Movement ecology in pelagic seabirds

Zuzana Zajková

Layout design by Arais Reyes Meza
Original illustrations in covers of chapters 1 to 4 by Esther Charles Jordán ©
Cover design by Esther Charles Jordán with contribution of José Manuel Reyes-González.

This thesis was financially suported by a pre-doctoral grant (APIF/2012) from the University of Barcelona.

Facultat de Biologia
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Programa de Doctorat en Biodiversitat

MOVEMENT ECOLOGY IN PELAGIC SEABIRDS

ECOLOGÍA DEL MOVIMIENTO EN AVES MARINAS

Memòria presentada per

ZUZANA ZAJKOVÁ

per optar al grau de Doctora per la Universitat de Barcelona

Barcelona, 2019

Supervisor and tutor:

Dr. Jacob González-Solís Bou
Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals
Facultat de Biologia
Universitat de Barcelona

Supervisor:

Dr. Frederic Bartumeus Ferré
Centre d'Estudis Avançats de Blanes
CEAB - CSIC

I have always liked to know birds as individuals, rather than as statistics. (…) No generalization in ecology is ever 100% valid. Somewhere, sometime, there is or will be a guillemot that plunges like a gannet and a tern that swims underwater. In an age when the computer speaks with the voice of unerring certainty, I find the unpredictable character of birds rather reassuring. They were here before us, and they will surely outlive us. Their lives have a reality and immediacy that may escape us in our increasingly secure and synthetic world.

Antony J. Gaston

- Seabirds. A natural history -

Acknowledgements

At the moment of choosing a topic for the final project of my Degree in Ecology, I choose to focus on plants and their conservation. Not only because I really like plants, the other reason which drove my decision, was that I found it pretty tough and challenging to study animals, as they are on a constant move. Who would say that much much later I would engage in a thesis to study animals, with a particular focus on an animal group with the most spectacular movements and migrations!

Any of the work you are about to read, would not be possible without supervisors of this thesis, Jacob González-Solís and Fede Bartumeus. Each of them contributed in different way, related to their research background. Thanks to Jacob, I learned a lot about seabirds' biology and ecology, his deep knowledge helped me to decipher the information coming from the small tracking devices. With Jacob I enjoyed my first seabird fieldwork on a remote island of Montaña Clara (Canary Islands), full of bites of Cory's shearwaters and Bulwer petrels, camping in a stone "house" and with a private lagoon!

I still remember the first time I met Fede in his office in Blanes, where I found myself staring at a white board (occupying the whole wall!) full of strange annotations. And I am glad that time later, also words like seabirds, geolocator and wet-dry started to appear in between all those strange annotations, together with a corner dedicated to a selection of visualizations of our work! I appreciate a lot his enthusiasm and patience and pragmatic approach to all of our discoveries.

Although I need to admit that finding an intersection of the two worlds of my supervisors (and mine, too) was not always easy and straightforward. Over this journey, we discovered several dead ends, but I think that at the end we could agree that our diverse backgrounds resulted in a very fruitful collaboration.

My time as PhD. student was almost equally split between the University of Barcelona and CEAB in Blanes. Starting at the University, I was lucky enough to become a part of great group of people. With all: Teresa, Vero, Laura, Fernanda and Jose we had funny times supported by regular consumptions of chocolate. Although the "new blood" Vir, Marta and Laura entered more less in the time I moved to Blanes, they greatly matched the mood of the group. And of course, it would have not been the same without having Francesc, Irene, Eli, Manolo, Mario, Alberto and Oriol around!

For the second part of my PhD. I moved to Blanes to work at CEAB. During almost two years I shared the office with an amazing person and polychaetes specialist, João. It was a unique opportunity for me to get deep insights about all those “worms”, not even talking about discovering all the amazing music of the world. I miss our regularly irregular beer-times in Casino, together with Nixon and Jose!

I would like to thank to the members of my PhD. evaluation committee, Maite Louzao, Robin Freeman and Raül Ramos, for their contributions and comments to my work developed especially over the first years of my doctoral studies.

I am thankful to all co-authors of the work contained in this thesis. Particularly, to Prof. Peter Becker, for giving me the possibility to contribute to their study by adding the analysis of activity data of Common terns, becoming the first published article of this thesis.

During the third year of my PhD. I had a great pleasure to spend two months at the lab at Max Planck of Ornithology in Radolfzell, lead by Dr. Kamran Safi. I received a great welcoming from the lab and I learned a lot, especially with the help of Kami, Bart and Anne, who helped me not to “re-invent the wheel” over and over again. How I enjoyed all the misty autumn days and nights, bike rides and walks around the Konstanz lake and the city. And of course the happy hours in nice company and talks and cakes!

Any of the analysis and visualizations would not be possible without the community of R enthusiasts. I am greatly doubted to all developers of plenty of R packages which I have used over the years. Here I want to thank to Joan Garriga, the man behind the R package used in the last chapter of this thesis. Thank you for your patience while teaching me how to use cluster computing to run all those immense calculations, with the objective to find out what the animals were doing.

My big thanks goes to Mara and Xavier, who believed that my skills which I developed focused on studying complex seabirds’ behaviour were applicable also in non-academic data science projects with totally different focus. Although I need to recognize that combining a full time job as a data scientist while finishing the PhD. was probably not the best idea ever, causing that things like “free time” somehow vanished from my vocabulary. Thank you both, together with David and Leandro, for being supportive and interested in my parallel academic journey, especially in the last moths.

I am lucky enough to have around people supporting me all the time to achieve my goals. All the friends which I have met at different space-times, some of them remain spatially close, many spread all around the world. Thank you Matias, Berta, Petr for our great adventures on the walls and in the mountains. Thank you Holger and Arais for always being around and for great jazzy parties at your place. Thank you Hugo for your coaching sessions, while hiking or searching for birds. Thank you Katka and your family for our regular winter wine meetings, Zuzka and the Vinklovci for being always close. And of course thank to Mazúrovci and Šutekovci for all the great time!

Maťko, thank you for encouraging all my decisions and steps for all those years, for always being around when needed. Most probably, there wouldn't be any thesis without our decision to start a new adventure in Spain. How many things we have learned and how many peaks and mountains have we climbed together here around! Looking forward for the next one. Ďakujem moc.

The huge thank you belongs to my great family, mum and dad, who always supported my decisions, my brother and sister for always being around. And even new members of the family, Mario and small Liam!

Ďakujem, mamina a ocino, Miro, Dada, za vašu podporu počas celých týchto bláznivých rokov, keď sme sa aj kvôli tejto práci videli pomenej, ale zato zas oveľa intenzívnejšie.

And last, but not least, to you, Jose, thank you for all. I would probably need all the pages of this thesis to write down everything I would like to mention to express my great gratitude for all your help during the process of this thesis. But as you know, it would probably take me years, therefore, thank you, my darling.

Arenys de Mar, Barcelona, September 2019

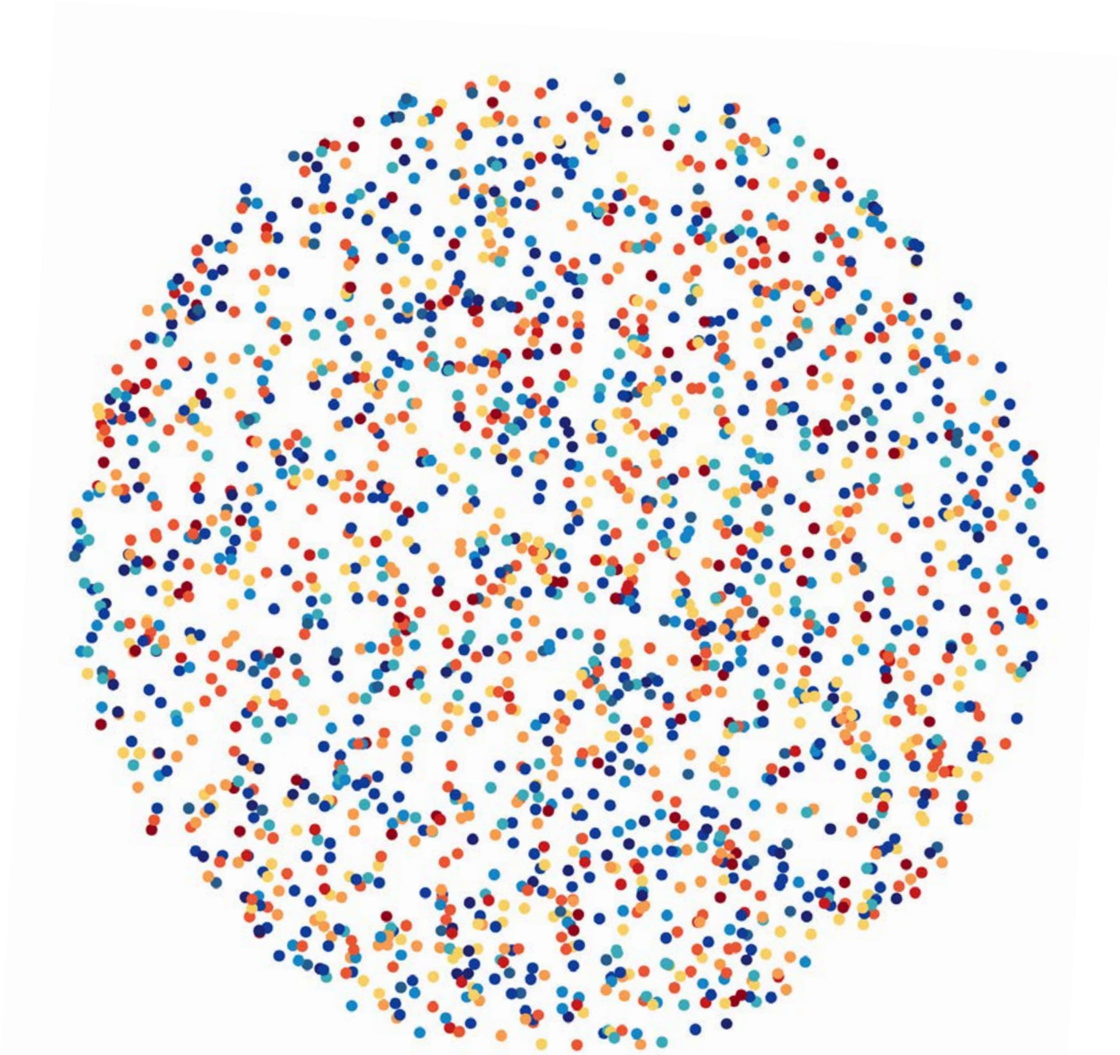
ABSTRACT

Movement is a fundamental component of behaviour and thus both are inextricably linked, so variation in movement patterns usually reflects different behaviours. The way individuals allocate time budgets to different behaviours within circadian rhythms and over the annual cycle will ultimately provide knowledge about evolutionary processes and adaptive capacity, which is also important to proper conservation actions of endangered species. Seabird movements have been studied over the last 20 years with the wide deployment of geolocator-immersion loggers, but wet-dry data seem underused according to literature published. Along 4 chapters this thesis presents novel insights about movements and behaviour of 4 little-known seabird species from the Atlantic Ocean: Boyd's shearwater (*Puffinus boydi*), Common tern (*Sterna hirundo*), Atlantic petrel (*Pterodroma incerta*) and Cory's shearwater (*Calonectris borealis*). Using wet-dry data alone or combined with positional data we uncovered the timing of major life cycle events and revealed circadian and circa-annual activity patterns of such species. In highly mobile migratory seabirds, the existence of radically different behavioural contexts linked to phenology and the need to exploit different marine environments over the year lead to different behavioural budgets. In the last chapter, we present a new analytical protocol based on state-of-the-art algorithms to decipher behaviours from wet-dry data. We reveal the hierarchical and modular nature of seabird behaviour at an unprecedented level of detail and used cutting-edge data visualization to highlight key insights. Our framework paves the way to use behavioural annotation for addressing old and new questions of interest in ecology from new perspectives using geolocator-immersion sensors. Overall, through this thesis I highlight the irreplaceable utility of wet-dry data to get unique insights in ecology and behaviour over the annual cycle of seabirds, a difficult-to-observe group of birds that remain out of the human sight most of their life. Geolocator-immersion sensors continue to be the most extended loggers to track year-round movements of seabirds, since they ensure the welfare of tagged individuals. Therefore, the results compiled in this thesis should encourage researchers to incorporate the use wet-dry data within hypothesis-driven frameworks, which surely would contribute to increase our knowledge of seabird ecology at sea.

RESUMEN

El movimiento es un componente fundamental del comportamiento animal, de forma que variaciones en los patrones de movimiento reflejan cambios comportamentales. El tiempo destinado a los diferentes comportamientos según los ritmos circadianos y a lo largo del ciclo anual puede ayudar a entender los procesos evolutivos y la capacidad de adaptación, algo importante también de cara a la conservación de especies amenazadas. La ecología de las aves marinas en mar abierto ha sido ampliamente estudiada en las dos últimas décadas gracias a los geolocalizadores por niveles de luz. Muchos modelos de geolocalizador registran datos de conductividad en agua salada, pero esta información parece infrautilizada a la luz de la literatura publicada. Esta tesis aporta nuevos conocimientos sobre la ecología en mar abierto de 4 especies de aves marinas del océano Atlántico: la pardela chica de Cabo Verde (*Puffinus boydi*), el charrán común (*Sterna hirundo*), el petrel atlántico (*Pterodroma incerta*) y la pardela cenicienta (*Calonectris borealis*). En esta tesis, usando los datos de conductividad solos o en combinación con datos de posicionamiento, desvelamos con detalle la fenología y los ritmos circadianos y anuales en el comportamiento de las aves marinas. En especies migratorias, la exposición a contextos diferentes a lo largo del año conduce a diferentes patrones comportamentales. En el último capítulo presentamos un nuevo protocolo analítico basado en datos de conductividad. Gracias al uso de algoritmos de aprendizaje automático desgranamos el comportamiento de las aves marinas a un nivel sin precedentes, desvelando su naturaleza jerárquica y modular. En conjunto, esta tesis remarca la enorme utilidad de los datos de conductividad para estudiar los patrones comportamentales a lo largo del ciclo anual en las aves marinas, un grupo animal difícil de observar al pasar la mayor parte del año en mar abierto. Los geolocalizadores provistos de sensor de conductividad siguen siendo los únicos aparatos de seguimiento remoto que aseguran el bienestar de las aves marinas instrumentadas durante largos periodos de tiempo. Los resultados expuestos en esta tesis deberían promover un mayor uso de los datos de conductividad, lo que contribuiría a aumentar nuestro conocimiento sobre la ecología de las aves marinas.

INDEX



PREAMBLE

This thesis is intended to provide new knowledge about movement and behaviour of seabird species, both for a better understanding of their ecology at sea and to bring new insights that hopefully can contribute to the conservation of this avian group. This thesis encompasses several aspects of seabird ecology at sea along 4 chapters focused on different species. Each of them was written as a self-contained piece of research and thus can be read and understood independently. Presenting them together I wanted to highlight how a very basic source of data, the wet-dry data recorded by geolocator-immersion loggers, can provide unique insights in behavioural and ecological studies. This data can reveal important aspects of movement and behaviour within the life cycle of seabirds, a difficult-to-observe group of birds as they remain out of the human sight most of their life.

GENERAL INTRODUCTION

Animal movement represents the continuous succession of locations of an individual over time. Movement is a feature governing different biological processes, from individuals to populations and communities, since every individual moves to engage in a variety of behaviours that determines fitness and ultimately population dynamics (Nathan 2008, Damschen et al. 2008, Jeltsch et al. 2013). Therefore, in vagile species, movement is a fundamental component of behaviour and thus both are inextricable linked. Behaviours mediated by movement represent the way animals react to internal and external stimuli, serving as mediators between the environment and individual fitness (Nathan et al. 2008). Indeed, variation in movement patterns usually reflects different behaviours, including those most glaring, such as foraging, dispersal, migration, social interaction, mate search or escaping from predators (Sutherland et al. 2013). Behavioural strategies, i.e. fine-scale behaviours that animals usually display interrelated, are the result of evolutionary processes exhibited in a population in certain environmental conditions, since behaviours evolve to maximize the fitness of individuals (van Buskirk 2012). Therefore, gathering information on movement and behaviour is fundamental for assessing how individuals and populations react in different environments. The way animals allocate behavioural budgets within circadian rhythm and over annual life cycles may ultimately provide knowledge about evolutionary processes and adaptive capacity to face changes in the environment (Sih et al. 2010, Wong & Candolin 2015).

Studying movement and behaviour over a wide range of scales and contexts, and from a multidimensional perspective, is a critical step to understand behavioural strategies and their relationship with environmental conditions. This has remained challenging and for a long time mainly restricted to description throughout *focal observation* bouts, thus leading to different degree of subjectivity and severely time constrained (Altmann 1974). Fortunately, during the last two decades the advances in remote tracking technologies have revolutionized the study of movement and behaviour of wild animals, even promoting the rise of a new research framework, the movement ecology (Nathan et al. 2008, Nathan & Giuggioli, 2013, Kays et al. 2015). The recent advent of biologging, i.e. the use of animal-borne sensors (Boyd et al. 2004, Cooke et al. 2004, Rutz & Hays 2009, Ropert-Coudert & Wilson 2005, Ropert-Coudert et al. 2012) provided the required bypass to address behavioural questions. Nowadays, we can find a full assortment of wearable devices fitted with multi-sensors, capable of recording not only location but a diverse array of ancillary data with unprecedented detail over a wide range of temporal and spatial scales (e.g. Wilmers et al. 2015, Chmura et al. 2018).

The difficulty to observe and study movement of wild animals in the marine environment had precluded addressing questions about behaviour in the context of their natural history-life and conservation. In this sense, the advances in tracking technologies have brought tremendous insights into the study of elusive marine megafauna (Block et al. 2011, McIntyre 2014, Roncon et al. 2018, Harcourt et al. 2019). In species such as sharks, tuna, cetaceans or seabirds, individuals can travel thousands of kilometers across ocean basins year round, playing a major role in the energy bal-ance and providing important goods and services across marine ecosystems (Tavares et al. 2019), and thus, biologging becomes essential for their study (Block et al. 2011, McIntyre

2014, Roncon et al. 2018, Harcourt et al. 2019). In the particular case of seabirds, their suitability as model species and the possibility to address many questions throughout biologging have led to a bloom in seabird research, including a proliferation of methods and analytical techniques, which has ultimately led to enhance our understanding of their ecology.

SEABIRDS AS MODEL SPECIES

Seabirds represent a diverse and polyphyletic avian group comprising several different families with complex natural life-history traits. Across seabird species, many ecological traits shaping their life style are shared, including extended immaturity, long-life and high adult survival, social and mostly sexual monogamy, low reproductive rates, small clutch size and an extended incubation and chick-rearing periods. Moreover, most seabirds are top-predators occupying the upper trophic level in marine and coastal food webs. But above all, what mainly represents seabird life-style is their high dependence on the marine environment for most part of their annual life cycle. Indeed, the most pelagic species spend most of their life at open sea and only come to land for breeding, as they need solid ground to lay the egg (Gaston 2004).

Living in the oceans imposes various constraints on seabird life style. Seasonal patterns and annual variations in climatic events shape highly dynamic environments in terms of productivity. Moreover, resources appear patchily distributed and are usually little predictable in space and time at medium or fine scale, thought they could be predictable at larger scales as also depend on static oceanographic features (e.g. shelf slopes, coastline shape, sea mountains) (Weimerskirch 2007). A singular trait of seabirds that has evolved to cope with these constraints is an extraordinary movement capacity. Flight performance and wing shape of many seabirds, especially the most pelagic species, allow them to fly over vast distances in relatively short times (Hertel & Balance 1999). In fact, seasonality in marine environments leads many species to perform long migratory movements year round, even moving between different ocean basins and across hemispheres to live in an "endless summer" in search of more abundant resources (Shaffer et al. 2006, González-Solís et al. 2007, Egevang et al. 2010). Moreover, even during the breeding period when seabirds become central-place foragers, after every visit to land they need to fly far away off-shore to forage (Phillips et al. 2017). Altogether, seabirds represent a particular case of free-range marine top-predators, as their movement and behaviour year round are severely constrained by their own phenology and the marine environment seasonality.

Lastly, it should be remarked that seabird conservation is a global concern, as they are one of the world's most rapidly declining vertebrate groups because of the effect of human activities (Croxall et al 2012, Dias et al. 2019). On land, seabirds suffer from the introduction of invasive predators (cats, rats, mice), poaching, human disturbance, habitat loss and light pollution (Croxall et al. 2012, Rodríguez et al. 2019). At sea, seabirds are threatened by fishing activities, by-catch, habitat degradation, pollution and climate change (Rodríguez et al., 2019, Díaz et al. 2019). Marine ecosystems are also recognized as globally threatened (Halpern et al. 2007). In this context, seabirds are sometimes considered as bio-indicators of marine ecosystem's health (Furness & Camphuysen 1997).

Nevertheless, their use as bio-indicators could improve with a comprehensive understanding of their behaviour at sea (Durant et al. 2009). Hence, every new insight about movement and behaviour of seabirds can greatly contribute to improve conservation and management actions of these species and their habitats (Croxall et al 2012, Lascelles et al. 2016, Dias et al. 2019).

STUDYING SEABIRD MOVEMENT AND BEHAVIOUR

A diverse array of tracking devices and tools have been used to study movement and behaviour of seabirds. The following is a brief introduction to the two main tools that have primarily contributed to the development of this thesis. I succinctly introduce them to ease understanding of their usage in the research shown in the next chapters.

Geolocation-immersion loggers

The study of year-round movement of pelagic seabirds at sea has been addressed over the last 20 years with the wide deployment of light-level geolocation loggers (Global Location Sensing units, GLS) (Burger & Shaffer 2008, Wilson & Vandenabeele 2012). These miniature archival data loggers, also known as solar geolocators, measure the ambient light in a regular schedule (measuring and recording resolution depend on the models) together with a time stamp in Greenwich Mean Time (GMT). Light records allow for determining latitude and longitude on a daily basis using astronomical algorithms (Wilson et al. 1992), but the method fails to infer latitude properly around the equinoxes and provides an average accuracy of 186 ± 114 km, being the error greater towards the equator (Phillips et al. 2004). Despite this low spatio-temporal resolution and the lack of reliability in latitude during the equinoxes (Hill & Bran 2001), GLS accuracy has been enough to reveal spectacular migrations and non-breeding areas of many seabird species (e.g. Shaffer et al. 2006, González-Solís et al. 2007, Egevang et al. 2010). Low spatio-temporal resolution is compensated by the size and weight of these devices (currently even < 1 g) and a long battery life (usually > 1 year) that allow for long tracking periods. The increasing miniaturization of GLS currently allows researchers to track also ever smaller species (e.g. Egevang et al. 2010, Quillfeldt et al. 2013, Pollet et al. 2014, Ramos et al. 2015).

Despite other kind of devices are available, GLS still are the single devices allowing the study of spatial ecology over long periods of time (Wilson & Vandenabeele 2012, López-López 2016). GPS loggers also need to be recovered to download the data but record high resolution spatio-temporal data. However, they have short battery life and are usually attached with TESA tape to back feathers, resulting in short-time attachment (days to few weeks), although technological improvements are rapidly cutting the distance between GLS and GPS loggers. Other devices, such as PTT, GPS-PTT or GPS-GSM, are usually equipped with solar panels and thus have no battery life limitations. Moreover, information can be retrieved remotely without the need of recapture. However, to track animals over long periods, these devices require long-lasting attachment systems such as harness, known to cause severe damage when used in some seabird species (Mallory & Gilbert, 2008). GLS, in contrast, are attached on a plastic or metallic ring placed on the tarsus of the birds, enabling even multi-year deployments and large sample sizes, with no detrimental effect observed on behaviour and fitness of birds (Igual et al. 2010, Vandenabeele et al. 2011, but see Brlík et al 2019). Therefore, GLS currently remain as the most cost-effective balanced tracking devices to get insights into the spatial ecology and movement of pelagic seabird species over the entire annual cycle while ensuring the welfare of tagged individuals (Vandenabeele et al. 2011, Vandenabeele et al. 2012, Kürten et al. 2019).

Together with ambient light intensity and time stamp, some models of GLS, frequently called geolocation-immersion loggers, also register wet-dry data. These devices detect conductivity between the anode and cathode terminals, which occurs in contact with saltwater, recording the time immersed. These data have been commonly used to study activity as a proxy of seabird behaviour (Wilson et al. 1995, Gutowsky et al. 2014). That is why in the literature wet-dry data from GLS may be also referred as saltwater immersion data or activity data. It is appropriate to mention here that high-resolution accelerometers can provide highly detailed behavioural information, particularly when combined with GPS devices (Cianchetti-Benedetti et al. 2017, Yoda 2019). However, they have similar disadvantages as those commented before for GPS, namely high energy and data-memory consumption, which precludes their use for extended periods of time (Yoda 2019). Some recent multi-sensor devices equipped with solar panels can store accelerometer plus GPS data over long periods and allow for remote downloading (Bouten et al. 2013), yet they also require harness for a long-lasting attachment, impeding their use to study at-sea behaviour of pelagic seabirds over long periods of time.

Data Visualization

According to the fast development in technology over the last two decades, the amount of movement and behaviour data collected from wildlife species have rocketed (Kays et al. 2015; Hays et al. 2016). Tracking data often provide enough information to immediately identify ecological insights, such as migratory pathways or home ranges of the species. However, as data size increases, more advanced graphics to unveil complex patterns are needed. In this sense, analysis of movement and behavioural data, as rich quantitative information, are an appropriate target to take advantage of data visualization tools. Effective data visualization can assist research bidirectionally, that is, as a knowledge-discovery tool helping to rise new hypotheses throughout exploration, or the other way around, helping to interpret results in the context of expectations and previous hypotheses (Tukey, 1977). Therefore, data visualization becomes an invaluable tool to assist research in movement ecology and animal behaviour.

STRUCTURE, USAGE, AND INSIGHTS FROM WET-DRY DATA

Studying how individuals allocate their time budget to different behaviours allows for better interpreting behavioural strategies within circadian rhythm, over annual life cycles and in different environments and conditions (Phillips et al. 2017). As commented above, GLS models used for seabird research also measure conductivity in saltwater, which have been used to infer activity patterns. The way GLS record wet-dry data varies according to models. In some of them, such as those initially produced by the *British Antarctic Survey* (Fox 2010), the default schedule stored data in 10-minutes blocks, where samples taken each 3s tested for contact with saltwater. This resulted in values ranging from 0 to 200 for each block (0 being dry the entire block, 200 being wet the entire block). Later models of GLS, such as those manufactured by *Biotrack Ltd*., store wet-dry data in a more continuous way by registering the time stamp of every change of state (wet to dry and vice versa). Lastly, most recent models (e.g. those models manufactured by *Migrate Technology Ltd*.) offer a variety of schedules to record wet-dry data, some of them matching schedules of previous models and thus being more frequently used by researchers.

The advent of GLS completely changed the way seabirds are studied. I carried out a systematic literature review to evaluate the use of GLS in seabird research over time but specially to evaluate the use of wet-dry data so far. Details about this review are included in Box 1. Once performed this review, the first evidence was that wet-dry data and activity patterns can provide useful insights on a variety of dimensions of seabird ecology, hard to obtain otherwise for elusive species. For example, in combination with positional information, wet-dry data have been used to define major important events over the breeding period. As a case in point, Militão et al. (2017) inferred the first visit to the colony and the duration of incubation stints in the endangered Cape Verde petrel (*Pterodroma feae*) by this means. In many seabird species, the arrival to breeding areas usually coincides with the equinox period, when positional data from GLS is unreliable and in such circumstances wet-dry data can help estimating the arrival date to the breeding colony. Regarding the breeding period, wet-dry data have also been used to compare at-sea activity patterns between successful and failed breeders (Catry et al. 2013, Ramos et al. 2018, Ponchon et al. 2019). Many researchers have commonly aggregated wet-dry data to assess the proportion of total time spent on water/in flight, and then looked at the variability between stages of the annual life cycle and across different groups, such as sexes (e.g. Pinet et al. 2012, De Felipe et al. 2019), ages (Catry et al. 2011, Missagia et al. 2015, Clay et al. 2018), or natal origin (e.g. Catry et al. 2011). These approaches usually evaluated circadian and circa-annual at-sea activity rhythms based on daylight/darkness activity (Phalan et al. 2007, Dias et al 2012), some of them also considering the effect of the moonlight (e.g. Yamamoto et al. 2008, Ramos et al, 2016). The proportion of daylight and darkness activity has also been used to calculate a night-flight index (Dias et al. 2012, Ramos et al. 2015, 2016). Some authors extended the use of wet-dry to broadly quantify foraging effort, estimating the number of landings/take-offs on hourly or daily time-scales (e.g. Phalan et. 2007, Mackley et al. 2010, Dias et al. 2012, Dias et al. 2016, Rayner et al. 2012). Some other approaches assumed wet-dry states and their alternation to be representative of basic behavioural modes. For example, some authors classified wet-dry data structured in ‘0-200’ schedule into three modes based on a simple threshold: ‘sitting on water’ (as representing resting or drifting, values from 195 to 200), ‘probable foraging’ (5-195) and ‘flying/roosting’ (0-5) (McKnight et al. 2011, Mattern et al. 2015). Guilford et al. (2009) used unsupervised clustering to infer those same three modes from 0-200 wet-dry data but estimated on a daily basis (i.e. assigning each day to a unique most probable mode). Wet-dry data from more recent GLS models, stored in a continuous way, have been used in similar way to calculate the duration and number of wet-dry changes as indicative of landing and take-off rate (Catry et al. 2004, Shaffer et al. 2001). Finally, few studies have actually taken advantage of transitions in wet-dry data recorded in continuous schedule to discern between foraging, flight and sitting on water (Dias et al. 2012, Gutowsky et al. 2014, Ponchon et al. 2019). More advanced approaches combining wet-dry data with information from other devices (GPS, time-depth recorders) have been used within a supervised machine learning framework to carry out behavioural annotation, although classifying again the three basic modes (‘flight’, ‘sitting on water’ and ‘foraging’, see Dean et al. 2012).

As shown above, a considerable research has been undertaken to uncover seabird behaviour from several perspectives. However, the second notable conclusion from the literature review was that wet-dry data seem underused, since only 53% of papers using GLS also made use of wet-dry data (see Table B1 in Box 1). Moreover, I found some less attended topics and remarkable gaps. Within these topics, the increase in the use of wet-dry data would probably contribute to provide important insights. In the following I comment some of the topics where I believe wet-dry data is clearly underused in seabird ecology studies:

- There are many seabird species with medium to small body size whose basic information regarding movements and behaviour at sea are unknown. Nevertheless, the progressive miniaturization and extensive use of GLS is allowing to fill this gap gradually. Lack about this basic knowledge also exists in medium-small sized species from tropical distribution, as a clear bias towards species with boreal and Antarctic/sub-Antarctic distribution has prevailed among researchers.

- Behaviour inferred from wet-dry data can easily enrich positional data to study the seasonal timing of life-history events (i.e. phenology). As major events over the annual cycle shape behaviour, the latter could easily inform the onset and duration of every event. For example, not only migratory schedules but also important events such as incubation shifts, duration of incubation stints, or hatching data, may be potentially inferred from a careful inspection or appropriate visualization of wet-dry data. This is particularly useful in species breeding in remote locations where on land recurrent nest monitoring may be difficult. However, wet-dry data have been underused for this topic, since only 15% of articles using wet-dry data evaluated aspects related to phenology at some extent.

- It is likely that physiological changes shape activity and behavioural budgets. In regards with physiology but also phenology, feather moulting is probably one of the most important processes that can constrain seabird behaviour and movement. However, and surprisingly, this effect has been rarely studied using wet-dry data (Cherel et al. 2016), despite once again a careful inspection or appropriate visualization of wet-dry data can greatly assist research in this regard. I found only 8% of articles using wet-dry data to relate at some extent with this topic, and many of them did not addressed the issue explicitly.

- Investigating the causes and consequences of movement and behaviour should consider carry-over effects, that is, how an individual previous experience explains its following performance

(O'Connor et al. 2014). Behavioural performance can be directly evaluated from wet-dry data. However, little research has been carried out in this sense: only 3% of articles using wet-dry data addressed this topic (Catry et al. 2013, Schultner et al. 2014, Shoji et al. 2015, Fayet et al. 2016, Ramos et al. 2018).

- Wet-dry data have been mostly used to investigate foraging: 39% of the articles using wet-dry data addressed this topic. Some of them, as commented above, went beyond wet-dry states and identified three behavioural modes, namely foraging, flying and sitting on water. In the literature review I only found one article using solely wet-dry data for behavioural annotation (also called behavioural classification, Guilford et al. 2009). Apart from inferring the same three behavioural modes, Guilford et al. (2009) based their analytical procedure on a predefined 24 h window upon which they aggregated the data. Therefore, virtually none of the articles published to date has intended to identify a greater array of behaviours using solely wet-dry data neither considering the natural temporal sequence of wet-dry events.

Certainly, there is still room to take advantage of wet-dry data, a source of information that has been available to researchers since more than a decade ago, but still clearly underused. Therefore, along this thesis I generally aimed to contribute with new insights and tools based on wet-dry data to fill these gaps.

BOX 1:

The use of geolocator-immersion loggers in seabird ecology research: a literature review

I carried out a systematic literature review to evaluate the use of light-level geolocators to study seabirds. I also evaluated to which extend researchers have taken advantage of wet-dry data from geolocation-immersion models to explore aspects of seabird ecology in more detail. I performed a search of published research articles using the Web of Science (WoS, Thomson Reuters & Clarivate Analytics). Using WoS I searched in *ISI Web of Knowledge* (*WoK*) and *Zoological Record* databases, filtering to report only peer-reviewed journal articles and truncating the search on 31 December 2018. I searched in both databases since I detected that some published articles on the issue were not included in *WoK*. At first, I used the following query, which I referred to as "spatial" for defining topics:

TS = (seabird AND (*geolocat* OR GLS))*

This search provided 224 published papers in which light-level geolocators were broadly used to produce positional data and investigate seabirds' spatial distribution in different ways.

Once gathered, I compiled titles and abstracts of the articles from the search and used Natural

Language Processing algorithms to create a text corpus. I calculated the most frequent words in the corpus as a proxy of most frequent topics and explored results with data visualization tools to evaluate the topics' representativeness (see Fig. B1 and B2).

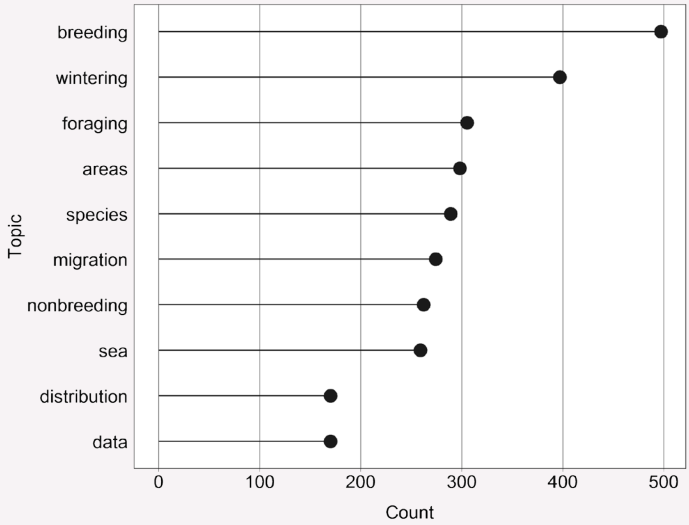


Fig. B1: Top 10 ranking of words by their frequency in published articles about seabird research using light-level geolocators.

Fig. B2: Word cloud of the 100 most frequent words computed from text included in titles and abstracts of published articles related to seabird research using light-level geolocators. The size relates to the frequency of each term in the whole dataset, so the visualization depicts the most frequent topics.

Topics as behaviour, activity or wet/dry were not included in the top 10 ranking (Fig. B1), but were present in the text content (Fig. B2). Next, I wanted to quantify the extent in the use of geolocators together with wet-dry data to investigate activity and behaviour of seabirds. To do so, I searched for published articles using the following query, which I referred to as "activity" topic:

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR wet OR dry OR "wet-dry" OR at-sea behaviour))*

This second search provided 120 articles, all of them already contained in the first "spatial" query results.

Last, I wanted to evaluate the number of articles published addressing some specific topics in which I thought wet-dry data could greatly contribute to foster seabird ecology research. These topics were "foraging", "phenology", "moult" and "carry-over", which I used in the following queries:

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR wet OR dry OR "wet-dry" OR at-sea behaviour) AND (foraging))*

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR wet OR dry OR "wet-dry" OR at-sea behaviour) AND (seasonal* OR phenolog*))*

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR wet OR dry OR "wet-dry" OR at-sea behaviour) AND (moult))*

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR wet OR dry OR "wet-dry" OR at-sea behaviour) AND (carry-over OR carryover))*

I also looked at the topic of using wet-dry as data source for behavioural annotation (also referred as behavioural classification):

TS = (seabird AND (*geolocat* OR GLS) AND (activit* OR "wet" OR "dry" OR "wet-dry" OR "at-sea behaviour") AND (behav* NEAR annotation* OR behav* NEAR classif*))*

The number of papers in each topic and relative representativeness are presented in Table B1. Note that a same article may be related with various topics. The bloom in the number of seabird articles over the last two decades thanks to the use of geolocator-immersion loggers is evident; the temporal trend of each topic is shown in Fig. B1. However, the last two years the number of articles has decreased (see Fig. B3).

Table B1. Number of articles (n) found in the systematic literature review for each topic selected. The column *Proportion* represent the percentage respect to the total, and this total corresponds to the topic "Spatial" (i.e. n=224). The column *Proportion respect to activity* represents the percentage of each topic respect to the number of articles in the topic "Activity" (i.e. n=119). Recall that a same article may be represented in more than one topic, so the values in proportion columns sum more than 100.

Topic	**Number of articles**	**Proportion**	**Proportion respect to "activity"**
Spatial	224	-	-
Activity	119	53.1	-
Foraging	87	38.8	73.1
Phenology	34	15.2	28.6
Moult	18	8.0	15.1
Carryover	6	2.7	5.0
Behavioural annotation	1	0.4	0.8

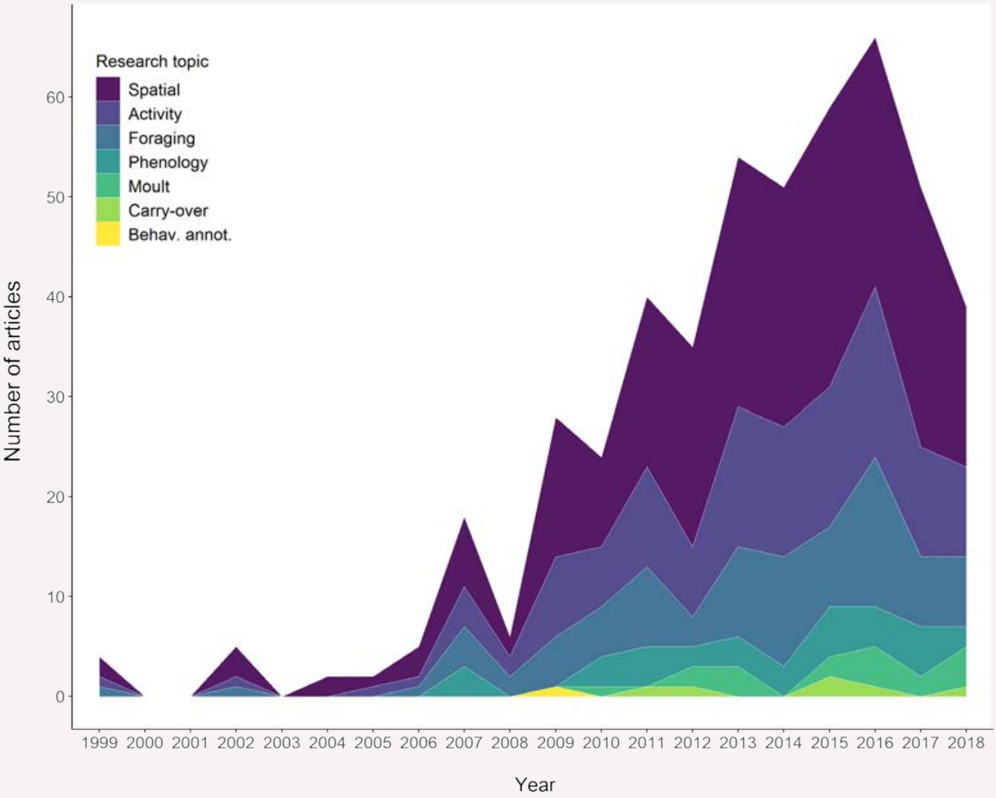


Fig. B3: Temporal trend of articles published related to each of the topics considered. The stacked area plot highlights that wet-dry (activity) data are underused for some of these topics.

STUDIED SPECIES AND FIELDWORK SITES

The work included in this thesis refers to seabird species from two different orders: Procellariiformes and Charadriiformes (Table 1), with studied colonies spread over different sites within the Atlantic Ocean and ranging from tropical to temperate to sub-Antarctic water distribution ranges (Figure 1).

Table 1: Studied species and studied colonies.

Species	Study colony
Order Procellariiformes	
Boyd's shearwater *(Puffinus boydi)*	Raso Is., Cima Is. (Cape Verde)
Cory's shearwater *(Calonectris borealis)*	Gran Canaria Is. (Canary Islands)
Atlantic Petrel *(Pterodroma incerta)*	Gough Island (Tristan da Cunha)
Order Charadriiformes	
Common Tern *(Sterna hirundo)*	Wilhemshaven (Germany)

Boyd's shearwater (*Puffinus boydi*, Order Procellariiformes, Family Procellariidae) is part of the Little−Audubon's shearwater complex (*Puffinus assimilis−lherminieri*) which encompass small-sized (140 - 290 g) dark-and-white shearwaters of pelagic habits and spread within tropical and temperate waters. Mainly due to their morphologic similarities, there has been a lot of controversy in the taxonomy and the species within this complex have been assigned to different taxa within 'assimilis' and 'lherminieri' groups (Cramp & Simmons 1977, Warham 1990, Carboneras 1992, Brooke 2004). The Boyd's shearwater is endemic to the Cape Verde Islands, where breeding sites are thought to be located on most islands and islets (Hazevoet 1995). Population is estimated of ca. 5 000 pairs (BirdLife International 2015). The species is thought to breed on most islands and islets of the archipelago, nesting in burrows in soft soil or in rocky cavities. Birds take a long breeding season (ca. 6 months), that generally starts during the boreal winter. After the females lays one single egg, both parents share breeding duties (Carboneras et al. 2016). Its diet is mostly based on squid and small pelagic and demersal fish (Neves et al. 2012, J. A. Ramos et al. 2015). Due to unsolved taxonomic status, the conservation status of taxa is 'Least Concern' (BirdLife International 2015, Carboneras et al. 2016).

Cory's Shearwater (*Calonectris borealis*, Order Procellariiformes, Family Procellariidae) is a large-sized shearwater (605-1060 g) of pelagic habits. The species breeds on islands and islets of the Macaronesian archipelago, in the North-East Atlantic Ocean. Females lay one single egg on late May-early June, in simple nests located inside burrows. Chicks fledge between late October and early November. Individuals migrate to several wintering areas in the southern Atlantic Ocean, returning early in February to the breeding colonies. Their diet is based mainly on epipelagic fish and squid (Reyes-González & González-Solís, 2016). It is considered as not globally threatened by the IUCN ('Least Concern', BirdLife International 2018a).

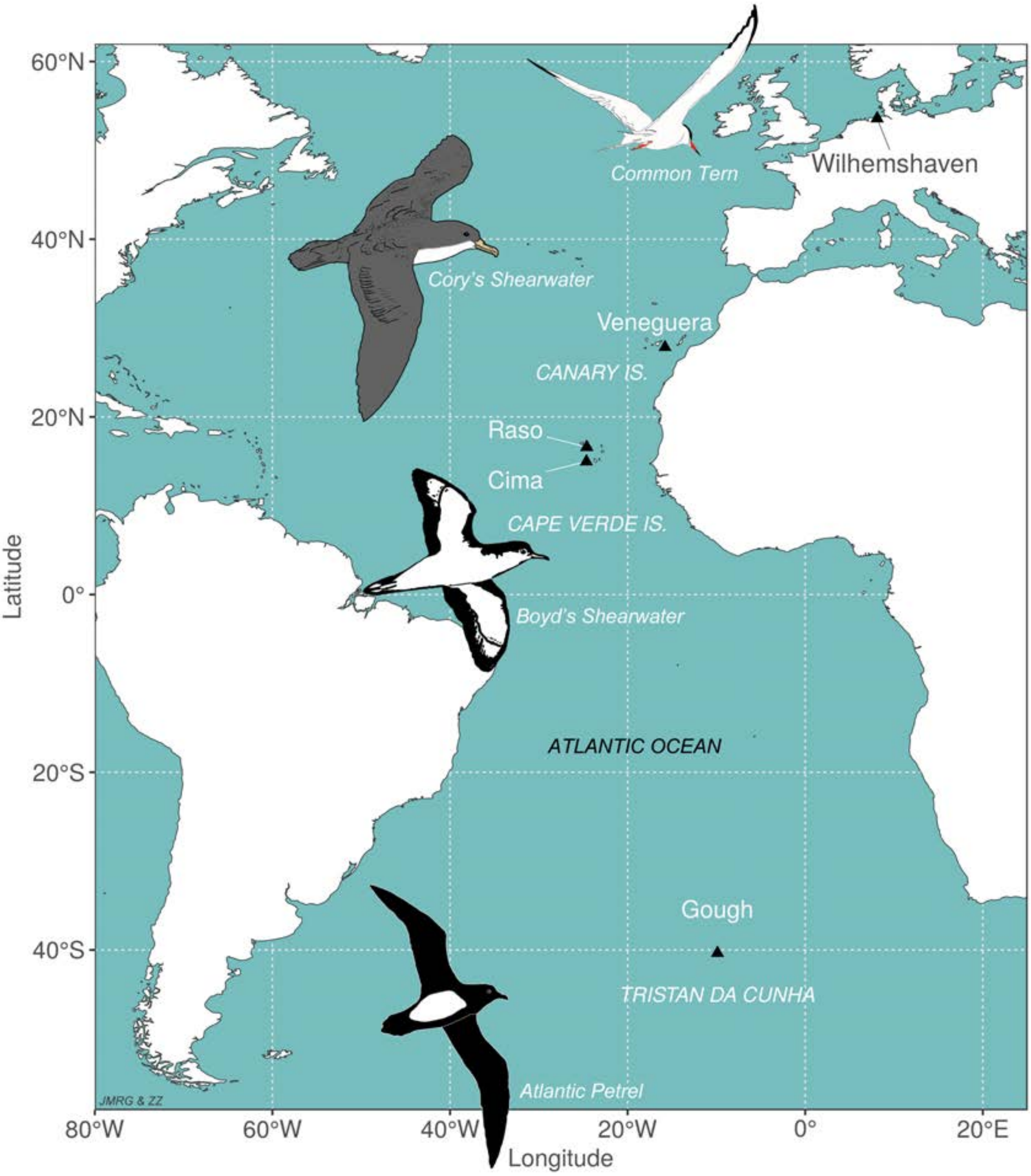


Fig. 1: Map showing the location of the breeding colonies (black triangles) of the seabird populations studied in this thesis.

The **Atlantic petrel** (*Pterodroma incerta*, Order Procellariiformes, Family Procellariidae) is a medium-sized (420 – 720 g) pelagic gadfly petrel (*Pterodroma* spp.). The species distribution is restricted to the South Atlantic Ocean (Enticott 1991, Orgeira 2001, Cuthbert 2004), with breeding sites located exclusively in the Tristan da Cunha group of volcanic islands, to which the species is endemic as breeder. Birds breed during the austral winter, females lay a single egg in a burrow in June-July, and chicks fledge in December (Richardson 1984, Cuthbert 2004). Diet is composed basically of squid (Klages & Cooper 1997). The population of Atlantic petrels is approximately 1 million pairs, breeding at Gough Island, but the strong population decline caused by the high rate of chick predation by introduced house mice (*Mus musculus*) has led to list the species as 'Endangered' by the IUCN (BirdLife International 2018b, Caravaggi et al. 2019).

Common Tern (*Sterna hirundo*, Order Charadriiformes, Family Laridae) is a small-sized seabird (120–135 g). The species' breeding distribution comprises the Palearctic and North America. It breeds in a variety of coastal and inland habitats (sand beaches, marshes, rocky islands, even nesting successfully on artificial nesting platforms), laying 2-3 eggs between April-June. Terns are considered inshore feeders since generally feed in waters not far from their colonies or roosting sites in their wintering grounds. They mostly feed on small fish, occasionally also on crustaceans and insects (Granadeiro et al. 2002, Bugoni et al. 2004). Common terns are strongly migratory, travelling to the southern hemisphere to winter. The species is considered as not globally threatened by the IUCN ('Least Concern') with a global population of 1 600 000–3 600 000 individuals (Gochfeld et al. 2019).

OBJECTIVES AND STRUCTURE OF THE THESIS

The main aim of this thesis was to provide new insights into the factors shaping the movement and at-sea behaviour of pelagic seabirds, highlighting the utility of wet-dry data from geolocator-immersion sensors. My specific objectives, and accordingly my role in the development of the studies presented as chapters of this thesis, were:

1. to extend our knowledge about the year-round movements and seasonal timing of life-history events in seabirds using wet-dry data,

2. to reveal the circadian and circa-annual at-sea activity rhythms of little-known seabird species,

3. to develop a novel methodological protocol based on wet-dry data to identify and annotate complex behaviours,

4. to quantify the relative prevalence and transition probabilities of behaviours in order to evaluate complexity in seabirds' behavioural strategies,

5. lastly, I additionally aimed to devise effective data visualizations to assist the process of research in animal movement and behavioural ecology.

The work contained in this thesis is organized in the following 4 chapters:

In **Chapter 1**, we used a combination of geolocation, wet-dry data and stable isotope analysis to reveal phenology, non-breeding distribution and migratory routes of a little-known tropical seabird endemic to Cape Verde Islands, the Boyd's shearwater *Puffinus boydi*. Using 5-year geolocation dataset, I described the onset and ending of major events over the annual life cycle, through combining positional with wet-dry data. This chapter contributes to objective 1 of the thesis.

In **Chapter 2**, we studied the temporal-spatial distribution of the Common tern *Sterna hirundo* along the East Atlantic Flyway. We unveiled migratory routes, stopover sites and non-breeding areas of the studied population. In this study, I used wet-dry data to disentangle differences in activity patterns at two hierarchical scales: on a daily basis and across stages of the annual life cycle. This chapter contributes to objectives 1 and 2 of the thesis.

In **Chapter 3**, we extended the knowledge about the spatial ecology of an endangered species, Atlantic petrel *Pterodroma incerta*. We used geolocation-immersion loggers to assess in detail phenology, at-sea distribution, behaviour and habitat preferences over the entire annual cycle. I combined positional and wet-dry data to describe in detail major events over the annual life cycle. Besides, I used data visualization in exploratory analyses to assist defining plausible hypotheses, which led us to find likely carry-over effects of breeding success on individual phenology and behaviour. This chapter contributes to objectives 1, 2 and 5 of the thesis.

In **Chapter 4**, we developed a novel protocol to provide new insights into behavioural organization of seabirds based uniquely on wet-dry data. In this protocol, I used a breakpoint algorithm to segment continuous wet-dry data, to which we later applied dimensionality reduction and unsupervised clustering algorithms. Throughout our approach, we built up continuous behavioural spaces and evaluated prevalence and transition probabilities of behaviours. Moreover, I introduced a novel application of network analysis to explore behavioural strategies throughout quantifying the changes in organization and importance of behavioural modes between the different stages of the annual life cycle. As a proof of concept, we applied the protocol on data from Cory's shearwater (*Calonectris borealis*), which allowed us to find a diverse array of behaviours and analyse them at various spatial and temporal scales. The study was firmly supported by data visualization, which we used to assist all steps along the research process. This chapter contributes to objectives 1, 2, 3, 4 and 5 of the thesis.

SUPERVISORS' REPORT

Dr. Jacob González-Solís and Dr. Frederic Bartumeus, as supervisors of the doctoral thesis entitled "Movement ecology in pelagic seabirds" certified that the dissertation presented here has been carried out by Zuzana Zajková and grant her the right to defend her thesis in front of a scientific panel. The dissertation work comprises two articles published and one accepted in highly ranked peer reviewed journals included in the Science Citation Index.

As supervisors, we have participated in the design, guidance and correction of the work and earlier drafts of the manuscripts included in this thesis. The contribution of the doctoral candidate to each manuscript and the impact factor (Thomson Institute for the Scientific Information) is detailed below:

CHAPTER 1

Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic

Zajková Z, Militão T, González-Solís J (2017) Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Marine Ecology Progress Series* 579:169-183.

Impact factor (2017): 2.292

Z. Zajková has contributed to the analysis of geolocator data, stable isotopes analysis and scientific writing.

CHAPTER 2

Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period

Becker, PH, Schmaljohann, H, Riechert, J, Wagenknecht, G, **Zajková, Z** & González-Solís, J (2016) Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period. *Journal of Ornithology* 157: 927– 940.

Impact factor (2015):1.419

Z. Zajková has contributed to the analysis of wet-dry immersion data and scientific writing.

CHAPTER 3

Spatial ecology, phenological variability and moulting patterns of the endangered Atlantic petrel, Pterodroma incerta

Marina Pastor-Prieto, Raül Ramos, ***Zuzana Zajková****, José Manuel Reyes-González, Manuel L. Rivas, Peter G. Ryan & Jacob González-Solís.* Accepted in *Endangered Species Research*. Biologging and Conservation Special issue.

Impact factor (2019): 2.122

Z. Zajková has contributed to the analysis of data and scientific writing.

CHAPTER 4

Air-water behavioural dynamics reveal complex at-sea ecology in global migratory seabirds

Zuzana Zajková*, José Manuel Reyes-González, Teresa Militão, Jacob González-Solís & Frederic Bartumeus.* To be submitted to Current Biology.

Impact factor (2018): 9.193

Z. Zajková has contributed to the study design, data analysis and scientific writing.

We also certify that any of the co-authors in the referred papers have used any or part of the work for their own doctoral theses.

Barcelona, 20th September 2019

Dr. Jacob González-Solís Bou
Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals
Facultat de Biologia
Universitat de Barcelona

Dr. Frederic Bartumeus Ferré
Centre d'Estudis Avançats de Blanes

Chapter 1:

Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic

Zuzana Zajková[1], Teresa Militão[1] & Jacob González-Solís[1]

[1] *Institut de Recerca de la Biodiversitat (IRBio) and Dept. Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 643, Barcelona 08028, Spain*

Published in: Zajková Z, Militão T, González-Solís J (2017) Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Mar Ecol Prog Ser* 579:169-183

ABSTRACT

Despite the proliferation of seabird tracking studies, there is a relative paucity of studies on small tropical seabirds. We present for the first time the distribution and movements of the little-known Boyd's shearwater *Puffinus boydi*, a Procellariiform endemic to the Cape Verde Islands. We tracked 28 birds from 2 breeding sites (Ilhéu Raso and Ilhéu de Cima) with geolocator loggers from 2007 to 2012. We also analysed stable isotopes of carbon and nitrogen in the 1st primary (P1), the 6th rectrice (R6) and the 1st (S1) and 8th (S8) secondary feathers to reveal moulting pattern and oceanic isotopic gradients. Birds migrated on average 1450 km westward, to the central Atlantic Ocean (5 to 15° N, 30 to 40° W), where they stayed on average 114 d, from May to August. Boyd's shearwaters exploited oceanic waters year-round and showed $\delta^{13}C$ values similar to other oceanic seabird species and $\delta^{15}N$ values indicating the lowest known trophic level among all central Atlantic seabirds. Isotope values in flight feathers suggest most animals moult their P1 and R6 around the breeding ground, whereas all birds moult S1 and S8 at the non-breeding quarters. Correlations of $\delta^{13}C$ and $\delta^{15}N$ values from S8 with the longitude of the non-breeding area indicate the existence of large-scale isotopic gradients matching those known at baseline levels. Combining geolocator tracking and stable isotope analyses in feathers not only allowed us to describe in detail the annual life cycle and distribution of the species, but also the oceanic isotopic gradients in the tropical Atlantic.

INTRODUCTION

Over recent decades, studies on the biology and ecology of tropical seabirds have been mainly focused on diet, foraging and performance at the breeding colonies (Ashmole & Ashmole 1967, Ballance & Pitman 1999, Spear et al. 2007). More recently, studies have been extended to include the relationship between breeding performance and environmental features (Surman et al. 2012, Catry et al. 2013). In contrast, at-sea distribution of many tropical seabirds remains poorly known and the sparse information available is mostly based on shipboard and coastal observations (Jaquemet et al. 2004, Ballance 2007). Despite the standardized approaches used in ship surveys (Tasker et al. 1984, Camphuysen & Garthe 2004), unreliable at-sea identification of some species (Ainley et al. 2012) and usually unknown origin and breeding status of observed individuals make these counts difficult to interpret.

In the last 2 decades, the rise in the use of extrinsic and intrinsic markers has underpinned an exponential increase in studies on the pelagic ecology of seabirds. Regarding extrinsic markers, the light level logger (geolocator) has become an essential device for studying year-round movements in much more detail than ever before, improving our understanding on the ecological needs and constraints of seabirds at sea (e.g. González-Solís et al. 2007, Guilford et al. 2012). However, the increasing use of geolocators to study seabird distribution and behaviour has been clearly biased towards species from temperate and subantarctic waters. Thus, there is still a clear lack of knowledge about the year-round at-sea ecology and distribution of tropical seabirds, with only a few species well studied (Catry et al. 2009, Pinet et al. 2011, Dias et al. 2015, Precheur 2015, Paiva et al. 2016, Ramos et al. 2016).

Similarly, intrinsic markers, such as stable isotope analysis (SIA) of $\delta^{13}C$ and $\delta^{15}N$ of various tissues have been widely used to study seabird trophic ecology. Typically, $\delta^{13}C$ values have been used to determine the diet of seabirds whereas $\delta^{15}N$ values reflect trophic level in a general manner (Hobson et al. 1994, Cherel et al. 2008). However, isotopic values of $\delta^{13}C$ and $\delta^{15}N$ at baseline are also known to vary geographically in the marine environment (McMahon et al. 2013a,b). Spatial maps of isotopic landscapes, so called 'isoscapes', reflecting this variability, are just now beginning to emerge, mostly based on large-scale studies on plankton (Somes et al. 2010, McMa- hon et al. 2013a,b). Whether this spatial isotopic variability propagates up to the food chain and can provide insights into the foraging movements or wintering areas of predators is still a matter of study (Quillfeldt et al. 2005, Cherel & Hobson 2007, Navarro et al. 2013). In this regard, combining SIA with tracking studies can help validate the relationship between isotope values and foraging movements (Jaeger et al. 2010). Despite increasing interest in linking isotope values of feathers to seabird movements, especially during the less known non-breeding season, only few studies showed a correspondence between $\delta^{13}C$ and $\delta^{15}N$ in feather isotope values and non-breeding distribution of seabirds tracked with geolocators (Phillips et al. 2009, González-Solís et al. 2011, Hedd et al. 2012).

The lack of basic knowledge regarding year-round distribution, phenology and trophic ecology becomes a matter of conservation concern in polytypic species difficult to identify at sea and with unclear taxonomic status. The Little–Audubon's shearwater complex (*Puffinus assimilis–lherminieri*, Procellariiformes), small-sized seabirds spread within tropical and temperate waters, is a particularly poorly known seabird complex as shown by the various taxonomic revisions that occurred over recent decades (reviewed in Austin et al. 2004). After many years of controversy, Audubon's shearwater is now suggested to include 3 subspecies, the Audubon's shearwater *P. l. lherminieri*, the Barolo shearwater *P. l. baroli* and the Boyd's shearwater *P. l. boydi*, with a conservation status of 'Least Concern' (BirdLife International 2015, Carboneras et al. 2016a), although in the present study we preferred to follow a precautionary principle and maintain the specific status of the taxon *P. boydi* (Hazevoet 1995, Robb & Mullarney 2008). Indeed, the conservation status and taxonomy of several closely related seabird taxa still remain controversial partly due to our lack of knowledge on their spatial ecology, since this is important for understanding migratory connectivity, reproductive isolation mechanisms, and therefore potential for lineage divergence (Ramos et al. 2016). Therefore, studies on the phenology and year-round distribution of species within seabird complexes with controversial taxonomic relationships are particularly timely.

Recent geolocation and stable isotope studies on Barolo shearwater breeding on the Macaronesian archipelagos of the Azores and the Salvagens (Neves et al. 2012, Paiva et al. 2016) showed this subspecies to disperse in the surroundings of the breeding colonies outside the breeding period. However, there is very little knowledge about detailed biology of the closely related Boyd's shearwater *P. boydi* Mathews, 1912, endemic to the Cape Verde Islands, especially those aspects related to phenology, year-round distribution and trophic ecology. Roscales et al. (2011) revealed the distribution and trophic position of Boyd's shearwaters only at the end of the breeding season, when animals foraged close to the colony. Away from breeding grounds, Boyd's shearwater has only been seen in small numbers off the Senegal coast in October (Hazevoet 1997, Dubois et al. 2009), in 1976 1 bird was trapped on St. Helena (Bourne & Loveridge 1978) and a suspected observation of 1 individual was reported from the Canary Islands in December 2012 (Velasco 2013). However, the majority of the observations of individuals of this species have been reported all year round in Cape Verde and surrounding waters (Bourne 1955, Hazevoet 1995, Dubois et al. 2009), which suggests a non-migratory behaviour, even though non-breeding grounds remain unknown.

To fill in this gap, we provide the first detailed study on the year-round movements and distribution of the Boyd's shearwater, based on geolocation and SIA of feathers over multiple years. We aim to (1) reveal main foraging areas during breeding and non-breeding seasons, the detailed phenology of their life cycle and, in particular, clarify whether Boyd's shearwater performs dispersal movements or oriented migration to a specific non-breeding area; and (2) to bring new insights into the existence of isoscapes and their potential use to study the movement of tropical top predators by linking the isotopic values of feathers with individual non-breeding areas.

MATERIALS AND METHODS

Study site and species

We conducted fieldwork during the breeding seasons of 2007 to 2012 in the Cape Verde Islands, on Ilhéu Raso (16° 36' N, 24° 35' W) and Ilhéu de Cima (14° 58' N, 24° 38' W), 2 islets 180 km apart. We visited the colonies during the incubation period, from February to early April, depending on the year. Additionally, we visited Raso in November 2009.

The Boyd's shearwater is a taxon within the Little−Audubon's shearwater complex (*Puffinus assimilis−lherminieri*, Procellariiformes) (reviewed in Austin et al. 2004). Traditionally, 'assimilis' and 'lherminieri' were recognized as 2 species groups, but with numerous taxa within each group (Cramp & Simmons 1977, Warham 1990, Carboneras 1992, Brooke 2004). In the last decade, a molecular study by Austin et al. (2004) proposed 3 geographically discrete clades of the complex identified in the North Atlantic, Southern (Australasia) and tropical Pacific and Indian oceans. A recent revision (Carboneras et al. 2016a,b) has suggested the separation of little shearwater *Puffinus assimilis,* distributed in the southern hemisphere, from the Audubon's shearwater *Puffinus lherminieri*, distributed in the North Atlantic Ocean and Caribbean Sea. Particularly, 2 North-Atlantic taxa, Barolo shearwater *Puffinus baroli* (breeding in the Azores, Madeira, and the Canary Islands) and Boyd's shearwater *Puffinus boydi* (breeding in the Cape Verde Islands) have been switched between 'assimilis' and 'lherminieri' groups by various authors over the years.

Hazevoet (1995) considered *P. boydi* as an independent species. The Boyd's shearwater is endemic to the Cape Verde Islands, where it is thought to breed on most islands and islets (not known from Maio and extinct on Sal) (Hazevoet 1995), with a population estimation of ca. 5000 pairs (BirdLife International 2015). Birds (body mass ≈ 160 g) nest in burrows in soft soil or in rocky cavities. Both parents share incubation of a single white egg that may take 44–60 d to hatch (Carboneras et al. 2016a) and breeding lasts from January to June. Birds are thought to disperse after breeding; however, some were reported visiting the breeding colony at the end of August (Bourne 1955) and throughout the year (Hazevoet 1995). Diet is not well known; the few stomachs examined by Bourne (1955) contained fish and cephalopods up to 8 cm. A closely related species (*P. baroli*) from the Azores feeds mostly on cephalopods and fish (Neves et al. 2012, J. A. Ramos et al. 2015).

Bird tracking and spatial data analysis

During the study period (2007–2012) we deployed a total of 90 geolocators on 68 individuals of Boyd's shearwaters. We captured breeding birds by hand in the burrow and deployed geolocators, which we retrieved after ≥1 yr. Over the course of the study, we used 3 different types of loggers from the British Antarctic Survey (BAS): Mk9 (n = 32), Mk13 (n = 15) and Mk18-H (n = 43). Each logger was attached with a cable tie to a plastic ring, which was deployed on the tarsus of the bird; weight of equipment was approximately 2 g (1.25 % of body mass). We deployed only 1 geolocator per breeding pair.

Geolocators recorded ambient light intensity, time and immersion in seawater. Light levels were measured every 60 s and, depending on the type of device, the maximum value within each 5 min (Mk18-H logger) or 10 min (Mk9 and Mk13 loggers) interval was recorded. We processed raw light data and visually supervised each transition using TransEdit from BASTrack software (British Antarctic Survey). The sunrise and sunset times were estimated applying the light threshold value of 20. To estimate sun elevation angle, we calibrated the loggers before deployment and after recovery on an open site without shading. The value of sun elevation angle was calculated and applied for each logger, ranging from −5.82 to −3.49 (mean −4.54). Light level data were converted into latitude derived from day length and longitude derived from the time of local midday with respect to Greenwich Mean Time, using BASTrack software. This process results in estimation of 2 positions of the animal per day (Delong et al. 1992, Hill 1994, Afanasyev 2004), with a mean error ± SD of 186 ± 114 km (Phillips et al. 2004). Furthermore, as the latitude estimates are highly sensitive to errors and changes in day length, positions in equatorial regions may present lower accuracy (Hill & Braun 2001). In addition, cloudy weather at sunrise and/or sunset may lead to error estimated to 340 km in latitude and 105 km in longitude (Nisbet et al. 2011).

It is worth mentioning that interpretation of geolocation positions especially in equatorial latitudes should be accepted with caution, especially the latitude estimations around equinoxes (Hill & Braun 2001, Ekstrom 2004, Lisovski et al. 2012). Detailed examination of error in latitude estimation is necessary to avoid the possible misleading interpretation of geolocation positions. Particularly in this study, previous visual examination of positions showed a clear pattern (Figs. S1 & S2 in Supplement 1 at www.int-res.com/articles/suppl/m579p169_supp/) repeated in all individuals during the breeding period and resulting from a shift in the latitudinal error between interequinoctial intervals: positions before spring equinox — reflecting mostly incubation and the early chick-rearing period — were distributed northerly from the colony, whereas the positions after the spring equinox — reflecting the chick-rearing period — were distributed southerly from the colony. To avoid possible misleading interpretation that during incubation animals forage in the north and during chick rearing in the south of the colony, we pooled together prelaying, incubation and chick-rearing as a breeding period.

Obtained positions were filtered for each logger separately applying a 3-level filtering method, removing positions (1) 15–30 d before and after equinoxes, (2) with obvious interference at dawn or dusk, and (3) when flight speeds sustained over a 48 h period were higher than 30 km h^{-1} applying iterative backward/forward speed filtering (McConnell et al. 1992). The speed threshold was defined after visual examination of distributions of flight speeds. We also excluded positions from the day of deployment and recovery of the logger. Overall, 66 % of original locations were retained for further analysis.

Kernel density utilization distribution (UD) estimates were generated from filtered locations (projection: Lambert Equal-Area Azimuthal, centred to the centroid of all locations) during different periods of the life cycle separately for each bird and year of tracking using package *adehabitatHR* (Calenge 2006) in R (R Core Team 2016). Kernel contours of 50 % ('core-area') were calculated using a smoothing parameter (h) equivalent to the mean error of the geolocators (Phillips et al. 2004). We examined various spatial parameters for each track: (1) the area exploited during the breeding and non-breeding periods (50% UD; in km^2); (2) location of the centroids of breeding and non-breeding areas (50% UD), which were calculated using 'centroid' function from package *geosphere* (Hijmans et al. 2012); (3) the total distance (great-circle) from the breeding colony to the centroid of the non-breeding area and (5) the accumulated distance covered within the non-breeding area (without migration), which were estimated using the functions 'distance' and 'distance-Track' from the *argosfilter* package (Freitas 2012), respectively.

Geolocators also recorded salt-water immersion data sampled every 3 s and registered summary value every 10 min (varying from 0, when the logger was dry the entire 10 min period, to 200, when the logger was permanently wet). This information was used to help define some phenological parameters (see next subsection).

Phenology

Dates defining the phenology of species were identified visually from geographical positions, light and immersion data. During equinox periods, when latitude estimation is not accurate (Hill & Braun 2001), we used only changes in longitude and in immersion data to detect changes in movements and estimate dates of arrival to and departure from the breeding colony.

We estimated various phenological parameters: last night spent at the colony (continuous dry record over prolonged period of time during darkness), departure from the breeding and non-breeding area (the first day that the bird's location was outside the cluster of previous day's positions and was followed by directed movement away from this area), duration of the non-breeding period and migratory movements, arrival to the breeding and non-breeding area (the first day the bird entered the cluster of positions after a directed movement towards that area), the first day and night an individual spent in the burrow (detected by a continuous dry record over a prolonged period of time during daylight and darkness), first day of incubation (min. 2 consecutive days spent in the burrow), duration of the incubation period (from the first day of incubation until the return from the last foraging trip, including time spent outside on foraging trips between incubation shifts), and, finally, incubation shift and foraging trip duration.

Parameters referring to incubation duration were estimated only for individuals with 2 or more continuous years of tracking data (with the same geolocator or the geolocator that was replaced during incubation and recovered the following year). For those individuals we could estimate the onset, duration and end of incubation from light and immersion data. As some loggers failed to collect data for the entire deployment period or some animals did not breed, sample sizes for different phenological parameters vary somewhat between analyses. Based on these parameters, we identified and considered 4 periods of the life cycle: (1) breeding, period between logger deployment and departure on migration and period between the arrival to the colony from migration and recovery of the logger, (2) postnuptial migration, (3) non-breeding, period between arrival to non-breeding area and start of prenuptial migration and (4) prenuptial migration. One individual did not migrate and spent the non-breeding season in the vicinity of the Cape Verde Islands, so we considered the last night the animal spent at the colony (burrow) as the end of the breeding period. Similarly, the start of the subsequent breeding season was assigned as the first night the animal visited the burrow.

We used repeated measures ANOVA with individual as an error term (to account for pseudo-replication as few individuals were tracked >1 yr) to test for differences between the duration of the post- and prenuptial migration and the size of the core range areas between the breeding and non-breeding periods.

Stable isotope analysis

Boyd's shearwater is expected to moult the first primary feather at the end of the breeding period, just before migration, reflecting the isotopic composition of the breeding area (Cramp & Simmons 1977, Roscales et al. 2011). Known primary moult patterns of similar shearwater species are described as descendent, i.e. from the innermost to the outermost primary feather, with a duration of 3−5 mo, while the outermost rectrice feather is among the last to be moulted (Monteiro et al. 1996, Bridge 2006, Ramos et al. 2009). Moult of secondary feathers of shearwaters has been previously linked with the non-breeding area (Neves et al. 2012, Paiva et al. 2016). In this study, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios were examined in different wing-feather types: 1st primary (the innermost), 1st and 8th secondary and 6th rectrices (the outermost) feathers (hereafter named as P1, S1, S8 and R6, respectively). All feathers were sampled when we recovered the geolocator and they were stored in plastic bags before the analysis. For birds with the same logger recovered after ≥ 2 yr, feather sampling also occurred at the point of logger recovery, but these feathers are only related with the last year of tracking. In total, the dataset for statistical analysis consisted of 32 sets of 4 feathers from 28 individuals (4 individuals with feathers from 2 different years).

To avoid any possible contamination, feather samples were washed in 0.25 M sodium hydroxide solution, rinsed with distilled water and oven dried at 40°C for 24 h. Subsequently, we manually cut each feather to small fragments using stainless steel scissors and weighed a sample of 0.30−0.32 mg on a precision scale. Stable isotope values are expressed in delta notation (δ) as parts per thousand (‰) according to the following: $\delta X = [(R_{sample}/R_{standard}) - 1]$, where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. $R_{standard}$ values for ^{15}N and ^{13}C were based on atmospheric N_2 and the Vienna Pee Dee Belemnite standard, respectively. Replicate measurements of laboratory standards (2 standards for every 12 unknowns) indicated measurement errors of approximately 0.2 and 0.1 ‰ for nitrogen and carbon, respectively. The analysis of stable isotopes was carried out at Scientific-Technical Services of the University of Barcelona.

Statistical analyses of isotopic data

We could not directly test for differences between the 2 colonies as they were sampled in different years (Ilhéu Raso: 2007 and 2008; Ilhéu de Cima: 2009, 2010 and 2011). After visual comparison, there was no indication in systematic differences in isotopic values between colonies; therefore, all the statistical analyses were performed with isotopic data of both colonies pooled together. To test for differences among feathers in isotopic data, we first checked $\delta^{13}C$ and $\delta^{15}N$ values for normal distribution using Q-Q plots and Shapiro-Wilks' test. We used linear mixed models (LMM, R package *lmerTest*; Kuznetsova et al. 2015) to compare isotopic values among feathers (fixed factor) and we accounted for pseudo-replication including individual and sampling year as random factors. The p-values were calculated from Type 3 F-statistics with Satterthwaite's approximation for degrees of freedom, while pairwise comparisons were calculated based on differences of least squares means (function 'difflsmeans' package *lmerTest*) and adjusted using Bonferroni correction.

Based on the isotopic differences found among feathers (see 'Results'), we inferred that the S1 and S8 were moulted during the non-breeding period. Because both showed similar isotopic values, and to allow a comparison with the isotopic data of previous studies on a closely related species (Neves et al. 2012, Paiva et al. 2016), we used S8 for subsequent analyses. To link isotopic values of S8 feathers with the non-breeding area of each individual we determined the individual centroids of 50% kernel of non-breeding area. We used LMM to examine whether the variation in S8 feather isotopic values could be explained by the location of their non-breeding area (latitude and/or longitude of centroid as fixed, individual and year as random factors; R package *lmerTest*; Kuznetsova et al. 2015). The best-supported model was selected using the Akaike Information Criteria corrected for small sample sizes (AICc) (R package *MuMIn*; Bartoń 2016). To understand the possible influence of the sampling year we verified its importance based on the likelihood ratio test (function 'rand' from package *lmerTest*) and by calculating the variance explained by the sampling year.

Statistical analyses were carried out using the R software version 3.2.1 (R Core Team 2016). All values are presented as means ± SD, and we assumed a significance level $p < 0.05$.

RESULTS

Recovery of loggers

We retrieved 43 loggers (recovery rate 47.8 %) from 32 unique individuals. Most loggers were recovered in the year following deployment; however, 7 loggers were retrieved after 2 consecutive years. Eight other individuals ($n = 6$ and $n = 2$, respectively) were tracked over 2 and 3 consecutive years, by recovering and deploying a new logger each year. Eleven loggers failed or did not contain enough data for further analysis. Overall, the final dataset contained 38 year-long tracks of 28 unique individuals (9 from Ilhéu Raso, 19 from Ilhéu de Cima), including 10 individuals with 2 yr of tracking. We calculated kernel UD density for 38 tracks for non-breeding (2007, 9 tracks; 2008, 3 tracks; 2009, 6 tracks; 2010, 12 tracks; 2011, 8 tracks) and 35 tracks for breeding season, as 3 tracks from 2010/2011 did not contain enough locations for kernel estimation.

Phenology of annual cycle

Boyd's shearwaters presented some variability in their phenological parameters, especially in the timing of the first day and the first night in the burrow (Table 1) and on the duration of the non-breeding period (Table 1, Fig. 1 with individual phenologies). Furthermore, the duration of the pre-nuptial migration was statistically longer than the postnuptial migration (repeated-measures ANOVA, $F_{1, 45} = 7.463$, $p = 0.009$), with birds travelling for 7.2 ± 6.0 d to reach the breeding colony on their prenuptial migration in contrast with 4.9 ± 2.6 d to reach the non-breeding area on their postnuptial migration (Table 1).

Seasonal changes in at-sea distribution

During breeding, birds dispersed in different directions around the breeding colony and in proximity to Cape Verde Islands. With 1 exception (bird ID 2007_047), which foraged in the neritic area of the African coast in November-December, the tracked birds did not forage in neritic waters but north of the breeding colonies, reaching up to 30° N (Fig. 2, Fig. S3 in Supplement 1 and the animation in Supplement 2 at www.int-res.com/articles/suppl/m579p169_supp/). The estimated individual core range area during the breeding season (50% kernel UD) ranged from 292 000 to 764 400 km^2 (470 600 ± 111 500 km^2, $n = 35$).

At the beginning of May, birds started their post-nuptial migration consistently in a west-

Table 1. Year-round phenology of Boyd's shearwaters from Ilhéu de Cima and Raso (Cape Verde), tracked with geolocators from 2007−2012; data are mean ± SD and range values over 5 yr of tracking study

Phenological parameter	n	Mean ± SD	Range
Last night colony	36	26 Apr ± 17.4	21 Mar - 28 May
Colony departure	38	4 May ± 16.5	4 Apr - 7 Jun
Non-breeding area arrival	38	9 May ± 16.6	7 Apr - 12 Jun
Non-breeding area departure	37	31 Aug ± 18.6	1 Aug - 16 Oct
Colony arrival	37	7 Sep ± 19.5	4 Aug - 22 Oct
First night burrow	33	18 Sep ± 28.5	4 Aug - 2 Dec
First day burrow	32	31 Oct ± 59.6	13 Aug - 11 Jan
Incubation start	24	9 Feb ± 12.2	22 Jan - 6 Mar
Number of incubation shifts	6	3.8 ± 0.8	3 - 5
Duration of incubation (d)	6	47.0 ± 2.8	42 - 50
Duration of incubation shift (d)	23	6.0 ± 1.9	2 - 10
Duration of incubation foraging trip (d)	23	6.3 ± 1.9	2 - 9
Duration of postnuptial migration (d)	38	4.9 ± 2.6	0 - 13
Duration of non-breeding period (d)	37	114.0 ± 18.1	50 - 140
Duration of prenuptial migration (d)	37	7.2 ± 6.0	0 - 33

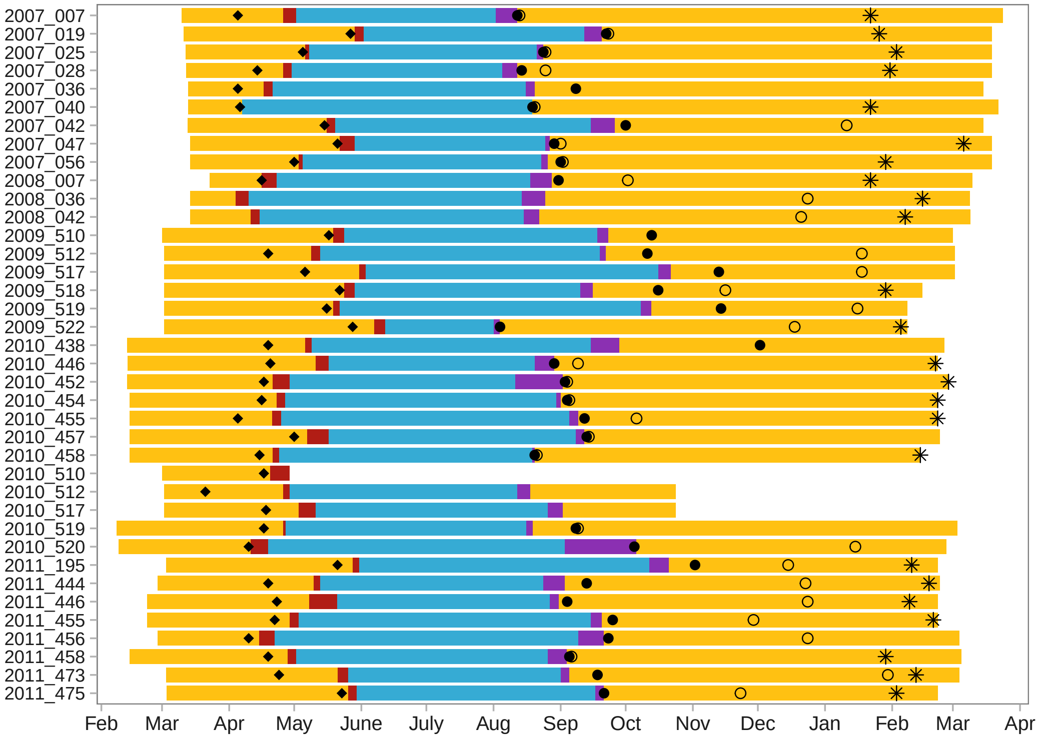


Fig. 1. Individual phenologies of Boyd's shearwaters, ordered by year of logger deployment (year of deployment_bird ID; n = 38). Each horizontal bar represents 1 yr of tracking, colours represent different stages of breeding cycle: breeding in yellow, postnuptial migration in dark red, non-breeding in blue, prenuptial migration in purple. Points refer to last night (◆), first night (●) and first day (○) the bird spent in the burrow, and onset of incubation (∗). Starts on the day of deployment, ends on the day of retrieval of the logger (or when logger stopped collecting data)

ward direction along a migration corridor between 7° and 15° N (Fig. S4). The mean distance between the breeding colony and non-breeding area (to the centroid of 50 % kernel UD) was 1450 ± 398 km (range 106–2391 km, n = 38). The main non-breeding area of Boyd's shearwaters was in the Central Atlantic Ocean, west of Cape Verde Basin, over the Mid-Atlantic Ocean Ridge, from 5 to 15° N and from 30 to 40° W (50% kernel UD; Fig. 3, Fig. S3 in Supplement 1, and Supplement 2). However, 1 individual migrated further west to 9° N, 43° W (bird ID 2009_510), while another went further north to 21° N, 36° W (bird ID 2007_007). The estimated individual core range area during the non-breeding season (50% kernel UD) ranged from 300 700 to 795 400 km^2 (467 700 ± 120 000 km^2, n = 38), which did not significantly differ from the size of core range areas during the breeding season (repeated measures ANOVA, $F_{1, 41} = 0.027$, p = 0.870, n = 35). During the non-breeding period, birds dispersed or steadily moved over a huge area. Total distance covered within the non-breeding area was on average 33 670 ± 5628 km (range 17 440–47 690 km, n = 38), moving on average 253.1 ± 32.8 km over approximately 24 h by a mean velocity of 10.5 ± 1.4 km h^{-1}. From all tracked birds, only 1 individual (bird ID 2007_040) did not migrate and stayed in the vicinity of Cape Verde Island year-round. The timing of pre-nuptial migration mostly overlapped with the autumn equinox period, but data for a few individuals suggest that animals use a similar route to return to breeding grounds (Fig. S4).

Stable isotope analysis

Boyd's shearwaters presented a wider range of nitrogen (6.39 to 12.60 ‰) than carbon values (−17.96 to −15.24 ‰) (Table 2, Fig. 4). Significant differences were found between feathers (P1, S1, S8 and R6) in both nitrogen (LMM, $F_{3, 94.323} = 29.965$, $p < 0.001$) and carbon values (LMM, $F_{3, 91.355} = 53.684$, $p < 0.001$). The differences in nitrogen values were between P1 and both S1 and S8 (pairwise comparison, both $p < 0.001$; Table S1 in Supplement 1). No difference was found between P1 and R6 (pairwise comparison, p = 0.719), or between S1 and S8 (pairwise comparison, p = 1.000). Significant differences were found between all feathers for carbon values (pairwise comparison, for all $p < 0.001$), except for S1 and S8 (p = 0.417). Although differences found between feathers were statistically significant, the magnitude of those differences was small (Table S1 in Supplement 1), comparing with variation among individuals (Fig. 4).

Geographic isotopic gradient (isoscapes)

The best-supported models (Table 3, Table S2a) suggest that the variation of isotope values of S8 was highly related with longitude (LMM, δ^{15}N: $F_{1, 29.915} = 57.945$, $p < 0.001$; δ^{13}C: $F_{1, 28.326} = 29.139$, $p < 0.001$; Fig. 5A,B), but not with latitude (LMM, δ^{15}N: $F_{1, 25.094} = 1.512$, p = 0.230; δ^{13}C: $F_{1, 29.200} = 0.511$, p = 0.485) values of the non-breeding centroid of Boyd's shearwaters. Indeed, the R^{2}m values, which describe the

Table 2. Isotopic values of δ^{15}N and δ^{13}C (‰) in the 1st primary (P1), the 1st (S1) and 8th (S8) secondary feathers and the 6th rectrice (R6) of Boyd's shearwaters breeding in the Cape Verde Islands. P1 and R6 feathers showed similar isotopic values but distinct than S1 and S8

Feather	n	δ^{15}N		δ^{13}C	
		Mean ± SD	Range	Mean ± SD	Range
P1	32	8.75 ± 1.12	7.29 to 12.60	-16.68 ± 0.43	-17.96 to -16.10
S1	32	7.61 ± 0.59	6.39 to 9.46	-16.04 ± 0.30	-16.93 to -15.59
S8	32	7.57 ± 0.61	6.44 to 9.82	-15.92 ± 0.35	-16.83 to -15.24
R6	32	8.51 ± 1.13	6.64 to 11.01	-16.37 ± 0.44	-17.20 to -15.51

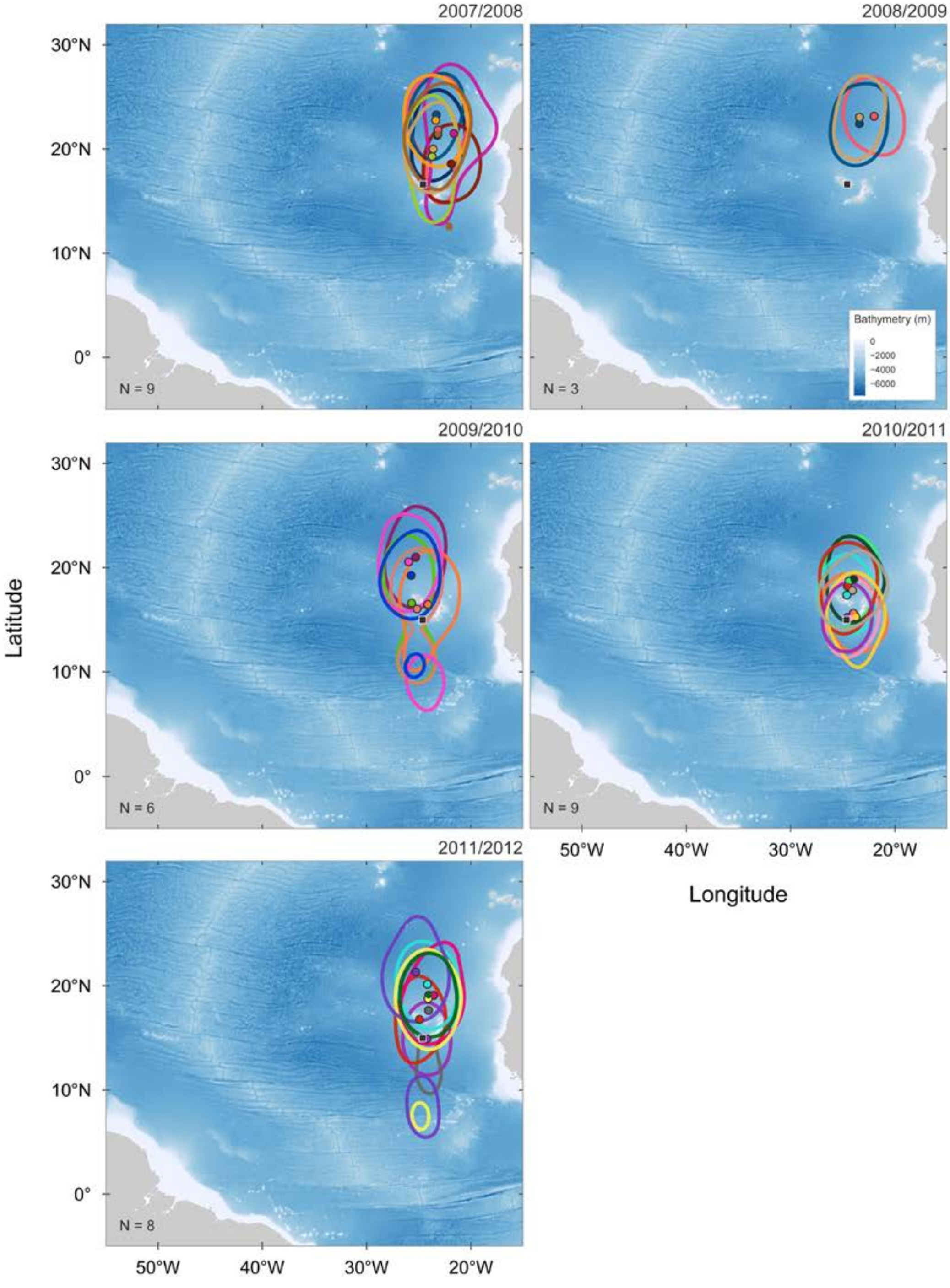


Fig. 2. Individual kernel density utilisation distributions for Boyd's shearwaters during the breeding season, tracked with geolocators during 5 yr (2007−2012). Ellipses: individual 50 % density contours; points: individual centroids of 50 % density contours; black square: breeding colony. Bathymetry used as background

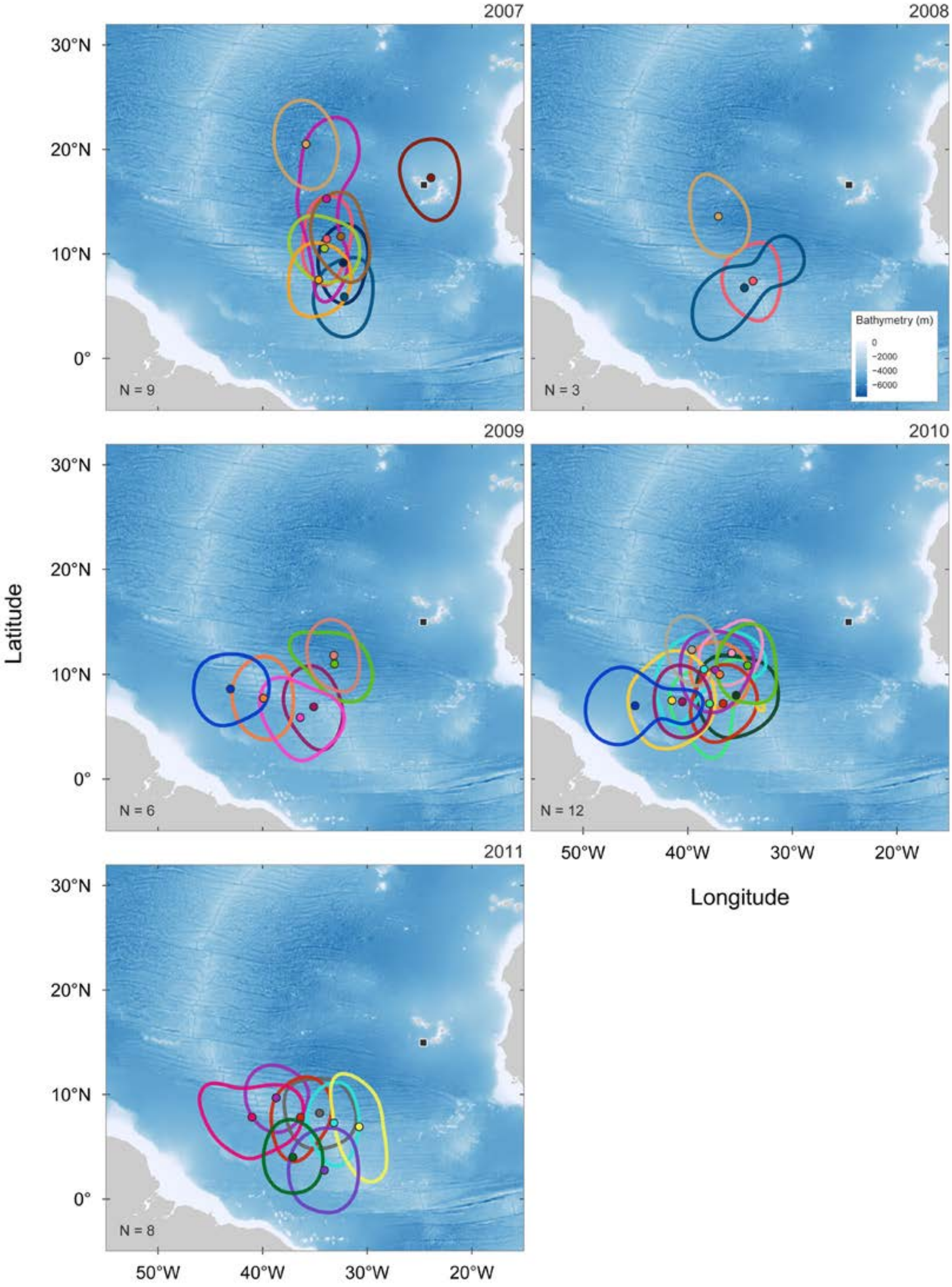


Fig. 3. Individual kernel density utilisation distributions for Boyd's shearwaters during the non-breeding season. Other details as in Fig. 2

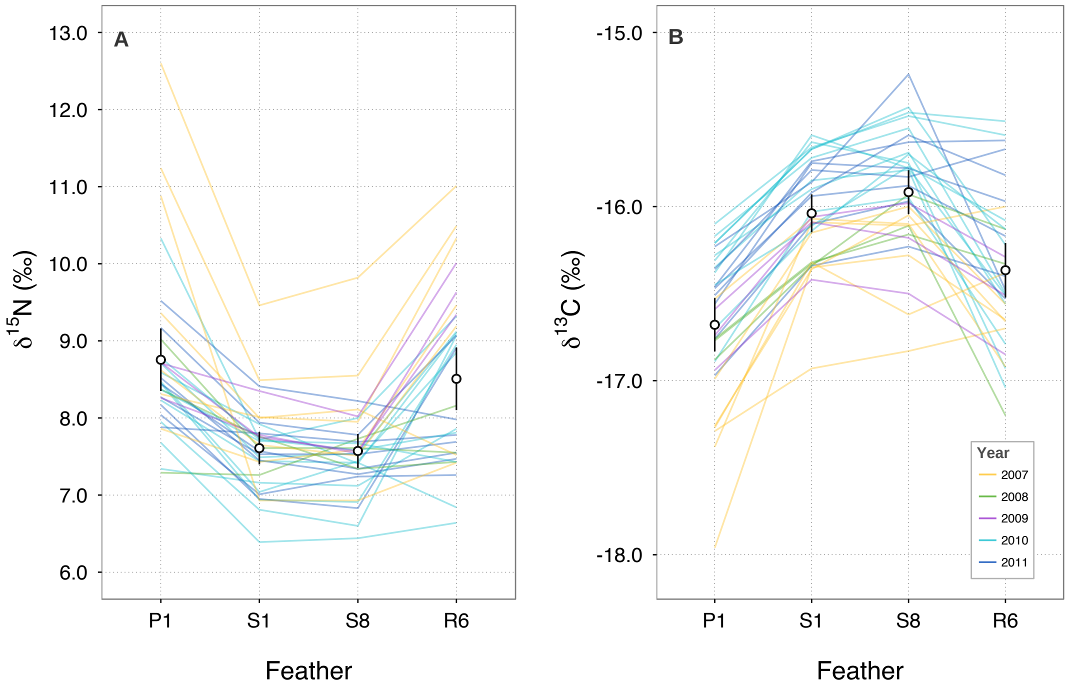


Fig. 4. Stable isotopes (A) δ^{15}N and (B) δ^{13}C of sampled feathers (P1: 1st primary; S1 and S8: 1st and 8th secondary, respectively; R6: 6th rectrice) of tracked Boyd's shearwaters breeding in the Cape Verde Islands (n = 32) in 2007−2012. Each line corresponds to 1 individual coloured by the year of tracking. Circle with range represents mean ± 95 % confidence interval

Table 3. Linear mixed models testing for spatial gradient in isotopic values of nitrogen and carbon of Boyd's shearwaters breeding in the Cape Verde Islands. Results of second-order Akaike's Information Criterion (AICc), delta AICc and Akaike weights are shown. The best supported model (in bold) includes longitude as fixed factor. All models include individual and year as random factors

Model	Df	δ^{15}N			δ^{13}C		
		AIC$_c$	ΔAIC$_c$	AIC$_c$ wt	AIC$_c$	ΔAIC$_c$	AIC$_c$ wt
Long	**5**	**37.56**	**0.00**	**0.81**	**0.75**	**0.00**	**0.82**
Long + Lat	6	40.49	2.93	0.19	3.79	3.04	0.18
Null	4	66.45	28.90	0.00	19.62	18.87	0.00
Lat	5	67.60	30.03	0.00	21.83	21.08	0.00

proportion of variance explained by the fixed factor alone, were high in the model with the fixed factor longitude (0.63 and 0.39 for δ^{15}N and δ^{13}C, respectively; Fig. 5A,B), but not in the ones with latitude (0.05 and 0.01 for δ^{15}N and δ^{13}C, respectively). Accounting for both longitude and latitude did not significantly improve the longitude-gradient model (LMM, δ^{15}N: $\chi^2 = 0.121$, df = 1, p = 0.729; δ^{13}C: $\chi^2 = 0.012$, df = 1, p = 0.913). Our best-supported models suggest that annual isotopic variability was negligible for nitrogen values of S8, accounting for 0 % of random variance ($\chi^2 = 0$, df = 1, p = 1.000) (Table S2b). In contrast, annual variation accounted for almost half (53.3 %) of the random variance of the carbon values ($\chi^2 = 7.630$, df = 1, p = 0.006).

DISCUSSION

This is the first study on the movements and year-round distribution of the Boyd's shearwater. We showed that Boyd's shearwaters perform oriented migratory movements and exploit oceanic habitats year-round. Furthermore, we revealed the existence of a longitudinal isotopic gradient in the tropical north Atlantic by relating the isotopic values of the feathers moulted during the non-breeding period and the location of the individual non-breeding area.

Boyd's shearwaters showed some variability in various aspects of their breeding phenology. Small species breeding in the tropics may experience relatively constant environmental conditions, which may cause minimal synchrony in breeding (Brooke 1990). The few individuals that started the postnuptial migration relatively earlier, in the beginning of April, were presumably failed breeders; however, we do not have breeding success information of each bird to confirm this hypothesis. The longer duration of prenuptial migration in relation to the postnuptial one is an opposite pattern to many long-distance migrants (Nilsson et al. 2013) and may be a consequence of prevailing trade winds which advantaged shearwaters during post-nuptial migration through a tailwind but disadvantaged them during pre-nuptial migration through a headwind (Liechti 2006). Birds started to arrive at the colony in early August, which confirms observations of shearwaters visiting Ilhéu de Cima at the end of August (Bourne 1955). After returning to the breeding colony, birds were asynchronous in terms of the first day spent in the burrow during daylight; these dates were spread over 4 mo. Those differences might be sex-related, with males visiting burrows earlier than females in some shearwater species (Hedd et al. 2012, Müller et al. 2014), probably due to their role in nest defence. However, this asynchrony was also observed in Barolo shearwaters, in a study where only males were tracked (Neves et al. 2012). As sex of animals tracked in this study was unknown and only 1 member of the breeding pair was tracked, we could not estimate the laying date and define the first incubation shift. However, we were able to estimate the beginning of incubation, on average February 9, which is earlier than Barolo's shearwaters in the Azores (Neves et al. 2012, but see Monteiro et al. 1996). Indeed, the incubation period (42–50 d) was slightly shorter than the periods reported for *Puffinus lherminieri* (44–60 d, Carboneras et al. 2016b), *P. assimilis assimilis* (55 d) breeding at Lord Howe Island (Priddel et al. 2003) and *P. a. haurakiensis* (54–57 d) on Lady Alice Island (Booth et al. 2000). Incubation shift length and duration of foraging trips during incubation were similar to Barolo shearwaters tracked in the Azores (Neves et al. 2012). However, the foraging-trip durations of Boyd's shearwaters differed from those of Barolo shearwaters foraging mostly within the Canary Current system (being longer than those of birds breeding in Salvagem Grande but shorter than those in Porto Santo) (Paiva et al. 2016). Since we would expect incubation behaviour and foraging strategies to be similar among such closely related taxa, this variability most likely reflects differences in environmental conditions across localities, such as differences in the distance to suitable foraging areas and their typically low predictability in tropical waters, which possibly results in differences in egg neglect episodes (and therefore duration of the incubation) and foraging trip length (and therefore duration of incubation shifts) across populations.

During the breeding period, Boyd's shearwaters mainly foraged around the Cape Verde archipelago. Individual core ranges seemed to fluctuate north and south of the archipelago, and some geolocator positions may have even reached the Canary Islands or the Azores (Fig. S3 in Supplement 1, and Supplement 2), but this is most likely due to the effect of the equinoxes on the latitudinal errors (Figs. S1 & S2). Since longitudinal errors of the geolocator methodology are relatively small and the African coast is just east of the archipelago, our results clearly showed that birds do not visit the African shelf to forage in neritic waters. With the exception of 1 individual for a few weeks, all birds were largely oceanic during breeding and over the 5 yr of the study (Fig. 2). Similarly, the closely related Barolo shearwaters breeding in Madeira and other small seabird species in Cape Verde also show oceanic distribution during the breeding period (J. A. Ramos et al. 2015, R. Ramos et al. 2015, 2016, Paiva et al. 2016). The oceanic behaviour of Boyd's shearwaters is also suggested by the low carbon values in their first primary feathers (P1), similar to those reported for other oceanic species, such as the Barolo shearwaters in several Macaronesian localities (Roscales et al. 2011, Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016), but also by Bulwer's and Fea's petrel in Cape Verde (Roscales et al. 2011). These results contrast with the importance of the continental shelf inferred for the Barolo shearwaters breeding on Salvagens (J. A. Ramos et al. 2015, Paiva et al. 2016) and also for Audubon's shearwaters breeding in the Caribbean (Precheur 2015, P. Jodice unpubl. data). Further studies using more accurate loggers are needed to confirm these results as this apparent neritic behaviour may just result from the latitudinal error of the geolocation method (Fig. S1).

After breeding, Boyd's shearwaters performed a longitudinal-oriented migration, heading westward to the oligotrophic waters of the central North Atlantic Ocean. Despite their short migration, Boyd's shearwaters constantly moved during the non-breeding season, covering on average more than 30 000 km. These movements may be a foraging strategy to increase the chances of finding prey in tropical oceanic waters, which typically show lower productivity and predictability of resources than upwelling systems (Weimerskirch 2007). However, distance calculations should be treated with caution as they may be overestimated due to the positional error. The longitudinal-oriented migration was noticeably consistent across years at coarse scale, wintering in the same area of the Atlantic (except 1 individual remaining around the Cape Verde Islands). All birds spending their non-breeding period in this area also showed clear oceanic habits. The lack of direct observations of Boyd's shearwaters from their migration and non-breeding grounds may be due to the lack of observers in those areas and/or to the problematic identification of the taxa at sea. To our knowledge, there are just a few sightings of individuals of the little shearwater complex of unknown provenance (RNBWS 2014), illustrating once again the enormous insights geolocation is providing into the spatial ecology of seabirds, particularly in closely related taxa with few morphological differences and unclear taxonomic status. In contrast with our results, previous tracking studies on Barolo shearwaters in the Azores and Salvagens mainly showed a dispersive behaviour after breeding (Neves et al. 2012, Paiva et al. 2016). In addition, there is no spatio-temporal overlap in distribution of the different taxa of the complex, pointing out substantial differences in their migratory behaviour and distribution and potential for lineage divergence, which deserves some attention when discussing the taxonomy within the little shearwater complex.

To understand year-round trophic ecology and study the existence of oceanic isoscapes through the analyses of stable isotopes in feathers it is essential to know the moulting patterns of the study model. Unfortunately, there is a lack of information about moult in Boyd's shearwater. Shearwaters usually show simple descendent moult that takes 3 to 5 mo to complete (Bridge 2006), starting with the innermost primary feather (P1), which in some species may be moulted even before the bird leaves the breeding area (Cramp & Simmons 1977, Monteiro et al. 1996). According to our geolocation data, birds spent on average 114 d outside of the breeding area, which theoretically should leave enough time to complete moult in the non-breeding area. Our SIA supports this hypothesis. P1 and R6 were isotopically similar, suggesting that they are moulted in the same area, probably near the breeding area at the end of the breeding and non-breeding period, respectively. These 2 feathers differed from the S1 and S8, which we inferred were moulted during the non-breeding period in the North Central Atlantic, since the isotopic values of the S8 showed a high correlation with the longitude of the centroid of the non-breeding area of each individual. We inferred P1 and R6 to be moulted in the same area (surroundings of the breeding colony), so we expected to find lower isotopic variability compared to S1 and S8, which were moulted in different non-breeding areas with potentially different baselines. Therefore, the larger range of isotopic values of the P1 and R6 than S1 and S8 may reflect the inter-individual variability in the phenology at the beginning and at the end of the moulting period, with some birds advancing or delaying their moulting patterns in relation to migration depending, for example, on their breeding success. Moreover, moulting pattern of rectrices is typically more asynchronic among and within individuals than the rest of the flight feathers (Ramos et al. 2009), adding variability in the timing of moult and in turn in the standard deviation and range of the isotopic values we found in R6.

The inter-annual variability in stable isotope values was low for nitrogen, but relatively high for carbon values. However, the broad pattern found in longitudinal gradients was similar over the years (Fig. S5). Baselines of nitrogen and carbon values are known to vary between seasons and years due to changing environmental factors (temperature) and/or productivity in marine environment (Goering et al. 1990, Rolff 2000, Graham et al. 2010). Inter-annual differences in stable isotopes were also found in Barolo shearwaters, but the origin is difficult to determine, since these differences may result from changes in diet, foraging areas and/or baseline conditions due to environmental factors, or a combination thereof (Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016).

Many seabird species cross the equatorial area of the Atlantic Ocean during their trans-equatorial migrations, but do not forage in this area for extended periods (González-Solís et al. 2007, Guilford et al. 2009, Hedd et al. 2012). So far, the only tracked species known to use the equatorial Atlantic waters as one of their main non-breeding areas is the Bulwer's petrel *Bulweria bulwerii* (Dias et al. 2015, R. Ramos et al. 2015), although in a different period than the Boyd's shearwater, since Bulwer's petrels breed during the non-breeding period of the Boyd's shearwaters. Temporal segregation in the breeding cycles of Bulwer's petrel and Boyd's shearwaters may suggest that this is driven by competition for food, but their segregation in trophic level, as indicated by the greater δ^{15}N in the former than in the latter (Roscales et al. 2011), would not support this interpretation. Instead, temporal segregation may partly result from competition for nesting sites (Fagundes et al. 2016). Indeed, previous studies on breeding seabirds of the tropical and subtropical Atlantic indicated that the trophic position of the Boyd's shearwater is the lowest among all pelagic seabirds, together with Barolo and Audubon's shearwaters (Roscales et al. 2011, Neves et al. 2012, Mancini et al. 2014, Paiva et al. 2016). No conventional dietary analysis of Boyd's shearwaters has been conducted so far (but see Bourne 1955), but its low trophic level indicates the consumption of small juvenile squid and fish and crustaceans, as found in the diet of the Barolo shearwater (Neves et al. 2012, J. A. Ramos et al. 2015). Previous studies have suggested seasonal changes in the diet of the Barolo shearwater (Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016), as indicated by an increase in δ^{15}N values in feathers moulted in the non-breeding season compared to those moulted in the breeding season, suggesting that shearwaters targeted prey with higher trophic level during the non-breeding season (Neves et al. 2012). We also found seasonal changes in the isotopic values quite consistent over 5 years, but changes in δ^{15}N were the opposite, i.e. we observed a decrease in δ^{15}N and an increase in δ^{13}C values from feathers moulted in the non-breeding (S1 and S8) compared to those grown in the breeding season (P1 and R6; Fig. 4). However, this opposite trend in δ^{15}N values and its significant correlation with longitude suggest that these changes just reflect baseline isotopic gradients in longitude (Fig. 5). Indeed, correlations between longitude of the non-breeding centroids with the isotopic values of feathers grown in this period broadly match isoscapes based on plankton samples from the same area (Somes et al. 2010, McMahon et al. 2013a). Spatial patterns indicating greater values of $\delta^{13}C$ and smaller in $\delta^{15}N$ in the central oligotrophic subtropical Atlantic Ocean were confirmed by a recent study on plankton biomass (Mompeán et al. 2013). Knowledge of baselines is also essential in any isotopic studies of trophic ecology, since baseline adjustment allows for the comparison of species from different geographical origin (Navarro et al. 2013). The strong longitudinal gradient in values of nitrogen and carbon found in this study suggests propagation of isotopic variability up to the food chain on a coarse scale. However, failure to find latitudinal gradients may be related to latitudinal error inherent to geolocation methodology. Another constraint in gradient models is the limitation in modelling techniques to incorporate all sources of uncertainty and error of location estimations. Furthermore, care should be taken, as the high isotopic variability among individuals and the reduction

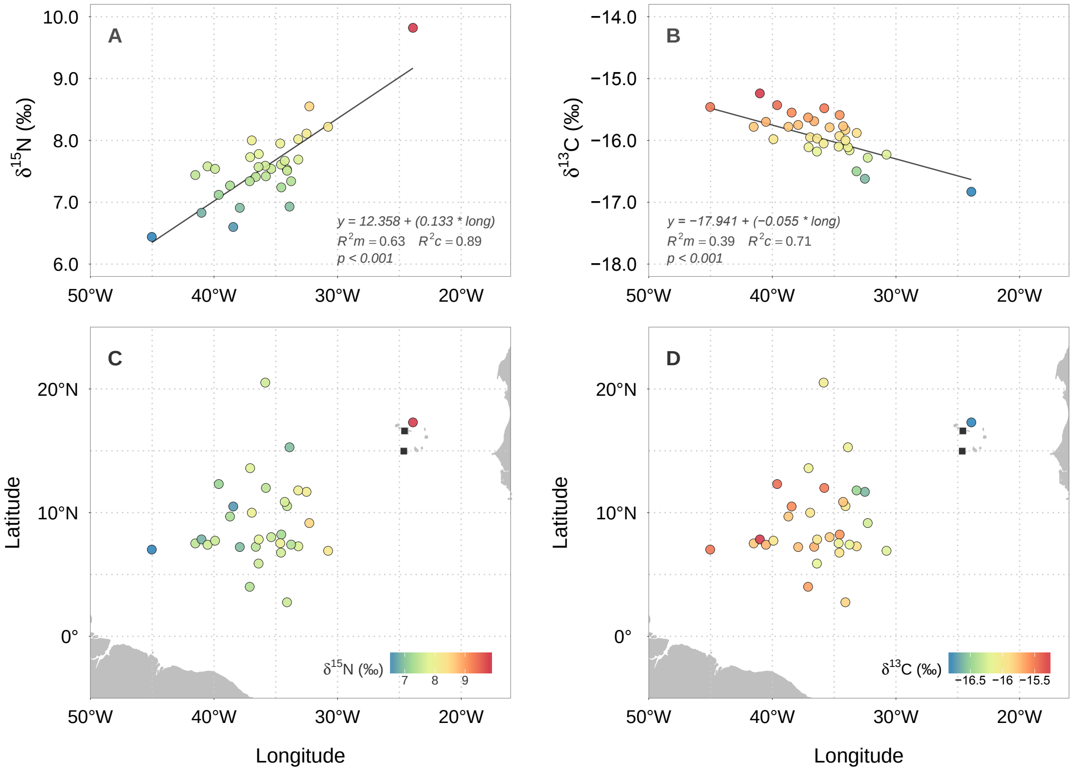


Fig. 5. Relationship between (A) $\delta^{15}N$ and (B) $\delta^{13}C$ values of 8th secondary feather (S8) of Boyd's shearwaters tracked with geolocators (n = 32; 2007−2012) and the longitude of the centroid, reflecting the area exploited during the non-breeding season (May−August). Points represent individual centroids of 50 % kernel utilization distribution during the non-breeding season. Equation (negative values for western longitude) and dark grey line refer to intercept and slope for fixed factors of linear mixed model (longitude as fixed factor, with year and individual as random) for all years pooled together. (C, D) Spatial distribution of individual centroids of 50 % kernel utilization distributions during the non-breeding season and their respective gradient in (C) $\delta^{15}N$ and (D) $\delta^{13}C$ values of S8. Black squares: breeding colonies (Ilhéu Raso and Ilhéu de Cima)

of the moulting area to a centroid may hinder the potential use of this isotopic gradient to infer the non-breeding areas of untracked birds. A study using data with more precise spatial resolution and more detailed knowledge about timing of moult would be required to create complex isoscapes and investigate the potential geographic assignment to foraging movements or non-breeding areas of top predators in the tropical Atlantic Ocean using SIA, but our results show some promising potential for this.

Overall, in this study we provided detailed information about the year-round distribution, trophic ecology, phenology and moulting patterns of Boyd's shearwater. The combined use of geolocators and SIA allowed us to bring new insights to the biology and ecology of a poorly known tropical species.

ACKNOWLEDGEMENTS

We thank all the people who helped us at several stages of fieldwork (S. Martins, R. Ramos, L. Zango). We are also grateful to the Direção Nacional do Ambiente of Cape Verde who provided logistical support and the necessary authorisations. Z.Z. was supported by a PhD grant (APIF) from the University of Barcelona (Spain) and T.M. by a PhD grant (SFRH/BD/47467/2008) from Fundação para a Ciência e Tecnologia (Portugal). This study was funded by the MICIN, Spain (CGL2009- 11278/BOS and CGL2013-42585-P) and Fondos FEDER. We are thankful to Sarah Saldanha for language corrections, Martin Stýblo for his encouragement and José Manuel Reyes-González for helpful discussions and comments on previous versions of the manuscript. We are also grateful to Steffen Oppel and an anonymous reviewer for their comments, which greatly improved the previous version of the manuscript.

LITERATURE CITED

Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. Mem Natl Inst Polar Res 58:227–233

Ainley DG, Ribic CA, Woehler EJ (2012) Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. Mar Ecol Prog Ser 451:231–243

Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus Nat Hist Yale Univ Bull 24

Austin JJ, Bretagnolle V, Pasquet E (2004) A global molecular phylogeny of the small puffinus shearwaters and implications for systematics of the little-audubon's shearwater complex. Auk 121:847–864

Ballance L (2007) Understanding seabirds at sea: why and how? Mar Ornithol 35:127–135

Ballance LT, Pitman RL (1999) Foraging ecology of tropical seabirds. In: Adams NJ, Slotow RH (eds) Proc 22 Int Ornithol Congr, Durban. BirdLife South Africa, Johannesburg, p 2057–2071

Bartoń K (2016) MuMIn: multi-model inference. https://cran. r-project.org/web/packages/MuMIn/index.html

BirdLife International (2015) *Puffinus lherminieri*. The IUCN Red List of Threatened Species 2015: eT45959182A 84678618

Booth A, Minot E, Imber M, Fordham R (2000) Aspects of the breeding ecology of the North Island little shearwater *Puffinus assimilis haurakiensis*. NZ J Zool 27:335–345

Bourne WRP (1955) The birds of Cape Verde Islands. Ibis 97: 508–555

Bourne WRP, Loveridge A (1978) Small shearwaters from Ascension and St. Helena, South Atlantic Ocean. Ibis 120:65–66

Bridge ES (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. Mar Ornithol 34:7–19

Brooke M (1990) The Manx shearwater. Academic Press, London

Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Camphuysen KCJ, Garthe S (2004) Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi-species associations. Atl Seabirds 6:1–32

Carboneras C (1992) Family Procellariidae (petrels and shearwaters). In: Del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, Vol 1. Lynx Edicions, Barcelona, p 216–271

Carboneras C, Jutglar F, Kirwan GM (2016a) Audubon's shearwater (*Puffinus lherminieri*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona

Carboneras C, Jutglar F, Kirwan G (2016b) Little shearwater (*Puffinus assimilis*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona

Catry T, Ramos JA, Le Corre M, Phillips RA (2009) Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. Mar Ecol Prog Ser 391:231–242

Catry T, Ramos JA, Catry I, Monticelli D, Granadeiro JP (2013) Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. Mar Biol 160:1189–1201

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cherel Y, Le Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar Ecol Prog Ser 366:281–291

Cramp S, Simmons KEL (1977) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, Vol I. Oxford University Press, London

Delong RL, Stewart BS, Hill RD (1992) Documenting migrations of northern elephant seals using day length. Mar Mamm Sci 8:155–159

Dias MP, Alho M, Granadeiro JP, Catry P (2015) Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel. J Ornithol 156: 955–962

Dubois PJ, Holmström N, Verneau A (2009) La péninsule du Cap-Vert à Dakar, Sénégal, est-elle la «Mecque» du sea- watching? Ornithos 16:220–232

Ekstrom PA (2004) An advance in geolocation by light. Mem Natl Inst Polar Res 58:210–226

Fagundes AI, Ramos JA, Ramos U, Medeiros R, Paiva VH (2016) Breeding biology of a winter-breeding procellariiform in the North Atlantic, the Macaronesian shearwater *Puffinus lherminieri baroli*. Zoology 119:421–429

Freitas C (2012) argosfilter: Argos locations filter. R package version 0.63. https://cran.r-project.org/web/packages/ argosfilter

Goering J, Alexander V, Haubenstock N (1990) Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a North Pacific Bay. Estuar Coast Shelf Sci 30:239–260

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 5:297–301

González-Solís J, Smyrli M, Militão T, Grémillet D, Tveraa T, Phillips RA, Boulinier T (2011) Combining stable isotope analyses and geolocation to reveal kittiwake migration. Mar Ecol Prog Ser 435:251–261

Graham BS, Koch PL, Newsome SD, McMahon CR, Aurioles-Gamboa D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson T, Tu KP (eds) Isoscapes: understanding movement, pat- tern, and process on Earth through isotope mapping. Springer, New York, NY, p 299–318

Guilford T, Meade J, Willis J, Phillips RA and others (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc Biol Sci 276:1215–1223

Guilford T, Wynn R, McMinn M, Rodríguez A and others (2012) Geolocators reveal migration and pre-breeding behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. PLOS ONE 7:e33753

Hazevoet CJ (1995) The birds of the Cape Verde Islands. An annotated check list. British Ornitologists Union, London Hazevoet CJ (1997) Notes on distribution, conservation, and taxonomy of birds from the Cape Verde Islands, including records of six species new to the archipelago. Bull Zool Mus Univ Amst 15:89–100

Hedd A, Montevecchi WA, Otley H, Phillips RA, Fifield DA (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. Mar Ecol Prog Ser 449:277–290

Hijmans RJ, Williams E, Vennes C (2012) Geosphere: spherical trigonometry. R package version 1.2-28. http://cran. r-project.org/web/packages/geosphere/geosphere.pdf

Hill RD (1994) Theory of geolocation by light levels. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkeley, CA, p 227–236

Hill RD, Braun MJ (2001) Geolocation by light level. In: Sibert JR, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Reviews: methods and technologies in fish biology and fisheries, Vol 1. Springer, Dordrecht, p 315–330

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Jaeger A, Lecomte VJ, Weimerskirch H, Richard P, Cherel Y (2010) Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. Rapid Commun Mass Spectrom 24: 3456–3460

Jaquemet S, Le Corre M, Weimerskirch H (2004) Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). Mar Ecol Prog Ser 268:281–292

Kuznetsova A, Brockhoff PB, Christensen RHB (2015) lmerTest: tests in linear mixed effects models. R package version 2.0-29. https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf

Liechti F (2006) Birds: blowin' by the wind? J Ornithol 147: 202–211

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol Evol 3:603–612

Mancini PL, Hobson KA, Bugoni L (2014) Role of body size in shaping the trophic structure of tropical seabird communities. Mar Ecol Prog Ser 497:243–257

McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct Sci 4:393–398

McMahon KW, Hamady LL, Thorrold SR (2013a) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697–714

McMahon KW, Hamady LL, Thorrold SR (2013b) Ocean eco- geochemistry: a review. Oceanogr Mar Biol Annu Rev 51:327–374

Mompeán C, Bode A, Benitez-Barrios VM, Dominguez- Yanes JF, Escanez J, Fraile-Nuez E (2013) Spatial patterns of plankton biomass and stable isotopes reflect the influence of the nitrogen-fixer *Trichodesmium* along the subtropical North Atlantic. J Plankton Res 35:513–525

Monteiro LR, Ramos JA, Furness RW, del Nevo AJ (1996) Movements, morphology, breeding, moult, diet and feeding of seabirds in the Azores. Colon Waterbirds 19: 82–97

Müller MS, Massa B, Phillips RA, Dell'Omo G (2014) Individual consistency and sex differences in migration strategies of Scopolis shearwaters *Calonectris diomedea* despite systematic year differences. Curr Zool 60: 631–641

Navarro J, Coll M, Somes CJ, Olson RJ (2013) Trophic niche of squids: insights from isotopic data in marine systems worldwide. Deep Sea Res II 95:93–102

Neves VC, Bried J, González-Solís J, Roscales JL, Clarke MR (2012) Feeding ecology and movements of the Barolo shearwater *Puffinus baroli baroli* in the Azores, NE Atlantic. Mar Ecol Prog Ser 452:269–285

Nilsson C, Klaassen RHG, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837–845

Nisbet ICT, Mostello CS, Veit RR, Fox JW, Afanasyev V (2011) Migrations and winter quarters of five common terns tracked using geolocators. Waterbirds 34:32–39

Paiva VH, Fagundes AI, Romão V, Gouveia C, Ramos JA (2016) Population-scale foraging segregation in an apex predator of the North Atlantic. PLOS ONE 11:e0151340

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272

Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160:795–806

Pinet P, Jaquemet S, Pinaud D, Weimerskirch H, Phillips RA, Le Corre M (2011) Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. Mar Ecol Prog Ser 423:291–302

Precheur C (2015) Ecologie et conservation du puffin d'Audubon (*Puffinus lherminieri lherminieri*) de la Réserve Nat- urelle des Ilets de Sainte-Anne (Martinique). PhD thesis, Zoologie des vertébrés, Université des Antilles

Priddel D, Hutton I, Carlile N, Bester A (2003) Little shearwaters, *Puffinus assimilis assimilis*, breeding on Lord Howe Island. Emu 103:67–70

Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: a review and case study of the Wilson's storm-petrel. Mar Ecol Prog Ser 295:295–304

R Core Team (2016) R: a language and environment for statistical computing. Version 3.3.0. R Foundation for Statistical Computing, Vienna. www.r-project.org

Ramos JA, Fagundes AI, Xavier JC, Fidalgo V, Ceia FR, Medeiros R, Paiva VH (2015) A switch in the Atlantic Oscillation correlates with inter-annual changes in foraging location and food habits of Macaronesian shearwaters (*Puffinus baroli*) nesting on two islands of the subtropical Atlantic Ocean. Deep Sea Res I 104:60–71

Ramos R, González-Solís J, Ruiz X (2009) Linking isotopic and migratory patterns in a pelagic seabird. Oecologia 160:97–105

Ramos R, Sanz V, Militão T, Bried J and others (2015) Leap-frog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). J Biogeogr 42:1651–1664

Ramos R, Ramírez I, Paiva VH, Militão T and others (2016) Global spatial ecology of three closely-related gadfly petrels. Sci Rep 6:23447

RNBWS (Royal Naval Birdwatching Society) (2014) World Database. www.rnbws.org.uk/search-2/ (accessed May 2, 2014)

Robb M, Mullarney K (2008) Petrels night and day: a sound approach. The Sound Approach, Dorset

Rolff C (2000) Seasonal variation in δ^{13}C and δ^{15}N of size-fractionated plankton at a coastal station in the northern Baltic proper. Mar Ecol Prog Ser 203:47–65

Roscales JL, Gómez-Díaz E, Neves V, González-Solís J (2011) Trophic versus geographic structure in stable isotope signatures of pelagic seabirds breeding in the Northeast Atlantic. Mar Ecol Prog Ser 434:1–13

Somes CJ, Schmittner A, Galbraith ED, Lehmann MF and others (2010) Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem Cycles 24: GB4019

Spear LB, Ainley DG, Walker WA (2007) Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. In: Marti CD (ed) Studies in avian biology, No. 35. Cooper Ornithological Society, Camarillo, CA, p 1–99

Surman CA, Nicholson LW, Santora JA (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. Mar Ecol Prog Ser 454:147–157

Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standarized approach. Auk 101:567–577

Velasco MC (2013) Mystery shearwater in Canary Islands in December 2012. Dutch Birding 35:186–189

Warham J (1990) The petrels: their ecology and breeding systems. Academic Press, London

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res II 54:211–223

Supplementary material

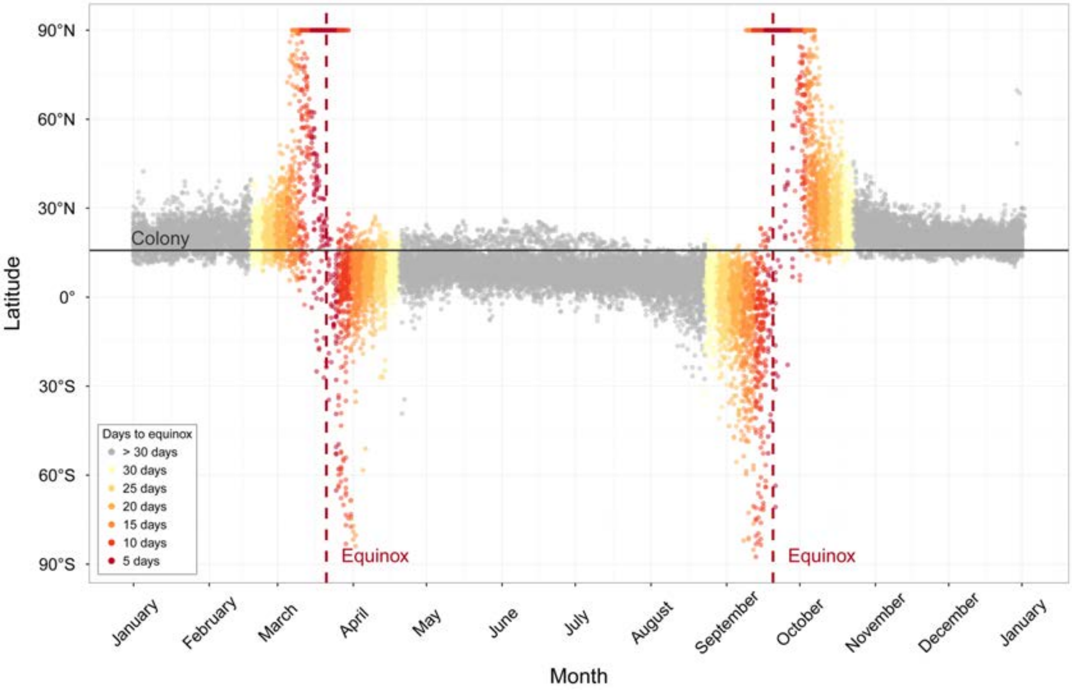


Fig. S1. Effect of equinoxes (red dashed lines) on estimation of latitude positions (using threshold method) of Boyd's shearwater tracked by geolocators in Cape Verde Islands from 2007 – 2012. Horizontal black line refers to mean latitude of two colonies (Ilhéu Raso and Ilhéu de Cima). Positions of all 38 unfiltered tracks are pooled together

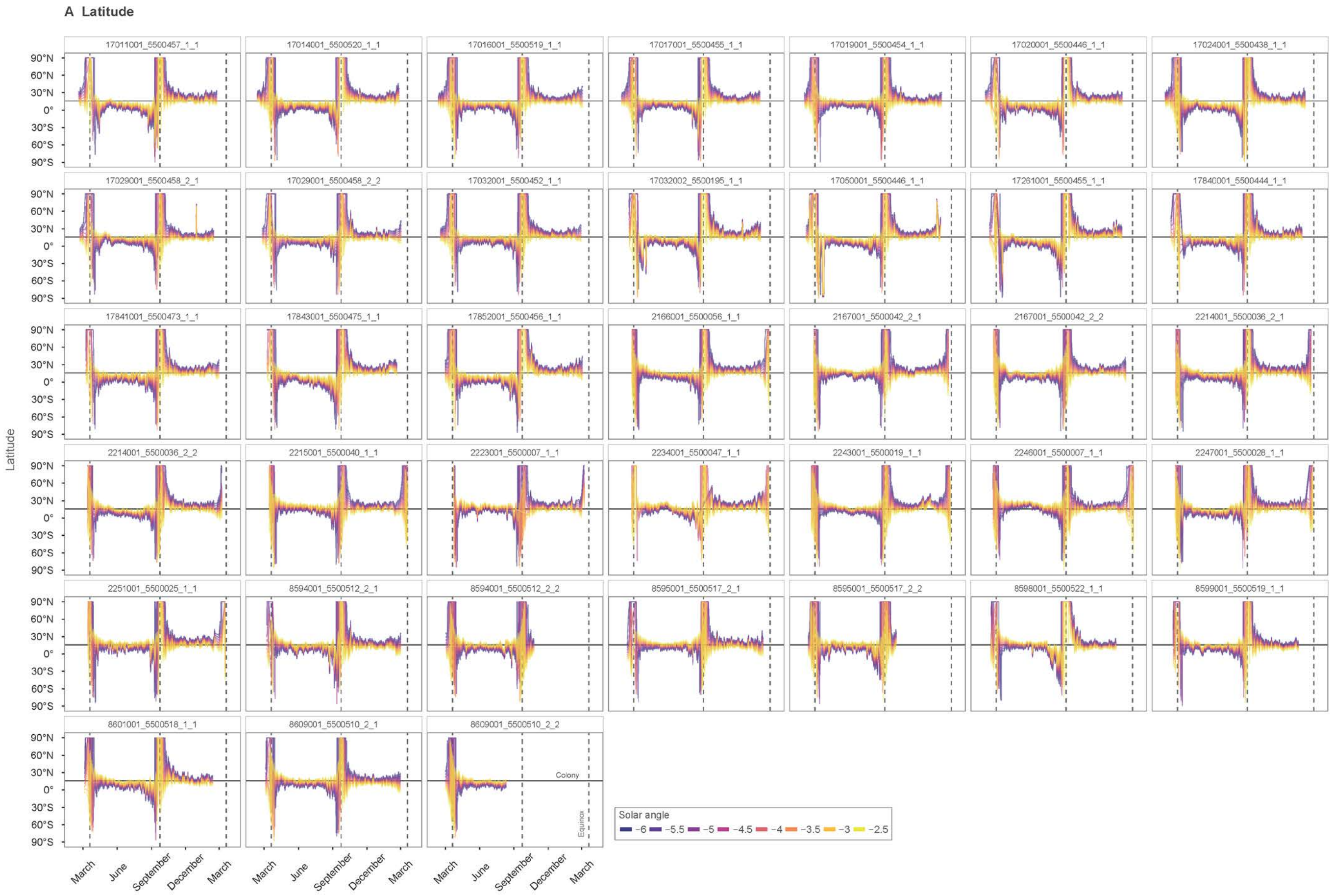
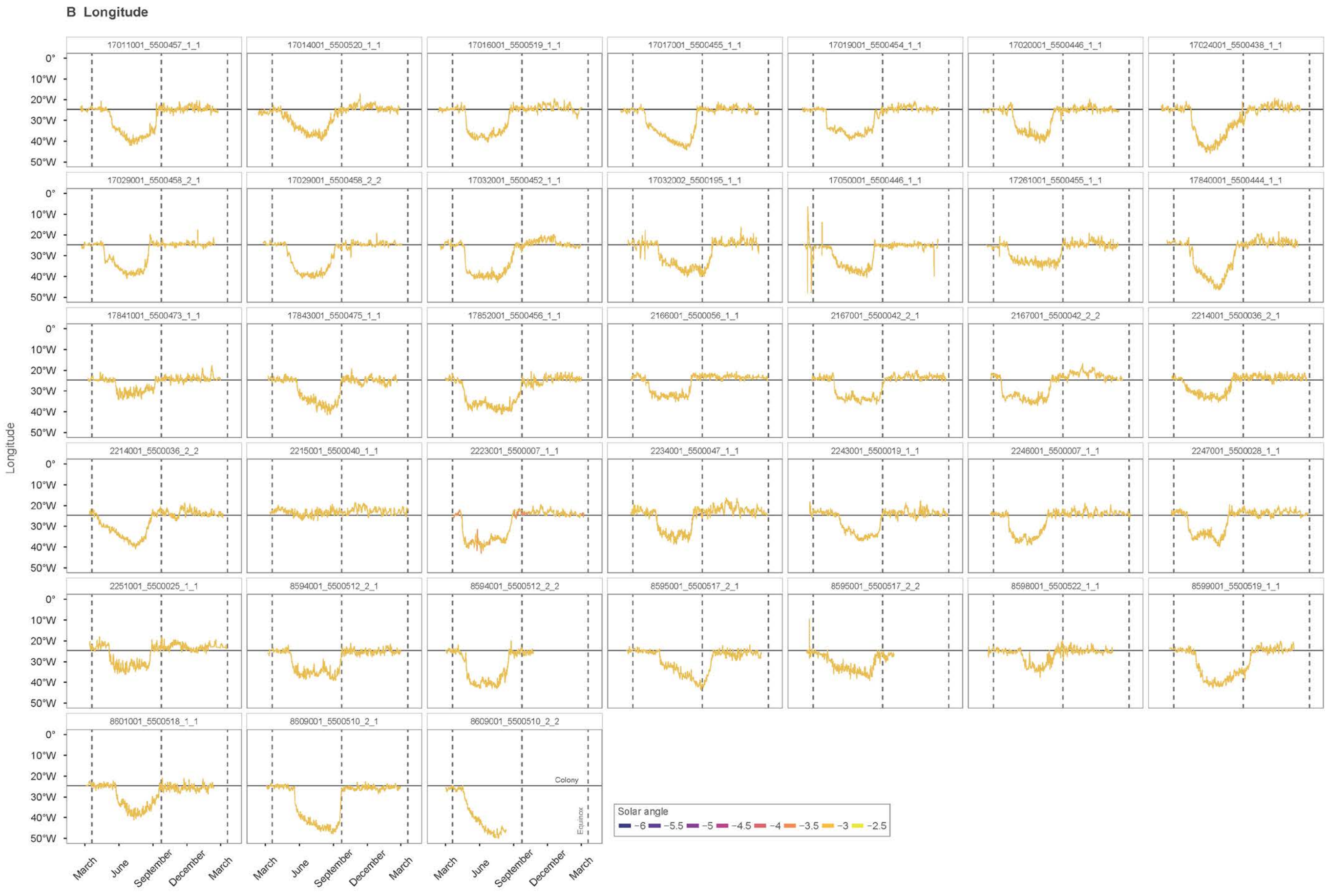


Fig. S2. Effect of equinoxes and solar angle on position estimations (using threshold method) of Boyd's shearwater tracked by geolocators in Cape Verde Islands from 2007 – 2012, for **(A)** latitude and **(B)** longitude. Horizontal black line refers to mean position of two colonies (Ilhéu Raso and Ilhéu de Cima), vertical dashed lines refer to spring (March) and autumnal (September) equinoxes. Figure visualize inherent systematic error of geolocation method, where latitude position can be more accurately estimated during solstices and at high latitudes, but more problematic during the equinox period and around the equator due to the little variation in day length (Hill 1994)



Furthermore, the error in latitude is not constant and is over- or underestimated depending on the proximity to vernal/autumnal equinox, hemisphere and mismatch between light threshold value and solar angle used for analysis (Lisovski et at. 2012).

Starts on the day of deployment and ends on the day of retrieval of the logger (or when logger stopped collecting data)

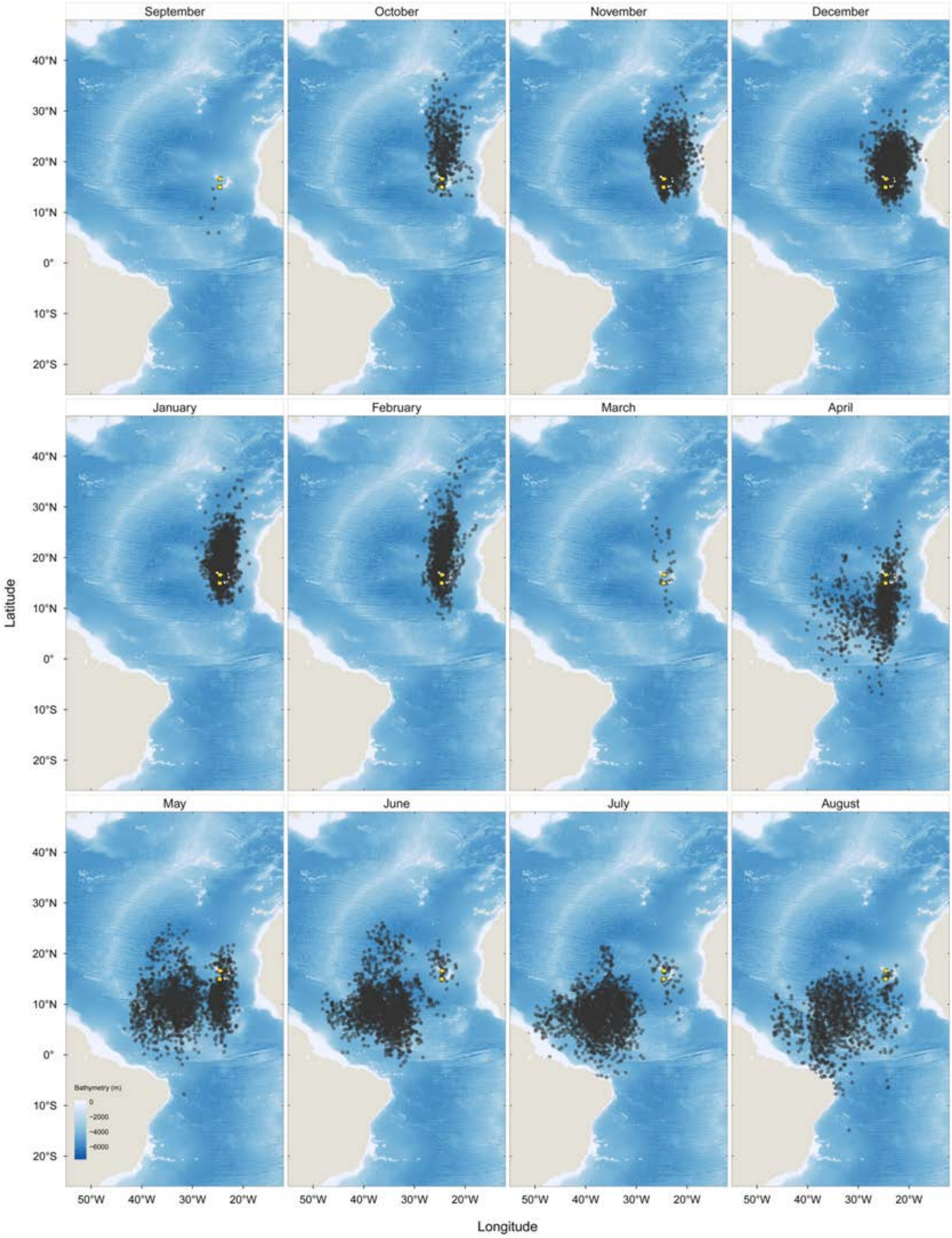


Fig. S3. Filtered monthly locations of Boyd's shearwaters (n = 38 tracks) tracked with geolocators on Cape Verde Islands (Ilhéu Raso and Ilhéu de Cima, marked as yellow squares) from 2007 – 2012, during their breeding (September – April) and non-breeding (May – August) period. The lack of locations in March and September is due to filtering process in which positions close to equinoxes were eliminated (see Methods). Bathymetry used as background

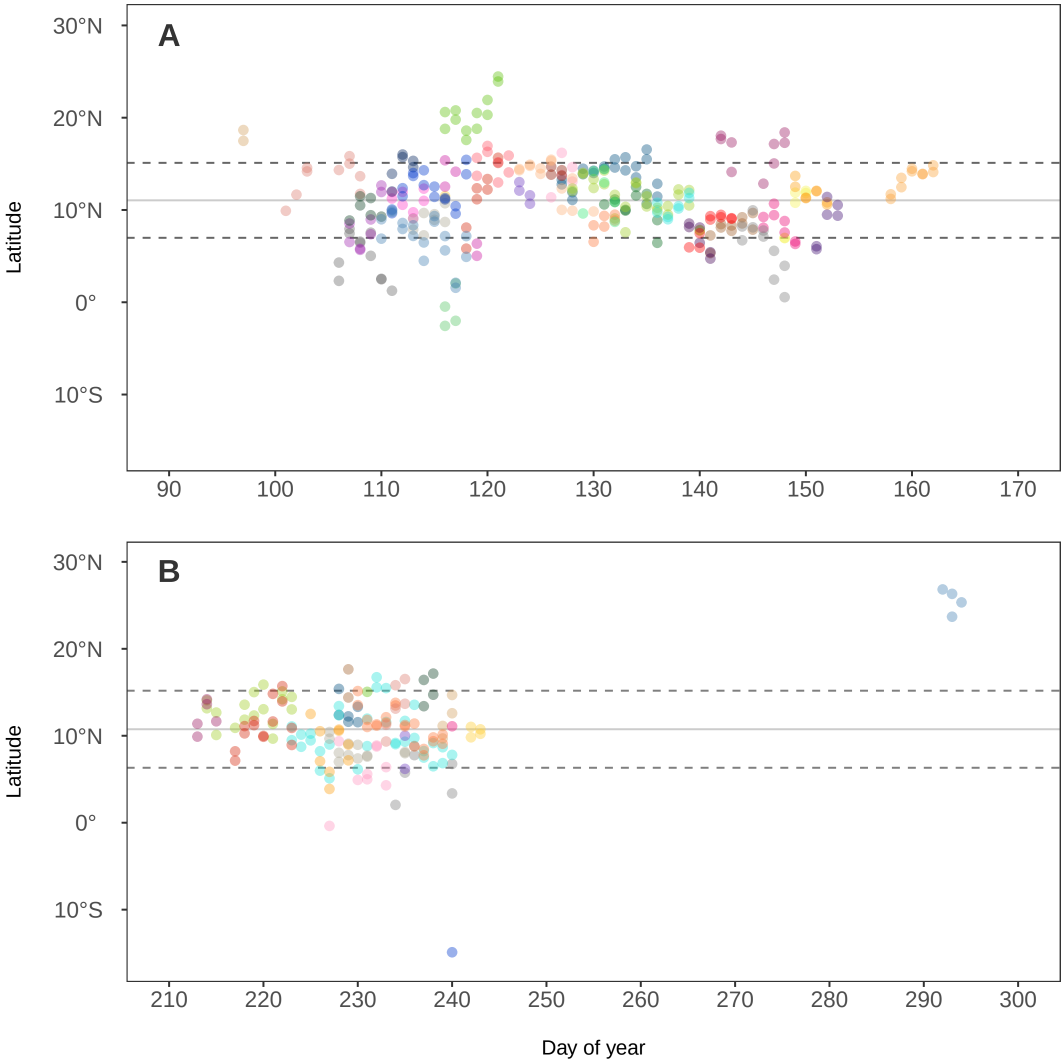


Fig. S4. Migratory corridors of Boyd's shearwaters tracked with geolocators from 2007 – 2012. All filtered latitudinal positions (see Methods) of (A) postnuptial migration ranged between 2ºS and 24ºN (n = 36), as a migratory corridor we defined a range between mean ± 1 SD of those positions, resulting in corridor between 7° – 15°N. (B) Prenuptial migration positions ranged between 15ºS and 27ºN (n = 20), resulting in corridor between 6º and 15ºN, which overlapped with postnuptial corridor. Solid and dashed lines represent mean ± 1 SD, respectively. Colours refer to different individuals, the same colour does not imply the same individual in (A) and (B).

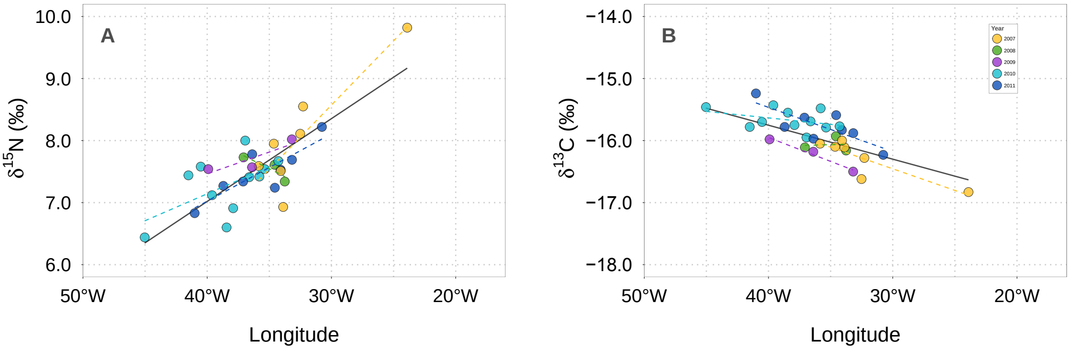


Fig S5. Relation between the (a) $\delta^{15}N$ and (b) $\delta^{13}C$ values of 8th secondary feather (S8) of Boyd's shearwaters tracked with geolocators (n=32, 2007-2012) and the longitude of the centroid, reflecting the area exploited during the non-breeding season (May-August). Points represent individual centroids of 50 % kernel utilization distribution during the non-breeding. Dark grey line refers to intercept and slope for fixed factor of linear mixed model (longitude as fixed factor, with year and individual as random, see Results and Fig. 5a-b) for all years pooled together. Dashed lines (coloured by year) refer to intercept and slope of simple linear regression of isotopic values and longitude to visualize that general pattern is maintained over years

LITERATURE CITED:

Hill RD, Braun MJ (2001) Geolocation by light level—The next step: Latitude. Electron Tagging Track Mar Fish:315–330

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol Evol 3:603–612

Table S1. a) Differences of least squares means and standard errors among sampled feathers (P1, S1, S8 and R6) of Boyd's shearwater based on the linear mixed effects models (LMM) that included individual and year as random factors (see Results). P-values are adjusted using Bonferroni correction; significant differences are highlighted in bold

	$\delta^{15}N$			$\delta^{13}C$		
Feather	Estimate	SE	p-value	Estimate	SE	p-value
P1 - S1	**1.146**	**0.158**	**< 0.001**	**-0.640**	**0.066**	**< 0.001**
P1 - S8	**1.183**	**0.158**	**< 0.001**	**-0.762**	**0.066**	**< 0.001**
P1 - R6	0.247	0.158	0.719	**-0.313**	**0.066**	**< 0.001**
S1 - S8	0.037	0.158	1.000	-0.122	0.066	0.417
S1 - R6	**-0.899**	**0.158**	**< 0.001**	**0.327**	**0.066**	**< 0.001**
S8 - R6	**-0.936**	**0.158**	**< 0.001**	**0.448**	**0.066**	**< 0.001**

(b) Variance of random effects explained in models

	$\delta^{15}N$			$\delta^{13}C$		
Random eff.	Variance	SD	%	Variance	SD	%
individual	0.322	0.567	39.31	0.029	0.171	20.20
year	0.100	0.317	12.24	0.045	0.213	31.26
residual	0.397	0.623	48.45	0.070	0.265	48.54

Table S2. (a) Model estimates and standard errors of linear mixed models (LMM) testing for spatial gradient in isotopic values of nitrogen and carbon of Boyd's shearwaters breeding in Cape Verde Islands. The best-supported models (in bold, see Results and Table 3) include longitude as fixed factor. All models include individual and year as random factors

		$\delta^{15}N$			$\delta^{13}C$		
Model	Term	Estimate	SE	t-value	Estimate	SE	t-value
Long	**(Intercept)**	**12.358**	**0.632**	**19.542**	**-17.941**	**0.373**	**-48.100**
	longitude	**0.133**	**0.018**	**7.612**	**-0.055**	**0.010**	**-5.398**
Long + Lat	(Intercept)	12.531	0.739	16.946	-17.933	0.414	-43.314
	latitude	-0.008	0.020	-0.385	-0.001	0.011	-0.062
	longitude	0.136	0.019	7.358	-0.055	0.010	-5.224
Null	(Intercept)	7.604	0.153	49.597	-15.990	0.127	-126.377
Lat	(Intercept)	7.242	0.318	22.775	-15.888	0.186	-85.536
	latitude	0.038	0.031	1.229	-0.011	0.015	-0.715

(b) Variance explained by random factors of best-supported longitudinal gradient model

	$\delta^{15}N$			$\delta^{13}C$		
Random effect	Estimate	SD	%	Estimate	SD	%
individual	0.103	0.322	69.26	0.000	0.321	0.00
year	0.000	0.000	0.00	0.036	0.000	53.38
residual	0.046	0.214	30.74	0.032	0.214	46.62


E. Ch

Chapter 2:

Common Terns on the East-Atlantic Flyway: Temporal-spatial distribution during the non-breeding period

Peter H. Becker[1], Heiko Schmaljohann[1,2], Juliane Riechert[1], Götz Wagenknecht[1], Zuzana Zajková[3], Jacob González-Solís[3]

[1] *Institute of Avian Research „Vogelwarte Helgoland", An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany*

[2] *University of Alaska, Fairbanks, AK, USA*

[3] *Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Animal, Universitat de Barcelona, Av Diagonal 643, 08028 Barcelona, Spain*

Published in: Becker, P.H., Schmaljohann, H., Riechert, J., Wagenknecht, G., Zajková, Z. & González-Solís, J. (2016) Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period. *J. Ornithol*. 157: 927– 940

ABSTRACT

We studied the temporal–spatial distribution of Common Terns *Sterna hirundo* along the East Atlantic Flyway. In 2009 and 2010 experienced adults from a colony on the German North Sea coast were tagged with geolocators recording light intensity and saltwater contact. Main objectives were the inter-individual temporal–spatial variation of migration routes and wintering areas, wintering site fidelity, and time spent at sea across the annual cycle. Geolocators had no effects on various traits of breeders, but their reproductive output suffered from egg breakage. This can be avoided by artificially incubating the eggs. Twelve routes of nine individuals were tracked. Transponder readings at the breeding site showed that birds left the colony 4 weeks before starting autumn migration. In spring and autumn, Common Terns stopped over around the Canary Islands. Main wintering distribution was the upwelling seas alongside the West African coast and similar between years, but different among individuals. Three females wintered further north and more offshore than six males. Pair mates wintered at different locations. Spring migration was longer (56 ± 8 days) than autumn migration (37 ± 17 days). During both migration and wintering the terns spent more time on salt water than during breeding and post-breeding. In most individuals saltwater contact was higher during the day than at night, reduced at sunrise and sunset likely due to foraging, and peaked about noon possibly related to resting or thermoregulation. Detailed ecological and behavioral studies of common terns during wintering are needed to clarify the results based on geolocators.

INTRODUCTION

Seabirds spend most of their non-breeding period far offshore at the oceans, e.g. Shaffer et al. (2006), Guilford et al. (2009), and Egevang et al. (2010). This makes it difficult studying their behavior during these times. By analyzing the stable isotope composition of feathers grown outside the breeding area, we gain information about the birds' diet composition and how this might affect other life-history stages, e.g. Sorenson et al. (2009). Ring recoveries might give us some indication about the birds' whereabouts during the non-breeding period, but these recoveries seem to be highly aged-biased in seabirds (Wendeln and Becker 1999; Bairlein et al. 2014). Although both methods can be used to study the ecology and the behavior of seabirds away from their breeding areas to a certain extent, different types of loggers offer the opportunity to estimate seabirds' behavior during migration and winter on a more precise scale. After recapture such loggers provide data about, e.g. GPS coordinates (Weimerskirch et al. 2002), light-level geolocations (Weimerskirch and Wilson 2000), three-dimensional acceleration (Sommerfeld et al. 2013), heart rate (Ropert-Coudert et al. 2006), water depth (Garthe et al. 2000), temperature (Wilson et al. 1992a), saltwater contact (Wilson et al. 1995), and others (Wilson et al. 2002). So far these studies have been limited to rather large seabirds, because neither the size nor the weight of the specific loggers have allowed deploying these devices to small seabirds, i.e., with body mass<100 g. Only little, therefore, was known about the whereabouts and their behavior during the migration and wintering period of such seabirds. The miniaturization of light-level geolocators now allows tracking also these smaller seabirds such as terns (e.g. Egevang et al. 2010; Nisbet et al. 2011a, b; Fijn et al. 2013; van der Winden et al. 2014).

Here we add to better knowledge about the ecology of seabirds during the non-breeding period by estimating the temporal–spatial distribution of European Common Terns (*Sterna hirundo*) along the East Atlantic Flyway. To do so we tagged adult Common Terns with data loggers at a breeding colony site in northwestern Germany (e.g. Becker et al. 2008) to record light levels and wet–dry conditions. The main objectives of this study were to estimate the inter-individual temporal–spatial variation of both their migration and wintering period, to explore potential sex-specific and within-pair differences of the wintering area, and to quantify the birds' behavior across the annual cycle in relation to the individual time spent on sea water.

METHODS

Study site

Common Terns considered in this study bred at a monospecific colony of about 400 breeding pairs located at "Banter See" at Wilhelmshaven on the German North Sea coast (53º36'N, 08º06'E, Becker et al. 2001, 2008; Becker 2010). This colony is the focus of an integrated, long-term population study, and about half of the breeders are aged, sexed, and marked with transponders (e.g. Szostek and Becker 2012). The colony site consists of six rectangular concrete islands (10.7 x 4.6 m), surrounded by a wall of 60 cm height. The walls are equipped with 44 elevated platforms for terns to land and rest on. Each platform contains an antenna reading transponder codes every 5 s, and half of them contain an electronic balance (accuracy ±1 g). This allows reliable automatic and remote detection of the birds' presence at the colony site, arrival, and body mass (Limmer and Becker 2007), with a reencounter probability of almost 1 (Szostek and Becker 2012). Colony site fidelity is very high (adult local return rate ca. 90 %; Ezard et al. 2006; Szostek and Becker 2012). The first and last transponder reading of an individual in a season indicated that the bird had arrived and left the breeding colony, respectively (Becker et al. 2008). For simplicity birds are called by individual names. Reproductive performance and output was determined for each clutch including those of geolocator-marked parents using standard protocols (e.g. Becker and Wink 2003; Zhang et al. 2015). For chicks, maximum mass, mass at fledging (±1 g), and age at fledging (±1 day) were recorded (Becker and Wink 2003).

Capture and deployment of light-level geolocators

Experienced breeders (9–14 years old, in 2009 and 2010 both pair members; Table S1) were identified by the transponder with a nest antenna and caught on the nest with an electronically released drop trap (or spring trap in exceptional cases) during incubation, on average 12 days after laying the first egg (Table S1). Before catching the birds, their eggs were replaced by dummy eggs to avoid egg breakage. The captured adults were weighed (±1 g, digital balance), measured (head and bill length ±0.1 mm; wing length 0.5 mm), and tagged with light-level geolocators (Fig. S9). Total handling time was 3–6 min. Most individuals returned to the clutch a few minutes after release and started incubation soon [on average after 13±11(2–38) min, n = 11]. No clutch was deserted owing to catching the breeders. In 2011 when light-level geolocators had to be only recovered, the eggs were removed immediately from the clutch after laying of the identified individuals, put in an incubator and were replaced by dummy eggs. Eggs remained in the incubator until light-level geolocators were retrieved from the adults to avoid any egg breakage. After that original eggs were exchanged again. Captures were performed earlier during incubation than in the previous years. Most individuals were captured in three successive years (Table S1).

Light-level geolocators

We used miniature light-level geolocators, Mk 10, from the British Antarctic Survey (BAS). They were fixed with layers of self-amalgamating tape to a plastic ring with cable tie (Fig. S9; 10 mm height, 5 mm internal diameter,1.0 mm thickness). In 2010, three geolocators were attached to an aluminum ring for a Black-headed Gull (*Croicocephalus ridibundus*, 10 mm height). Mass of the ring and fixing materials was <1.7 g (about 1.3 % of Common Tern body mass). At recapture, the geolocator from the previous year was removed and replaced by a new one (Table S1). During the pre-calibration period light-level geolocators experienced the unhindered natural change in light conditions at the colony site for 7–19 days. After removal a post-calibration was conducted with each light-level geolocator for 5–18 days (in 2011 at the colony, in 2009 and 2010 at the Institute of Avian Research, 53º33’N, 08º06’E). Twelve of the 24 geolocators had failed (see Table S1); reasons for data loss were infiltrated water, non-realistic shift in longitude due to internal clock shifts (Fig. S8), or insufficient lifetime of batteries.

Light-level geolocators used in the present study archive maximum light intensity every 10 min. Sunrise and sunset times allow inferring length of day and night and the timing of midday and midnight, and finally estimate latitude and longitude twice a day (Wilson et al. 1992b; Hill 1994). As a matter of principle, latitude cannot be estimated on about 10 days around the equinoxes (Wilson et al. 1992b; Hill 1994; Lisovski et al. 2012). The general uncertainty of the estimated locations is generally on the order of magnitude of about 150 km (Phillips et al. 2004; Fudickar et al. 2012; Lisovski et al. 2012).

Light-level geolocation data were analyzed using the statistical software R 3.1.2 (R Core Team 2014) and the freely available *SGAT* package (https://github.com/SWo therspoon/SGAT). This packages combines tools of the R package *GeoLight* (Lisovski and Hahn 2012), which uses the threshold approach (Hill 1994; Ekstrom 2004), and the R package *tripEstimation* (Sumner et al. 2009), which uses the curve-fitting approach (Ekstrom 2004; Nielsen and Sibert 2007) to estimate the animals’ locations. Here a threshold-based approach was used to estimate the birds’ locations via an Estelle model. A probability distribution of these locations is derived from the Markov chain Monte Carlo method with a metropolis sampler. In comparison to other methods of estimating birds' locations from light-level geolocation data, here a priori knowledge can be used to estimate locations by considering (1) a species-specific movement model, which is described by a bird's ground speed, (2) a species-specific land mask model, and (3) that the errors in the twilight times, which follow a log normal distribution. Following these assumptions, probability distributions of the locations are estimated. The movement model defines the density distribution of travel speed, which is described here by a gamma distribution. As air speed of common terns is about 11 m/s (Bruderer and Boldt 2001; Pennycuick et al. 2013) and as terns in general exploit favorable wind conditions (Egevang et al. 2010), we arbitrarily set mean ground speed to 15 m/s. To determine the density distribution of ground speeds, all locations of a bird were initially estimated with the threshold-sensitivity twilight function *threshold.path* and used to estimate the ground speed for the initial track. This was on average 14.66 ± 1.05 m/s (mean ± SD; n = 11) and similar to the arbitrarily chosen ground speed. In a second step, we excluded extremely high speeds which are associated with erroneously estimated locations. The mean and SD of these remaining speed values were used to estimate both the shape parameter (1.51) and rate parameter (0.13) of the corresponding gamma distribution (Becker et al. 1988). This gamma distribution fitted well the density distribution of the ground speed during the tracking period (Fig. S1). The land mask model allows setting different probabilities for the bird being on land or on water. We set the probability of a Common Tern to be near or over water two times higher than being over land because Common Terns are typical seabirds (Harrison 1997; Nisbet et al. 2011a; Neves et al. 2015) and because the vast majority of ring recoveries from mid-European breeding populations comes from the West African coast and not from inland sites, indicating the wintering grounds to be on or even off the West African coast (Wernham et al. 2002; Bairlein et al. 2014). When sunrise and sunset events are not affected by artificial light, light cannot be detected before sunrise or after sunset by the light sensor. Hence, twilight errors are not normally distributed, but described by a lognormal distribution, as twilight error of recorded light cannot be negative (Fig. S2).

We considered these assumptions in our analyses of estimating birds' locations (for details and R-code see https://github.com/SWotherspoon/SGAT). The resulting estimates in respect of longitude and latitude and their corresponding 95 % confidence intervals are given for each individual in the electronic supplemental material (Fig. S3).

We defined departures and arrivals from stationary sites, i.e., breeding area, stopover sites, and wintering grounds, as obvious changes in longitude and/or latitude (Fig. S3). In the latter, changes were only considered outside 10 days before and 10 days after the equinoxes. Because of corrupt data and heavy outliers (Fig. S3) the *changeLight* function of the *GeoLight* R packages (Lisovski and Hahn 2012) to estimate the migration schedule did not work properly. The values describing the individual migratory schedules should be treated cautiously. The estimated start of spring migration, e.g. in Cornelia and Joachim (Table 1; Fig. S3) could also be attributed to the start of movements in the wintering area. Some light-level geolocators broke before detachment, and in some the internal geolocator clock drifted (Figs. S3, S8). The area that was visited during winter time was individually estimated based on light-level geolocation estimates (Fig. S3; Table S2). However, we did not consider location estimates derived before 1 November and after 28 February to minimize the influence of the equinoxes on the latitudinal estimates (Table S2). The centroid of the wintering ground for each individual was estimated as the mean ± SD of the estimated locations which are all shown in the corresponding figures. Stopover sites could only be determined for three individuals (Table S2). Kernel densities (45, 75, and 95 %; Epanechnikov kernel) were calculated for wintering grounds of different sets (sex, year) of individuals using the *kernelUD* function of the R-packages *adehabitatHR* (Calenge 2006). The ad hoc method was used for the smoothing

Table 1 Departure and arrival dates (day–month) of common terns at the breeding and wintering area based on tracks by light-level geolocators and on remote identification by transponders at the colony site
Twelve tracks of nine individuals were achieved. Pair mates are italicized
ND no data, not analyzed, *Diff* difference of date of first or last record at colony, date based on geolocator data given in days. Only three individuals had fledged young

Bird			Departure date at breeding area			Wintering area		Arrival date at breeding area		
Name	Sex	Year	Last record colony	Geo-locator	Diff (days)	Arrival date	Departure date	Geo-locator	First record colony	Diff (days)
Joachim	M	2009/10	02-09	02-09	0	22-10	18-02	27-04	28-04	1
		2010/11	02-09	21-09	-19	23-10	ND	ND	23-04	-
Moses	M	2009/10	31-07	12-09	-43	08-10	03-03	27-04	03-05	6
		2010/11	12-07	06-09	-56	28-10	ND	ND	ND	-
Kasimir	M	2009/10	12-07	12-09	-62	11-10	ND	28-04	25-04	-3
Cornelia	F	2009/10	28-07	28-07	0	08-10	ND	ND	26-04	-
		2010/11	22-07	22-07	0	29-07	19-02	14-04	14-04	0
Heiner[a]	M	2010/11	24-08	06-09	-13	01-11	15-02	11-04	18-04	7
Ayla[a]	F	2010/11	24-08	06-09	-13	25-10	15-02	18-04	14-04	-4
Ernst[a]	M	2010/11	07-08	21-09	-45	28-10	23-02	13-04	14-04	1
Wieland	M	2010/11	26-07	11-09	-47	12-10	08-03	23-04	ND	-
Marianna	F	2009/10	15-07	30-08	-46	21-10	ND	ND	25-04	-
Mean			04-08	02-09	-31[b]	13-10	22-02	20-04	22-04	1[b]
± SD			± 20	± 19	± 23	± 25	± 8	± 7	± 7	± 4

[a] Care of juveniles on migration
[b] Calculated for the individual differences

parameter. The grid was set to 500. The same settings were applied when estimating kernel densities for stopover sites. The distance between the breeding area and the average wintering ground was calculated as the great circle distance between these locations.

Time spent on salt water

The Mk 10 BAS geolocators also recorded saltwater immersion every 3 s and stored number of positive records ranging from 0 (continuously dry) to 200 (continuously wet) at the end of each 10-min period (“wet– dry” information). Immersion data were available for eight individual tracks (two females, six males, Table S3). We estimated the average proportion of time spent on saltwater per hour (0–24 h, Greenwich Mean Time, GMT) and per day (in hours or % of 24 h, and for wintering at the latitude of Dakar, Senegal, we differentiated between daylight (7:30–18:45) and night hours (18:45–7:30).

Defining stages of the annual cycle

Based on the individual light-level geolocation data combined with data from transponders at the colony site (Table 1; Fig. S3) we defined for each individual six different annual stages:

Breeding stage: the bird was at the colony.

Post-breeding stage: the bird had left the colony, but remained in the vicinity of the German Bight and did not start its autumn migration.

Autumn migration: the bird was on the move, but had not reached its wintering area.

Wintering: the time after arrival at the wintering area and before spring migration.

Spring migration: the bird started its spring migration and had not reached the colony.

Pre-breeding: spring migration was finished, but the colony site not reached (sufficient data only in one individual, Table S3).

Defining these stages based on light-level geolocation data was a rough estimate, and small differences between these stages with respect to saltwater contact should be interpreted cautiously.

Statistics

Data were analyzed using the statistical software R 3.1.2 (R Core Team 2014). To assess whether individual birds being tracked for two consecutive winters showed significantly higher winter area fidelity than the population on average, we performed a randomization test, randomly selecting 10,000 pairs of mean wintering locations from our data set. We did not allow that a pair of mean locations consisted of the same locations. If the within-individual difference of the two tracked mean wintering locations were shorter than the 250 shortest distances between randomly selected pairs of mean wintering locations, birds were assessed more faithful than expected by chance.

We tested for seasonal differences in at-sea activity between stages (without the pre-breeding period, owing to insufficient data) using GLMRM (generalized linear model for repeated measurements, SPSS 22). The Mann–Whitney *U* test was applied when comparing non-parametric differences between two groups. The Wilcoxon signed-rank test was used as a non-parametric test for paired samples. If not otherwise stated values are reported as mean ± 1 SD.

RESULTS

Retrieval of geolocators

Twenty-five out of the 29 tagged birds, i.e., 86 %, returned to the breeding colony the year after deployment. All individuals carrying a light-level geolocator bred in their returning year (Table S1). No bird showed any signs of leg injuries when light-level geolocators were removed. One female had lost her light-level geolocator (Table S1). Twelve of the 24 light-level geolocators contained analyzable data by nine adults (three females and six males, including three pairs).

Potential effects of geolocators

Carrying light-level geolocators did not significantly affect both arrival and laying date, mass at arrival, mass at catching, clutch size, body mass growth of chicks, and ability to fledge chicks (see chapter "Additional information about potential effects of geolocators on common terns" in Electronic Supplementary Material). However, we recorded a strong and significant deterioration of hatching success from 86 to 43 % reducing reproductive output of pairs marked with geolocators severely (Tables S5, S6). The reduced hatchability was caused by eggshell breakage owing to fine fissures increasing with time advancing of incubation by the marked individuals (Figs. S9, S10). In 2011, i.e., the last year of this study, reproductive success of geolocator-birds was successfully increased by exchanging pairs' original eggs with dummy eggs, and incubating the original eggs in an incubator until geolocators were retrieved. These measures had increased hatching success to 89 % (for details see Electronic Supplementary Material, Table S6).

General temporal–spatial distribution of Common Terns during the non-breeding period

As Common Terns mainly migrated during both equinoxes (Fig. S3), we dispensed with a detailed temporal–spatial analysis of individual movements between the colony and the wintering areas.

Birds left the colony on average on 4 August ±20 days (range 12 July–2 September) and abandoned the German Bight on 2 September

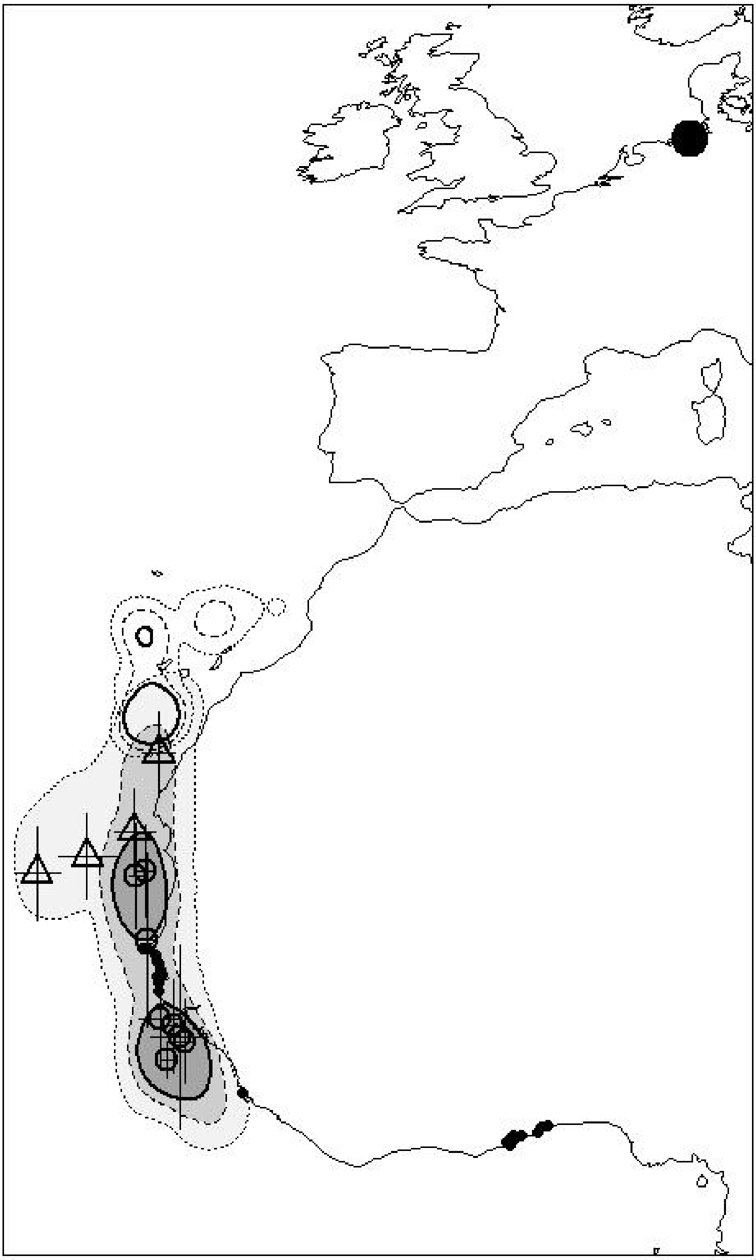


Fig. 1 Wintering and stopover locations at Canary Islands of 12 routes of nine Common Terns tracked with light-level geolocators between 2009 and 2011. Breeding site *large black dot*. *Large black triangles* (females) and *black circles* (males) mean wint er locations ±SD. *Dotted lines* 95 kernel densities; *dashed lines* 75 kernel densities; *solid lines* 45 kernel densities. Kernel densities at wintering sites were highlighted in three different shades of *grey*. Birds migrated to their winter locations by flying mainly over water. *Small black dots* indicate African ring recoveries during December and January of adult common terns from northwest German breeding sites (Helgoland ringing center, n = 30; age at ringing older than 1 year or period between ringing and recovery date >3 years; cf. Bairlein et al. 2014). Map is Mercator projection

±19 days (22 July–21 September; Table 1). In general, the data suggested that common terns moved along the East Atlantic Flyway and that they predominantly used offshore migration routes (Fig. S3). The sea around the Canaries was identified as a stopover area (Fig. 1; Table S2): two individuals stopped there during autumn migration. One remained in this area approximately for 7 days (Moses in 2010) and the other slightly less than a month (Cornelia in 2009; Table 1, Table S2). Also, during spring migration one individual (Kasimir) stopped there (Table S2). Within 13 days after resuming migration from this stopover area the bird (Kasimir) reached the colony (Table 1, Table S2).

Common Terns arrived at the wintering areas on 13 October ± 25 days (29 July–1 November, Table 1). Mean wintering period lasted 136 ± 34 days (n = 7, calculated by the individual differences, cf. Table 1). Their preferred wintering areas were the upwelling seas alongside the West African coast of Morocco, Western Sahara, Mauritania, Senegal, The Gambia, Guinea Bissau, Guinea, and Sierra Leone (Fig. 1). Mean great circle distance between the colony and the individual mean wintering locations was 4,782 ± 467 km (range 3,881–5,368 km, n = 12). In autumn, this distance was covered in 41 ± 17 days (n = 12, calculated by the individual differences, cf. Table 1). The mean distances covered per day during southward migration was 158 ± 132 km (n = 12). The four females spent the winter further north (females 20 ± 2.5°N, range 18–24°N, males 13 ± 3.8°N, range 9–19°N; Mann–Whitney U test: U = 30, p = 0.016; Fig. 1) and seemingly more offshore than the eight males (males 107 ± 57 km, range 30–217 km; females 293 ± 255 km, range 86–624 km; Mann–Whitney U test: U = 44, p = 0.174).

The winter distributions were not obviously different between the 2 years (Fig. S5). There was no indication for significant wintering site fidelity, however, as the within- individual distance of the tracked mean wintering locations were not shorter than expected by chance in comparison to the between-individual distance of the mean wintering locations (Figs. S4–S6).

In the three pairs for which light-level geolocation data were available for both partners (Table 1), the general wintering areas and the estimated mean wintering locations did not overlap between the sexes (Fig. 2). There was some spatial overlap of the general wintering area of Cornelia and Kasimir (Fig. 2), but they seemed to be temporally separated (Fig. S3). Distance of pair members' mean wintering locations was 897 ± 320 km (530–1,120 km, n = 3) and with longer than the median great circle distance (647 km) of the 10,000 randomly chosen mean wintering location pairs (Fig. S4). These sex-specific differences in the mean location of the general wintering areas within breeding pairs supported the general picture of females wintering further off-shore and unrelated to their mates.

Spring migration started on average on 22 February ± 8 days (15 February–8 March, Table 1). Common terns arrived at the breeding grounds on 20 April ± 7 days (11–28 April) so that total time of migration was about 56 ± 8 days (mean ± SD, n = 7) in spring. The mean distance covered per day during northward migration was 88 ± 20 km (n = 7). For these seven birds spring migration lasted significantly longer than autumn migration (autumn: 37 ± 17 days; Wilcoxon signed-rank test: V = 0, p = 0.036, n = 7). Common Terns spent about 117 ± 8 days (n = 11) at the breeding colony or in the vicinity of the colony during the reproductive season. Based on transponder data only the tracked common terns stayed 96 ± 23 days (n = 16) at the colony site.

The within-individual variation of the migration schedule between 2 years varied in general by a few days (Table 1). In 2009 Joachim and Cornelia and in 2010 only Cornelia left the colony and the breeding area on the same day, i.e., autumn migration started on the day individuals were last recorded at the colony by their transponder. Cornelia arrived at the wintering area in the beginning of October in 2009, but to the end of July in 2010. This between-year difference in the estimated arrival time at the wintering area was not explained by the between-year variation in the start of autumn migration (about 1 week). The return of the young of Ayla,

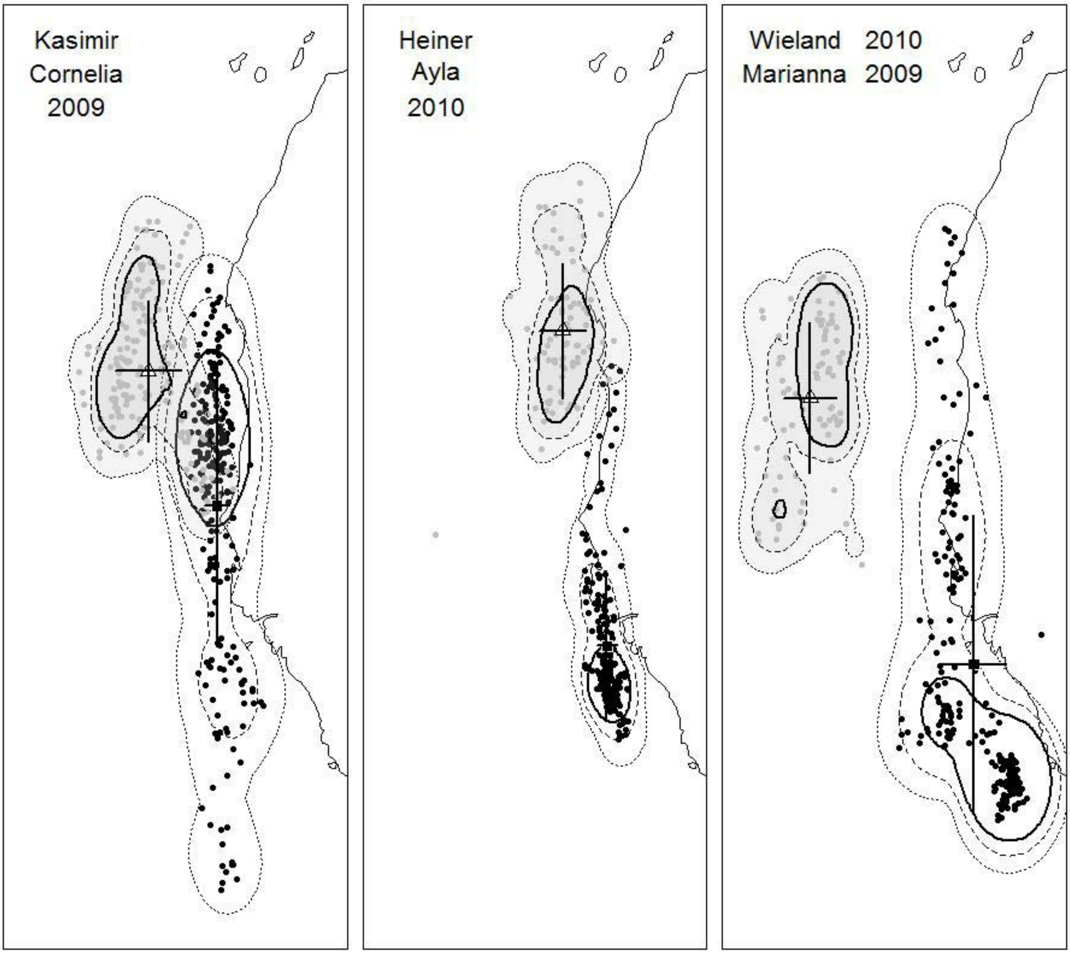


Fig. 2 Wintering areas of pair mates tracked during the same winter (Ayla, Heiner 2009/2010; Cornelia, Kasimir 2010/2011) or with male one winter later (Marianna 2009/2010, Wieland 2010/2011). *Grey dots* female; *black dots* male locations. *Symbols* and kernel densities (females highlighted in *grey*) as described in Fig. 1

Heiner, and Ernst (Table 1) as prospectors to the colony 2 years later showed that post-fledging parental care of these parents was successful. The temporal patterns of Ayla's, Heiner's, and Ernst's autumn migration, however, were not distinctively different from the adults failing to produce fledglings (Table 1).

Arrival and departure dates at the colony site: a comparison of transponder data and light-level geolocation estimates

After leaving the breeding colony (transponder data) it took on average 31 days before Common Terns started their autumn migration (Table 1; Fig S3). Only two birds had left both the colony site and the breeding area on the same day (Joachim and Cornelia, Table 1; Fig S3). In spring, however, arrival date at the breeding colony detected with the transponder recording system was similar to the estimated arrival date by light-level geolocation data (Table 1).

Saltwater contact during the annual cycle

The proportion of time spent on salt water varied among individuals and stages (Fig. 3, Fig. S7; Table S3). The differences between the stages of the annual cycle were highly significant (F = 10.228, p < 0.001, n = 6; 3 stages, F = 11.711, p = 0.002, n = 8; Fig. 3). During breeding and post-breeding, common terns spent only a small proportion of time on saltwater (1.1–3.5 %). During autumn migration, wintering, and spring migration, however, individuals spent significantly more time on salt water (8.6–13.9 %; Fig. 3, Fig. S7; Table S3 with statistics among single periods). Inter-individual differences were consistent between stages: during all periods, e.g. Ayla or Joachim spent more time at sea than, e.g. Heiner and Moses (between subject effects, F = 37.325, p = 0.002, n = 8; Fig S7; Table S3). There was a tendency that individuals wintering more offshore had more water contact than birds wintering closer to the coast (correlation between proportion of time at sea water with distance from the coast, Pearson, r = 0.624, p = 0.098, n = 8). Furthermore, the daily proportion of time spent at seawater during winter was significantly and positively correlated with the latitude of mean wintering locations of the com- mon terns studied (Pearson, r = 0.743, p = 0.035, n = 8).

The time spent with saltwater contact varied over the course of the day with respect to the stages of the annual cycle (Fig. 4). During both autumn and spring migration and during winter, Common Terns spent about 10–15 % of the time on salt water during the night. At times around sunrise and sunset proportion of water contact was minimal, but highest between these events (Fig. 4), peaking between 11 and 15 GMT. There was no clear daytime pattern for the other stages of the annual cycle (Fig. 4). With respect to day and night differences in winter, five out of seven individuals had more saltwater contact at daylight than during the night, for the other two individuals it was vice versa (Cornelia and Joachim, who also had most saltwater contact in total, cf. Table S3).

DISCUSSION

Our results show that common terns from the breeding colony in Germany winter in the fish-rich upwelling off the West African coast (Grecian et al. 2016; Fig. 1). Females' wintering areas were situated further to the north by 7° than that of males. The proportion of time birds had direct contact with salt water varied between the different stages of the annual cycle: while at the breeding area saltwater contact was low, it was high during the migration and wintering periods (Fig. 3). This difference across the annual cycle might be explained by the daily variation of saltwater contact (Fig. 4).

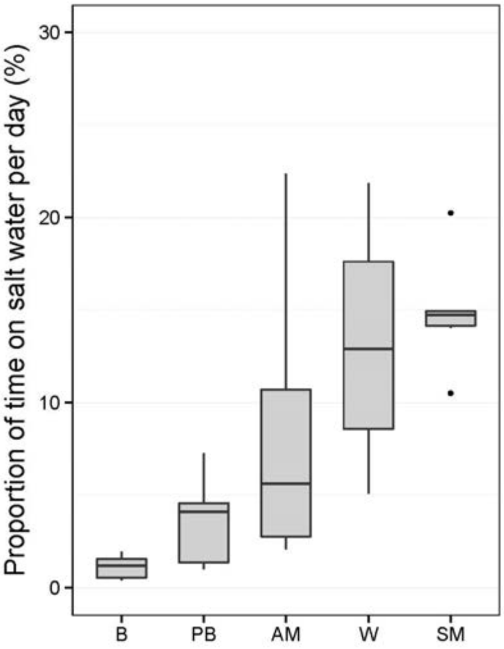


Fig. 3 Seasonal variation in the temporal proportion of saltwater contact across different stages of the annual cycle. Means of daily percentage of time eight common terns had contact with salt water recorded by using saltwater immersion data from geolocators (*B* breeding, *PB* post-breeding, *AM* autumn migration, *W* wintering, *SM* spring migration)

Potential effects of geolocators

Despite the phenomenon of egg breakage (Fig. S10 and below) we found no adverse effects of birds being tagged at the tarsus with a light-level geolocator neither on return rate, body condition, nor arrival date after spring migration or laying date. Return rate to the colony was

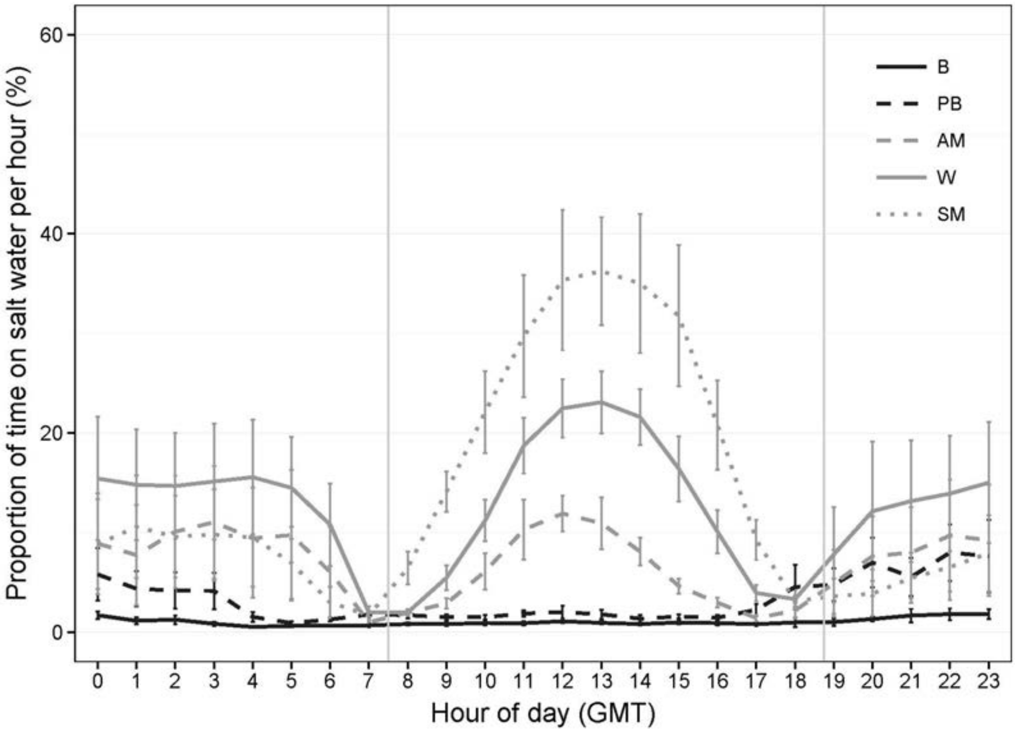


Fig. 4 Daily saltwater contact pattern. Mean hourly percentage of time spent on salt water ± standard error of seven common terns recorded using geolocation-immersion loggers during different stages of the annual cycle. Means of values were first calculated for individual birds, then averaged for all birds (without Ayla owing to clock shift, Fig. S8). Vertical lines refer to mean sunrise and sunset hour during wintering. Codes for stages as in Fig. 3

in the range known for this and other colonies of the common tern (Ezard et al. 2006; Szostek and Becker 2012; Nisbet and Cam 2002; Breton et al. 2014; Palestis and Hines 2015). Return rate of tagged birds was also similar to the rates as reported from other light-level geolocation studies of *Sterna* terns in general (Nisbet et al. 2011a; Fijn et al. 2013). Returned Common Terns equipped with geolocators were in good physical condition like Arctic Terns (*Sterna paradisaea*, Egevang et al. 2010; Fijn et al. 2013) and showed no reduction of body mass at arrival or when recaptured. This is in contrast to the findings of Nisbet et al. (2011a) in Common Terns and Mostello et al. (2014) in Roseate Terns *Sterna dougallii*. Neither arrival date of the birds repeatedly measured before, during, or after deployment of the geolocators nor laying date was affected (for further details see Electronic Supplemental Material). Thus, the various parameters recorded in the individuals tagged with light-level geolocators make us confident that the geolocators did not negatively affect the temporal-spatial distribution of the Common Terns during their non-breeding period.

After return all experimental birds produced normal clutch sizes (in contrast to Arctic Terns, Egevang et al. 2010), but suffered from increased egg breakage (cf. Nisbet et al. 2011a). This was caused by the geolocator and dependent on the number of days the eggs were incubated by a parent carrying a geolocator. Thus, effects of geolocators on the individual fitness can be serious (cf. Scandolara et al. 2014 for barn swallows *Hirundo rustica*). This effect, however, can be minimized by exchanging natural eggs with dummy eggs soon after laying and by artificially incubating the natural eggs until deployment of the geolocator, or even until hatching.

General temporal–spatial distribution of common terns during the non-breeding period

In agreement with recoveries of adult Common Terns ringed during the breeding period in Germany, this study confirms that individuals from our study site mainly winter in coastal West Africa (Fig. 1). However, ring recoveries suggested that the wintering area of adults from eastern, but also from western Germany is further extended to the south of western Africa than pictured by the birds from Banter See colony (Fig. 1, cf. Neubauer 1982; Bairlein et al. 2014). Common Terns made use of the upwelling zone supplied by the cold Canary current off the northwest African coast (Brenninkmeijer et al. 2002), where primary productivity is higher than in other areas (McGregor et al. 2007; Ar´ıstegui et al. 2009). Accordingly, the coastline of about 2,200 km along Mauritania, Senegal, Gambia, Guinea Bissau, Guinea, Sierra Leone to Liberia is a very attractive and important wintering area for many seabird species (Grecian et al. 2016). To reach and leave this area, Common Terns might make use of stopover sites at the seas around the Canary Islands (Fig. 1), similarly to Black Terns *Chlidonias niger* (van der Winden et al. 2014). Like other tern species passing West African waters, Common Terns mainly use offshore migration routes (Figs. 3, 4, Figs. S3, S7), cf. Arctic Terns (Fijn et al. 2013) and Black Terns (van der Winden et al. 2014).

Wintering site fidelity is described for some seabird species (Phillips et al. 2005; Guilford et al. 2011; Dias et al. 2013). On average the three birds tracked for two seasons did not revisit the exact same wintering area (see “Results”), suggesting a low wintering site fidelity at a narrow spatial scale. However, this may result from a low sample size and indeed site fidelity varied substantially among individuals (Figs. S5, S6). The habitat which common terns seek for wintering is not fixed to a certain location, because biotic and abiotic environmental conditions are on the move with the actual currents. Hence, we do not predict a similar level of high winter site fidelity as found in terrestrial bird species, e.g. Salewski et al. (2000).

The general data indicate that Common Tern females wintered further north than males (Fig. 1), which was supported by within-pair data (Fig. 2). Causes are unknown, but could be related to different nutritional requirements between male and female Common Terns: Nisbet et al. (2002) showed that pair members of Common Terns breeding at Bird Island, MA, USA, had different diets in winter. Females were supposed to feed on a higher trophic level than males. A stable-isotope analysis of feathers from individuals whose gender and wintering site are known could enlighten these interesting findings. Based on our light-level geolocation data, we argue that pair mates do not meet during their wintering period and that in consequence they likely migrated separately from their mate to the colony. Similar results have been found for other seabird species, e.g. the Cory’s Shearwater *Calonectris borealis* (Müller et al. 2015).

Time schedule of the annual cycle

The general timing of the stages within a year was similar between Common Terns on their East and West Atlantic Flyways (Table 1, cf. Nisbet et al. 2011a). In contrast to the more general pattern that avian spring migration is faster than autumn migration (Nilsson et al. 2013), Common Terns reached their seasonally appropriate migratory goal in on average 41 days in autumn, but 55 days in spring. This may be a consequence of prevailing winds, rotating clockwise in the North Atlantic and offering tailwind during autumn migration, but headwind during spring migration (Liechti 2006). For the few birds tracked along the West Atlantic Flyway, however, spring migration was faster than autumn migration (Nisbet et al. 2011a) again in agreement with prevailing wind directions. However, these results should be treated cautiously given the location error in light-level geolocation estimates and the low sample sizes.

Most adult Common Terns lingered for 4 weeks around the breeding area, as inferred by the time passed between the last detection at the colony site by the transponder system and the first sign of migration from geolocation. A similar pattern was described by Nisbet et al. (2011a) showing that adult Common Terns stayed about 100–200 km to the east or the west of the breeding colony before starting autumn migration. The reason for this behavior remains speculative. Possibly, adults care for their offspring, which they may guard and feed up to several weeks after fledging (Burger 1980; Becker and Ludwigs 2004; Nisbet et al. 2011b: at least until end of September; for other tern species see Ashmole and Tovar 1968). Parents may familiarize their offspring with the extended surroundings of the colony site or to reach more productive feeding grounds (cf. Fijn et al. 2013). Adults may also accumulate energy, in terms of fat and muscle mass, as a preparation for the upcoming migrations. Our light-level geolocator data indicated that the delay until the final departure of adults for migration was independent of sex (Table 1). This is in contrast to the findings of Nisbet et al. (2011a, b) showing that females started earlier than males presumably because the post-fledgling guarding is mostly provided by the fathers (Nisbet et al. 2011b).

Saltwater contact during the annual cycle

Common terns spent small proportions of time resting on saltwater during the breeding period (Figs. 3, 4). This saltwater contact was likely explained by bathing as Common Terns do not swim in the breeding area (PHB personal observations; Nisbet 2002; Nisbet et al. 2011a). During the non-breeding season, however, the birds spent more time on salt water, confirming observations of Common Terns from the West Atlantic Flyway (Nisbet et al. 2011a; Neves et al. 2015). The inter-individual differences in saltwater contact during both migration periods and wintering along the West African coast might be due to individual selection of habitats. In contrast to other individuals who spent most time resting at sea water during the day, Cornelia and Joachim showed high saltwater contact during the night, which they obviously had spent offshore (Fig. S8). Perhaps inter-individual variation in wintering habitat selection may be influenced by an extended parental care; hence, wintering on the coast might be beneficial if parents still care for their offspring (e.g. potentially in Heiner, Ayla and Ernst), so that juveniles in poor body condition can easily find sites for resting on beaches or sandbars (e.g. Bugoni et al. 2005; Blokpoel et al. 1982, 1984). Whether Common Terns care for their offspring at wintering sites is still unclear, but juvenile Royal Terns *Thalasseus maximus* were fed by adults during wintering in Peru in December and January, when they were about 7 months old (Ashmole and Tovar 1968).

Changes in the daily routines of Common Terns as suggested by the saltwater contact data could likely be explained to a certain extent by their daily foraging pattern. Radio-tracked Common Terns spending the non-breeding season in southern Brazil usually started foraging from roosting sites on the beach or sandbars in the morning or late afternoon (Bugoni et al. 2005). The low proportion of saltwater contact during sunrise and sunset (Fig. 4) is, therefore, likely to be related to the foraging behavior of Common Terns, considering that during the short plunge dives no saltwater contact was recorded, cf. in the breeding period (Figs. 3, 4). Another explanation of the high proportion of saltwater contact during the non-breeding period in common terns on the West (Nisbet et al. 2011a) and East Atlantic Flyways could be thermoregulatory necessities: during noon at areas close to the equator (Fig. 4) they may cool down their body temperature, which might be heated up considerably by the high solar irradiation. This is corroborated by the significant positive correlation of Common Terns' saltwater contact per day with higher latitude of the wintering locations coming along with decreasing sea water temperatures. Moreover, water contact was highest during spring migration (Figs. 3, 4) when also sunshine duration is highest in Senegal and Mauretania, concomitant with lowest sea surface temperatures due to upwelling (19–20 °C, February and March; e.g. Hayward and Oguntoyinbo 1987; http://www.iten-online.ch/klima/afrika) that the temperature gradient between birds' legs and sea water should warrant body heat release. Another explanation of longer resting times at sea during noon (Fig. 4) may be related to winds, since wind speed is typically higher at midday than at sunrise and sunset, possibly handicapping the terns' flight. Gannets *Sula bassana*, too, wintering off West Africa spend more time on the sea water during daylight than conspecifics wintering at the Bay of Biscaya or the North Sea (Garthe et al. 2012). There is a need of detailed behavioral observations of terns and other seabirds in their wintering areas to clarify these speculations on persisting parental care and thermoregulation by offshore swimming.

General migration patterns of Common Tern populations studied by geolocation

Our study adds to the three investigations published to date of Common Tern migration based on light-level geolocators (Nisbet et al. 2011a, b; Neves et al. 2015; Moore et al., personal communication). Overall, these studies clearly show a strong east–west separation in their migration routes and wintering areas among breeding populations and connectivity at broad spatial scales (Fig. 5). Some studies on pelagic seabirds have also found a certain degree of migratory connectivity (e.g. Cory's Shearwater *Calonectris diomedea*, González-Solís et al. 2007, Bulwer's petrel *Bulweria bulwerii*, Ramos et al. 2015), but Common Terns are more coastal seabirds and their longitudinal change in migratory routes parallel those found in terrestrial birds of the Palearctic–Tropical and Nearctic–Neotropical migratory systems (e.g. Trierweiler et al. 2014; Hallworth et al. 2015). Such knowledge is important to understand migration strategies and for conservation concerns. Based on information about the migratory connectivity we can recognize and elucidate impacts of population-level threats during the non-breeding period, which may affect demographic rates or traits of migration timing (e.g. in Common Terns: Szostek and Becker 2015; Szostek et al. 2015). The differences in the wintering areas and migratory flyways of Common Terns breeding, in geographical terms, in relative close vicinity to each other are striking for seabirds. Common Terns breeding in northwest Germany and on the Azores are separated to a larger scale in winter when visiting the West African coast or the eastern South American coast, respectively, than in summer. A similar pattern exists for the breeding populations in North America: Common Terns from the northeast Atlantic coast (Bird Island) spent their winter along the eastern South American coast and mix with birds from the Azores breeding population, whereas Common Terns from the Great Lakes winter along the eastern Pacific coast in South America (Fig. 5). Ring recoveries suggest similar divergence of wintering sites for further common tern populations (Neubauer 1982; Bairlein et al. 2014; Cohen et al. 2014). The origin and causes of the population-specific migration patterns and wintering areas in Common Terns may be driven by geographical structures and barriers such as mountains, coastline courses, wind patterns, currents, water bodies, or oceans.

ACKNOWLEDGMENTS

We thank Christina Bauch, Alexander Braasch, Julia Spieker, Lesley Szostek, Katharina Weißenfels, Silas Wolf, and Christian Wolter for their help with field work. Simeon Lisovski helped with analyzing the light-level geolocation data. Kathrin Hüppop helped preparing the figures. We thank Dave Moore giving access to unpublished data of migration of common terns breeding at the Great Lakes and Olaf Geiter for providing ring recovery data of common terns. The manuscript was improved by helpful comments of Franz Bairlein and two anonymous

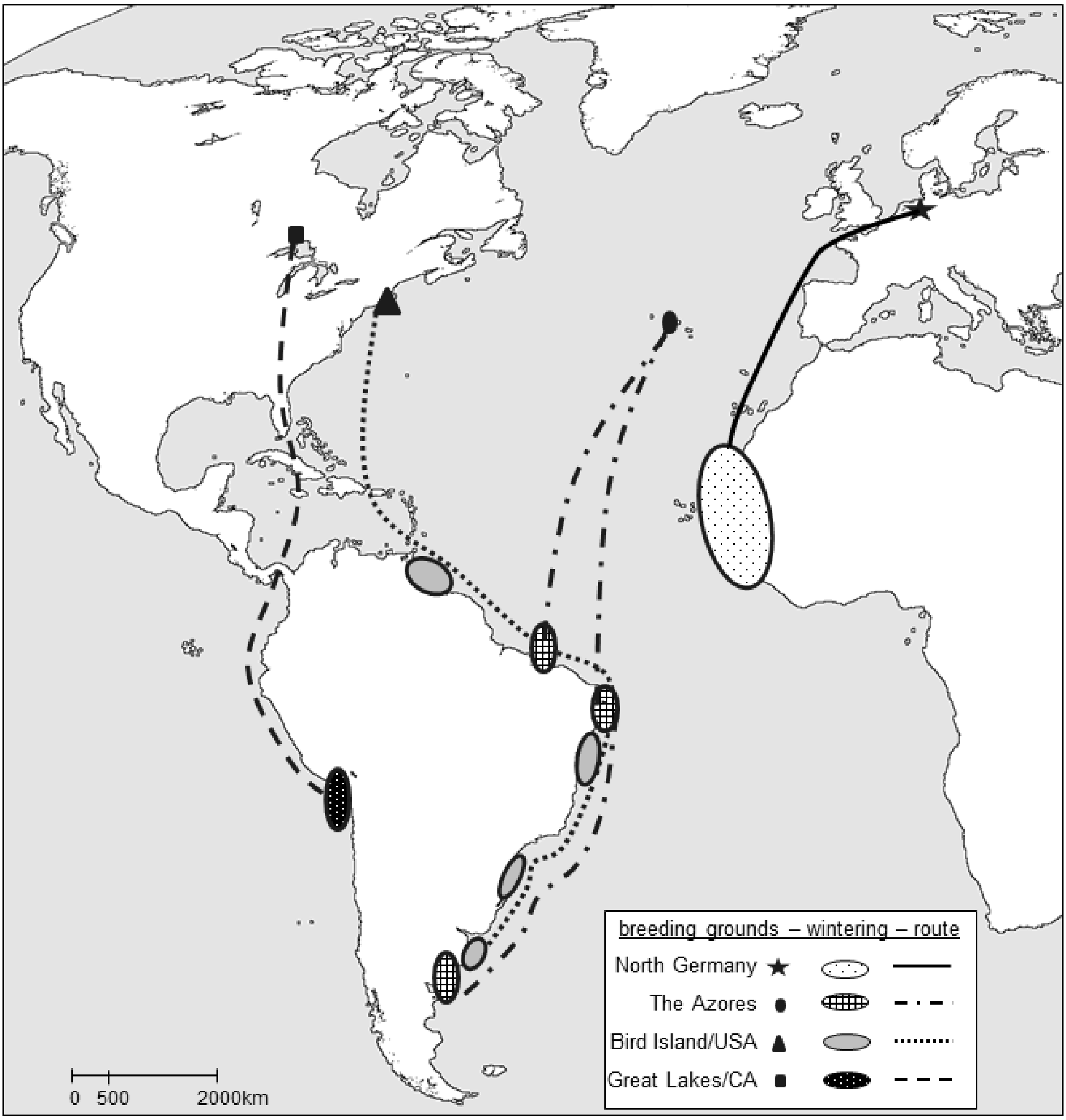


Fig. 5 Breeding grounds (indicated by different symbols), migration routes (diverse lines), and wintering areas (differently shaded areas) of Common Terns tracked with light-level geolocators. Migration routes are rough estimates. Data are from four populations of Common Terns breeding in north Germany (this study), on the Azores (Neves et al. 2015), at MA, USA (Nisbet et al. 2011a, b), and Great Lakes, Canada (Moore et al., personal communication)

reviewers. The studies were performed under license of the Nds. Landesamt für Verbraucherschutz und Lebensmittelsicherheit Oldenburg and of the Stadt Wilhelmshaven. H.S. is financed by the Deutsche Forschungsgemeinschaft (SCHM 2647/1-1) which also supported the project (BE 916/8 and 9).

REFERENCES

Arístegui J, Gasol JM, Duarte CM, Herndl GJ (2009) Microbial oceanography oft he dark ocean's pelagic realm. Limnol Oceanogr 54:1501-1529

Ashmole NP, Tovar HS (1968) Prolonged parental care in Royal Terns and other birds. Auk 85:90-100

Bairlein F, Dierschke J, Dierschke V, Salewski V, Geiter O, Hüppop K, Köppen U, Fielder W (2014) Atlas des Vogelzugs. AULA. Wiebelsheim

Becker PH (2010) Populationsökologie der Flussseeschwalbe: Das Individuum im Blickpunkt. In: Bairlein F, Becker PH (Hrsg.) 100 Jahre Institut für Vogelforschung „Vogelwarte Helgoland". Aula, Wiebelsheim, pp 137-155

Becker PH, Dittmann T, Ludwigs J-D, Limmer B, Ludwig SC, Bauch C, Braasch A, Wendeln H (2008) Timing of anitial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. PNAS 105:12349-12352

Becker PH, Ludwigs J-D (2004) *Sterna hirundo* Common Tern. In: Parkin D (ed) BWP Update Vol. 6 Nos 1/2 , 93-139. Oxford University Press

Becker PH, Wendeln H, González-Solís J (2001) Population dynamics, recruitment, individual quality and reproductive strategies in Common Terns marked with transponders. Ardea 89 (special issue):239-250

Becker PH, Wink M (2003) Influences of sex, sex composition of brood and hatching order on mass growth in Common Terns (*Sterna hirundo*). Behav Ecol Sociobiol 54:136-146

Becker RA, Chambers JM, Wilks AR (1988) *The New S Language*. Wadsworth and Brooks/Cole

Blokpoel H, Morris R, Tessier G (1984) Field investigations of the biology of Common Terns wintering in Trinidad. J Field Ornithol 55:424-434

Blokpoel H, Morris R, Trull P (1982) Winter observations of Common Terns in Trinidad, Guyana, and Suriname. Colonial Waterbirds 5:144-147

Brenninkmeijer A, Stienen EWM, Klaassen M, Kersten M (2002) Feeding ecology of wintering terns in Guinea-Bissau. Ibis 144:602-613

Breton AR, Nisbet ICT, Mostello CS, Hatch JJ (2014) Age-dependent breeding dispersal and adult survival within a metapopulation of Common Terns *Sterna hirundo*. Ibis 156:534-547

Bruderer B, Boldt A (2001) Flight characteristics of birds: 1. Radar measurements of speeds. Ibis 143:178-204

Bugoni L, Cormons TD, Boyne AW, Hays H (2005) Feeding grounds, daily foraging activities, and movemnts of Common Terns in Southern Brazil, determined by radiotelemetry. Waterbirds 28:468-477

Burger J (1980) The transition to independence and post fledging parental care in seabirds: In: Burger J, Olla BL, Winn HE (eds.) *Marine Birds. Behavior of Marine Animals, Vol.4*:367–447. Plenum Press, New York.

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modelling 197:516-519

Cohen EB, Hostetler JA, Royle JA, Marra PP (2014) Estimating migratory connectivity of birds when re-encounter probabilities are heterogenous. Ecol Evol 4:1659-1670

Core Team R (2014) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Dias MP, Granadeiro JP, Catry P (2013) Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. Anim Behav 86:359-364

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proc Natl Acad Sci 107:2078-2081

Ekstrom PA (2004) An advance in geolocation by light. Memoirs Natl Inst Polar 58:210–226

Ezard T, Becker PH, Coulson T (2006) The Contributions of Age and Sex to Variation in Common Tern Population Growth Rate. J Anim Ecol 75:1379-1386

Fijn RC, Hiemstra D, Phillips RA, Winden J van der (2013) Arctic Terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctica. Ardea 101:3-12

Fudickar AM, Wikelski M, Partecke J (2012) Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Methods Ecol Evol 3:47-52

Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit plunning by northern gannets (*Sula bassana*) “feeding on capelin (*Mallotus villosus*)”. Proc R Soc B 267:1717-1722

Garthe S, Ludynia K, Hueppop O, Kubetzki U, Meraz JF, Furness RW (2012) Energy budgets reveal equal benefits of varied migration strategies in northern gannets. Mar Biol 159:1907-1915

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 5:297–301

Grecian WJ, Witt MJ, Attrill MJ: Multi-species top predator tracking reveals link between marine biodiversity and ocean productivity. Biol Letters (in revision)

Guilford T, Meade J, Willis J, Phillips RA, Boyle D, Roberts S, Collet M, Freeman R, Perrins CM (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc R Soc B 276:1215-1223

Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. PloS ONE 6:e21336

Hallworth MT, Sillett TS, Van Wilgenburg, SL, Hobson KA, Marra PP (2015) Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecol Appl 25:336–347

Harrison P (1997) Seabirds of the World. Princeton, Princeton

Hayward DF, Oguntoyinbo J (1987) The climatology of West Africa. Hutchinson, London

Hill RD (1994) Theory of geolocation by light levels. Elephant Seals: Population Ecology, Behavior, and Physiology. In: Burney J, Boeuf BJ, Laws RM (eds)), pp. 227–236. University of California Press, Berkeley

Liechti F (2006) Birds: Blowin’ by the wind? J Ornithol 147:202-211

Limmer B, Becker PH (2007) The relative role of age and experience in determining variation in body mass during the early breeding career of the Common Tern (*Sterna hirundo*). Behav Ecol Sociobiol 61:1885-1896

Lisovski S, Hahn S (2012) GeoLight–processing and analysing light-based geolocator data in R. Methods Ecol Evol 3:1055-1059

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol Evol 3:603-612

McGregor HV, Dima M, Fischer HW, Mulitza S (2007) Rapid 20th-century increase in coastal upwelling off Northwest Africa. Science 315:637-639

Mostello CS, Nisbet ICT, Oswald SA, Fox JW (2014) Non-breeding season movements of six North American Roseate Terns *Sterna dougallii* tracked with geolocators. Seabird 27:1-21

Müller MS, Massa B, Phillips RA, Dell’Omo G (2015) Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes? Anim Behav 102:267-276

Neubauer W (1982) Der Zug mitteleuropaeischer Flusseeschwalben (*Sterna hirundo*) nach Ringfunden. Ber Vogelwarte Hiddensee 2:59-82

Neves VC, Nava CP, Cormons M, Bremer E, Castresana G, Lima P, Azevedo jun SM, Phillips RA, Magalhães MC, Santos RS (2015) Migration routes and non-breeding areas of Common Terns (*Sterna hirundo*) from the Azores. Emu 115:158–167

Nielsen A, Sibert JR (2007) State-space model for light-based tracking of marine animals. Can J Fish Aquatic Sci 64:1055-1068

Nilsson C, Klaassen RH, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837-845

Nisbet ICT (2002) Common Tern. The Birds of North America 618: 1-39.

Nisbet ICT, Cam E (2002) Test for age-specificity in survival of the Common Tern. J Appl Statistic 29:65-83

Nisbet ICT, Montoya JP, Burger J, Hatch JJ (2002) Use of stable isotopes to investigate individual differences in diets and mercury exposures among Common Terns *Sterna hirundo* in breeding and wintering grounds. Mar Ecol Prog Ser 242:267-274

Nisbet ICT, Mostello CS, Veit RR, Fox JW, Afanasyev V (2011a) Migrations and winter quarters of five Common Terns tracked using geolocators. Waterbirds 34:32-39

Nisbet ICT, Szczys P, Mostello CS, Fox JW (2011b) Female Common Terns *Sterna hirundo* start autumn migration earlier than males. Seabird 24:103-106

Palestis BG, Hines JE (2015) Adult survival and breeding dispersal of Common Terns (*Sterna hirundo*) in a declining population. Waterbirds 38:221-228

Pennycuick CJ, Åkesson S, Hedenström A (2013) Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. J R Soc Interface 10:20130419

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265-272

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 86:2386-2396

Ramos R, Sanz V, Militão T, et al. (2015) Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer’s petrel (*Bulweria bulwerii*). Journal of Biogeography 42:1651-1664.

Ropert-Coudert Y, Wilson RP, Grémillet D, Kato A, Lewis S, Ryan PG (2006) Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. Mar Ecol Prog Ser 328:275–284

Salewski V, Bairlein F, Leisler B (2000) Recurrence of some palaearctic migrant passerine species in West Africa. Ringing & Migration 20:29-30

Scandolara C, Rubolini D, Ambrosini R, Caprioli M, Hahn S, Liechti F, Romano A, Romano M, Sicurella B, Saino N (2014) Impact of miniaturized geolocators on Barn Swallow *Hirundo rustica* fitness traits. J Avian Biol 45:417-423

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Nat Acad Sci 103: 12799-12802

Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013) The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. J Avian Biol 44:531–540

Sorenson MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that non-breeding diet quality influences reproductive success. J Anim Ecol 78:460-467

Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian estimation of animal movement from archival and satellite tags. PLoS One 4:e7324

Szostek KL, Becker PH (2015) Marine primary productivity in the wintering area influences survival and recruitment in a migratory seabird. Oecologia 178:643-657

Szostek KL, Bouwhuis S, Becker PH (2015) Are arrival date and body mass after spring migration influenced by large-scale environmental factors in a migratory seabird? Front Ecol Evol 3:42

Szostek L, Becker PH (2012) Terns in Trouble: Demographic Consequences of Low Breeding Success and Recruitment on a Common Tern Population in the German Wadden Sea. J Ornithol 153:313-326

Trierweiler C, Klaassen RGH, Drent RH, Exo K-M, Komdeur J, Bairlein F, Koks BJ (2014) Population specific migration routes and migratory connectivity in a long-distance migratory raptor. Proc Royal Soc B London 281:1471-2954

Winden J van der, Fijn RC, Horssen PW van, Gerritsen-Davidse D, Piersma T (2014) Idiosyncratic migrations of Black Terns (*Chlidonias niger*): diversity in routes and stopovers. Waterbirds 37:162-174

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp H-P (2002) GPS tracking of foraging albatrosses. Science 295:1259

Weimerskirch H, Wilson RP (2000) Oceanic respite for wandering albatrosses. Nature 406:955-956

Wendeln H, Becker PH (1999) Significance of ring removal in Africa for a Common Tern *Sterna hirundo* colony. Ring Migration 19:210-212

Wernham CV, Toms MP, Marchant JH, Clark JA, Siriwardena GM, Baillie SR (2002) The migration atlas: movements of the birds of Britain and Ireland. T & AD Poyser, London

Wilson RP, Cooper J, Plötz J (1992a) Can we determine when marine endotherms feed? A case study with seabirds. J Exp Biol 167:267-275

Wilson RP, Ducamp JJ, Rees G, Culik BM, Niekamp K (1992b) Estimation of location: global coverage using light intensity. Wildlife Telemetry: Remote Monitoring and Tracking of Animals. In: I.G. Priede IG, Swift SM (eds), pp. 131–134. EllisHoward Ltd, Chichester

Wilson RP, Weimerskirch H, Lys P (1995) A Device for Measuring Seabird Activity at Sea. J Avian Biol 26:172-175

Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, Schäfer-Neth C, Scolaro JA, Bost C-A, Plötz J, Nel D (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar Ecol Prog Ser 228:241–261

Zhang H, Vedder O, Becker PH, Bouwhuis S (2015) Age-dependent trait variation: the relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. J Anim Ecol 84:797–807

Supplementary material

1. ADDITIONAL INFORMATION ABOUT LIGHT-LEVEL GEOLOCATION

Table S1 Information of Common Terns being tagged with light-level geolocators. Given were their name, sex, year of birth, ring number (no.), geolocator number (no.), deployment (deploy.) date, removal date, and name of mate./ = no return of adult; lost = return but geolocator lost; highlighted grey = non/breeding movements tracked

Bird				2008			2009			2010			2011
name	sex	year of birth	ring no.	geol. no.	de-ploy. date	mate name	geol. no.	re-moval/ deploy. date	mate name	geol. no.	re-moval/ deploy. date	mate name	re-moval date
Alitze	f	1998	7731970	7153	31-05	Cadfael		/					
Eli	f	1994	7729088	7149	31-05	Victor		/					
Wieland	m	1997	7732141	7150	27-05	Antonia	7414	03-06	Marianna	21166	29-05	Marianna	18-05
Kasimir	m	1994	7729014	7152	27-05	Cornelia	7406	20-05	Cornelia	21157	27-05	Cornelia	/
Nina	f	1997	7731348	7151	31-05	Moses	7407	26-05	Moses	21168	31-05	Moses	18-05
Salome	f	2000	7783558				7408	28-05	Ernst	21164	29-05	Ernst	13-05
Minna	f	1998	7700408				7409	28-05	Joachim	21167	29-05	Joachim	18-05
Cornelia	f	1995	7731633				7410	28-05	Kasimir	21162	29-05	Kasimir	01-06
Moses	m	1997	7732149				7411	28-05	Nina	21165	29-05	Nina	19-05
Joachim	m	1999	7782159				7413	01-06	Minna	21158	27-05	Minna	19-05
Ernst	m	1999	7782099				7405	20-05	Salome	21160	27-05	Salome	12-05
Marianna	f	1997	7732696				7415	05-06	Wieland	21159	27-05	Wieland	16-05
Werner	m	1996	7729699				7412	28-05	Claire		/		
Claire	f	1996	7729678				7404	20-05	Werner		lost		
Heiner	m	1999	7782380							21163	29-05	Ayla	10-05
Ayla	f	2000	7783506							21161	27-05	Heiner	09-05

Table S2 Estimated mean longitude and mean latitude positions ± standard deviation (SD) of individual wintering areas of 9 common terns, 2009 – 2011. For three birds wintering areas were estimated for more than one year. Number of locations considered for the estimated mean wintering area (n loc.). For three birds a stopover either during autumn or during spring migration could be estimated. As for the wintering area estimated mean longitude and latitude positions ± standard deviations (SD) were given. The period of stopover was indicated. NA= Not analysed

bird, year			wintering area			stopover during autumn or spring		
name	sex	zear	longitude mean±SD	latitude mean±SD	n loc.	longitude mean±SD	latitude mean±SD	period
Joachim	m	2009/10	-17.77±0.37	18.8±2.52	232			
		2010/11	-17.37±0.35	18.44±2.19	183			
Moses	m	2009/10	-16.32±0.34	9.39±0,86	228			
		2010/11	-16.68±1.0	11.37±2.21	138	-13.76±1.14	30.58±0.52	13-10 – 20-10
Kasimir	m	2009/10	-17.30±0.51	15.14±4.17	240	-17.39±0.35	29.16±1.12	NA – 12-04
Cornelia	f	2009/10	-20.08±1.34	19.13±2.08	166	-17.04±0.44	25.85±0.48	08-08 – 05-09
		2010/11	-16.73±0.77	24.06±2.04	220			
Heiner	m	2010/11	-16.07±0.41	10.99±2.23	212			
Ayla	f	2010/11	-17.87±0.96	20.33±2.0	77			
Ernst	m	2010/11	-15.51±0.44	10.27±2.03	228			
Wieland	m	2010/11	-15.77±1.33	10.44±4.41	222			
Marianna	f	2009/10	-22.42±1.08	18.33±2.24	82			

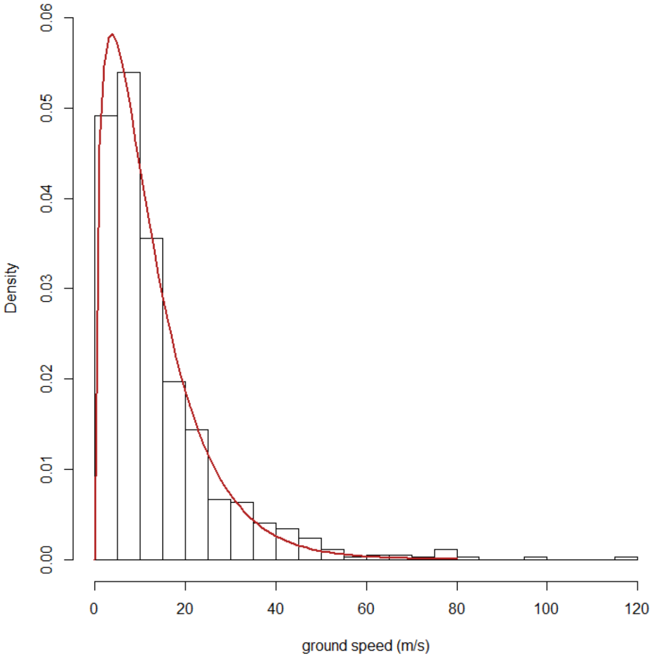


Figure S1 Density distribution of ground speed of the entire track (bars) and the corresponding gamma distribution (shape = 1.51, rate = 0.13, red line) exemplary for one bird (Kasimir tracked in 2009 to 2010)

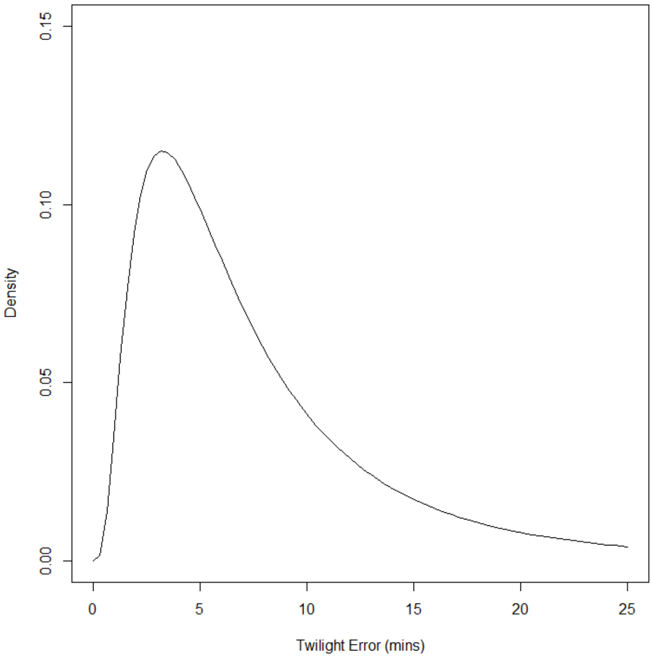


Figure S2 Lognormal distribution of twilight errors (mean of the distribution = 1.792, standard deviation of the distribution = 0.788; both on a log scale)

Figures S3 individual light-level geolocation data. Longitude and latitude estimates (red lines) over time for each individual. Blues lines indicate 95% confidence intervals. Black lines indicate obvious changes in bird's whereabouts. These dates were used to define departures and arrivals of stationary periods, i.e. breeding area, stopover sites, and wintering grounds (see Table 1, Table S2). Grey dashed lines indicate longitude/latitude of the breeding area and first/last reading of transponder at the breeding colony. Outlier estimates are clearly recognizable; these were excluded for estimating wintering grounds. Some light-level geolocators produced corrupt data at certain times of the recording which could not be corrected for. This decreased the precision of our data and should be kept in mind when interpreting the data. Grey bars indicate ten days around (± 10 days) each equinox. As only latitude estimates were affected by the equinoxes, grey bars are only indicated in the plots showing latitudinal estimates over time. In Table S2 the number of locations considered to estimate mean wintering areas are given for each individual

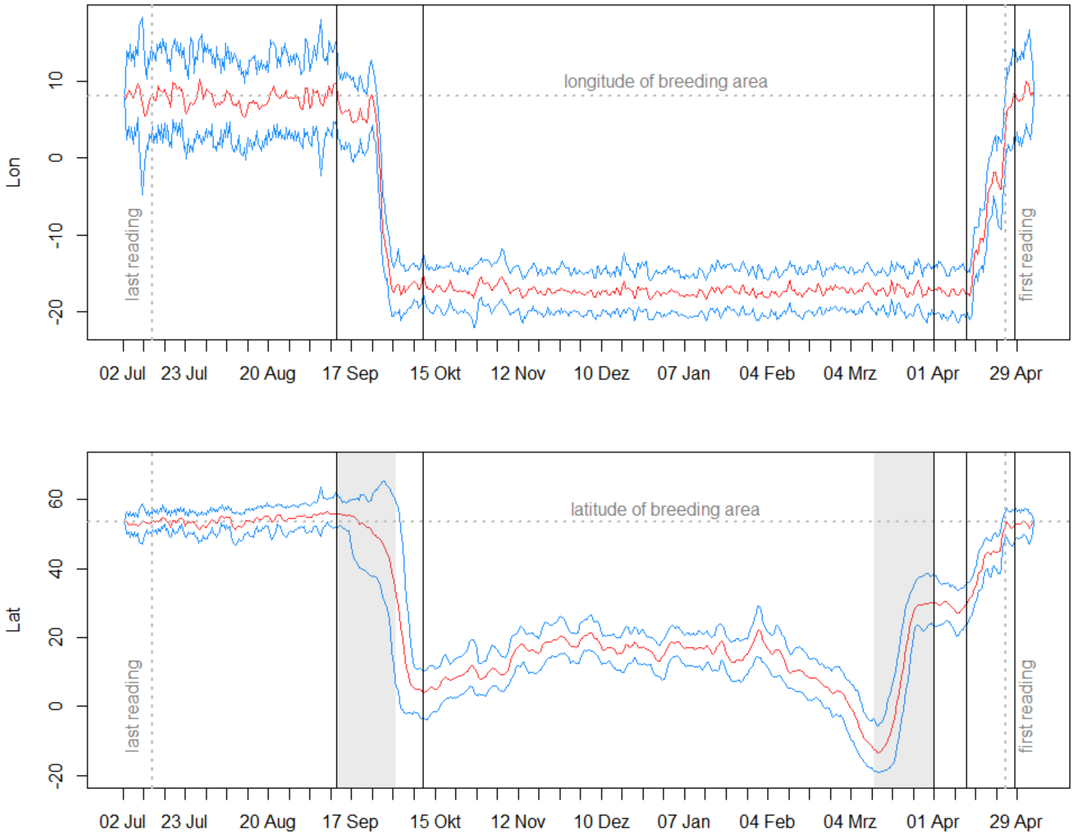


Figure S3a LGeolocator number 7406 = Kasimir 2009 – 2010

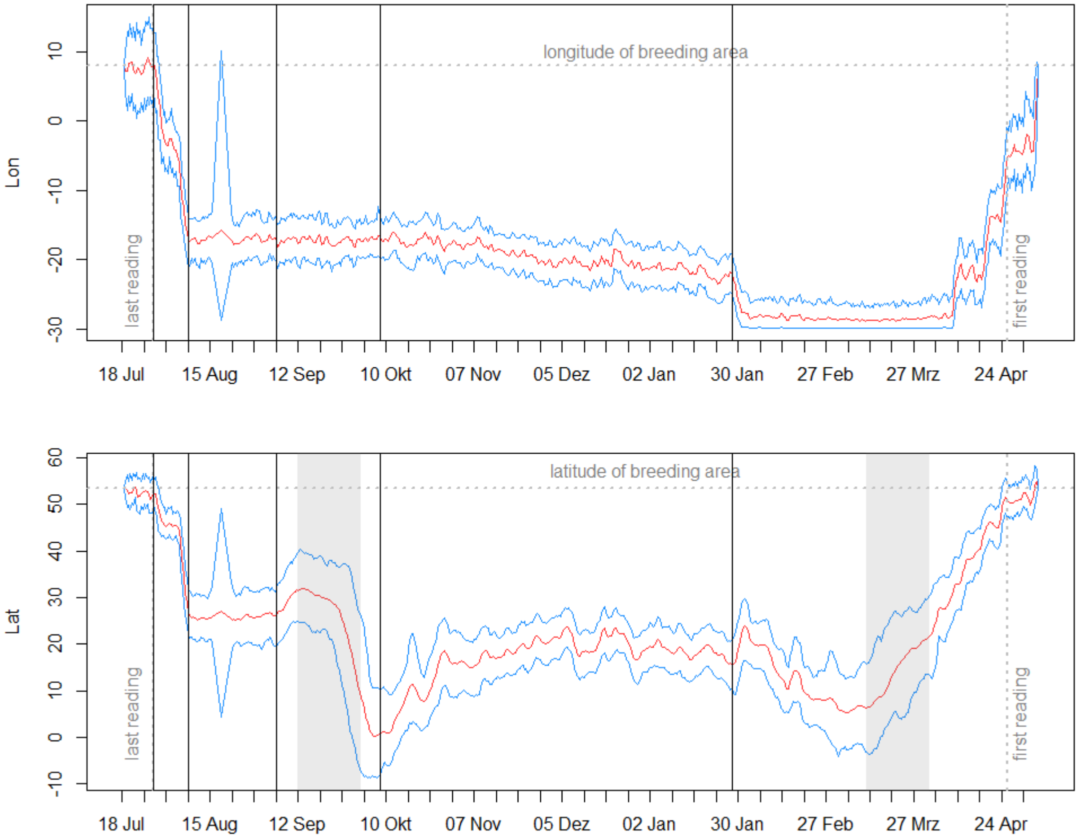


Figure S3b LGeolocator number 7410 = Cornelia 2009 – 2010
The internal geolocator clock drifted during the winter so that longitude could not be estimated correctly. Based on the plot longitude over time, we estimated that the internal geolocator clock started drifting on the 28rd of January 2010. We, therefore, did not consider locations after that date for estimating the wintering ground and also not for determining start of spring migration

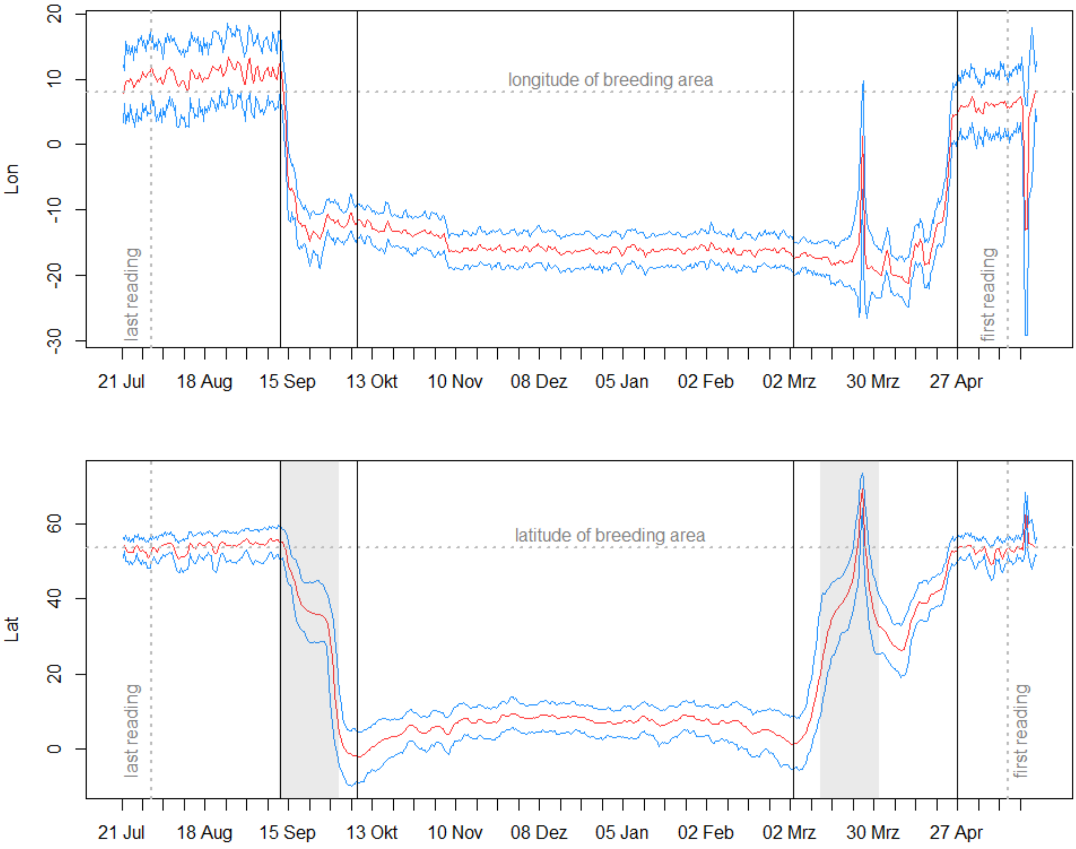


Figure S3c LGeolocator number 7411 = Moses 2009 – 2010
Both higher longitude estimates in summer 2009 and lower longitude estimates in spring 2010 in comparison to longitude of the breeding colony suggest a drift of the internal geolocator clock over the year. Whether this shift occurred gradually over the season or whether the marked shift in longitude in the beginning of November 2009 was responsible for the low estimates of longitude in spring 2010 remained unclear. Therefore, we did not control for this time shift here, but assume that the bird was at the colony on the 27th of April though longitude estimate was slightly too low

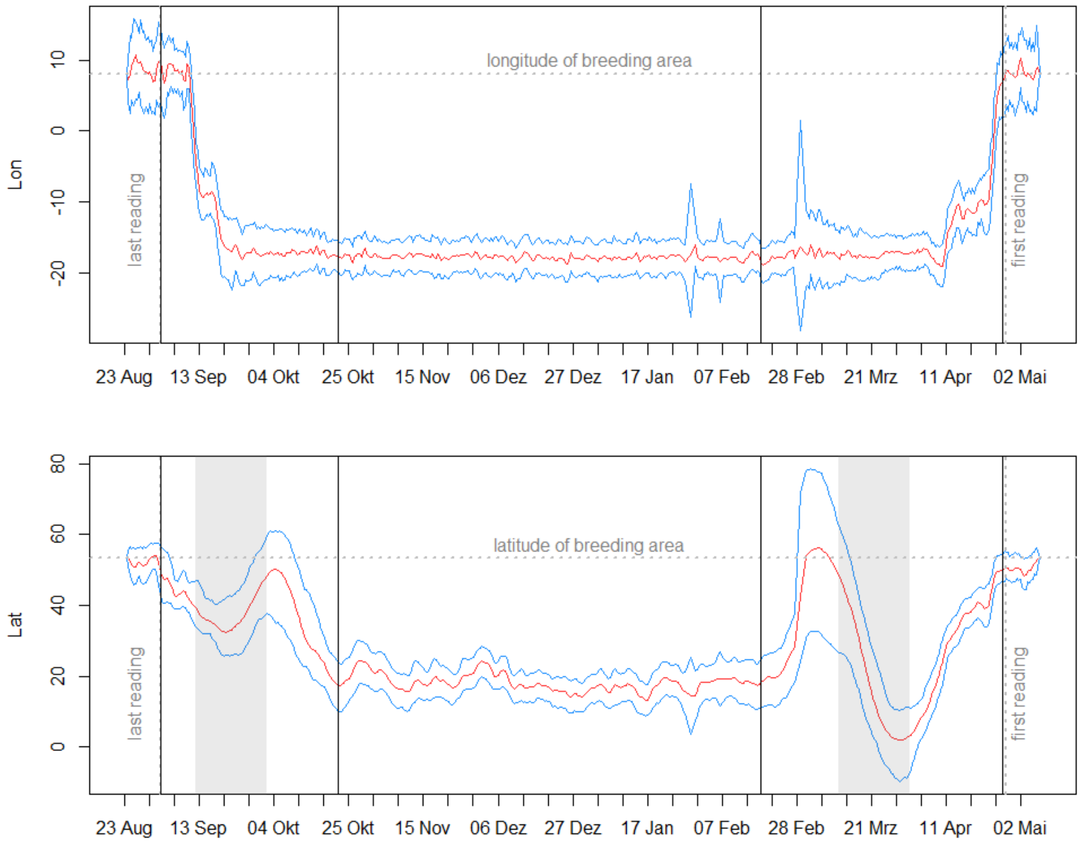


Figure S3d Geolocator number 7413 = Joachim 2009 – 2010

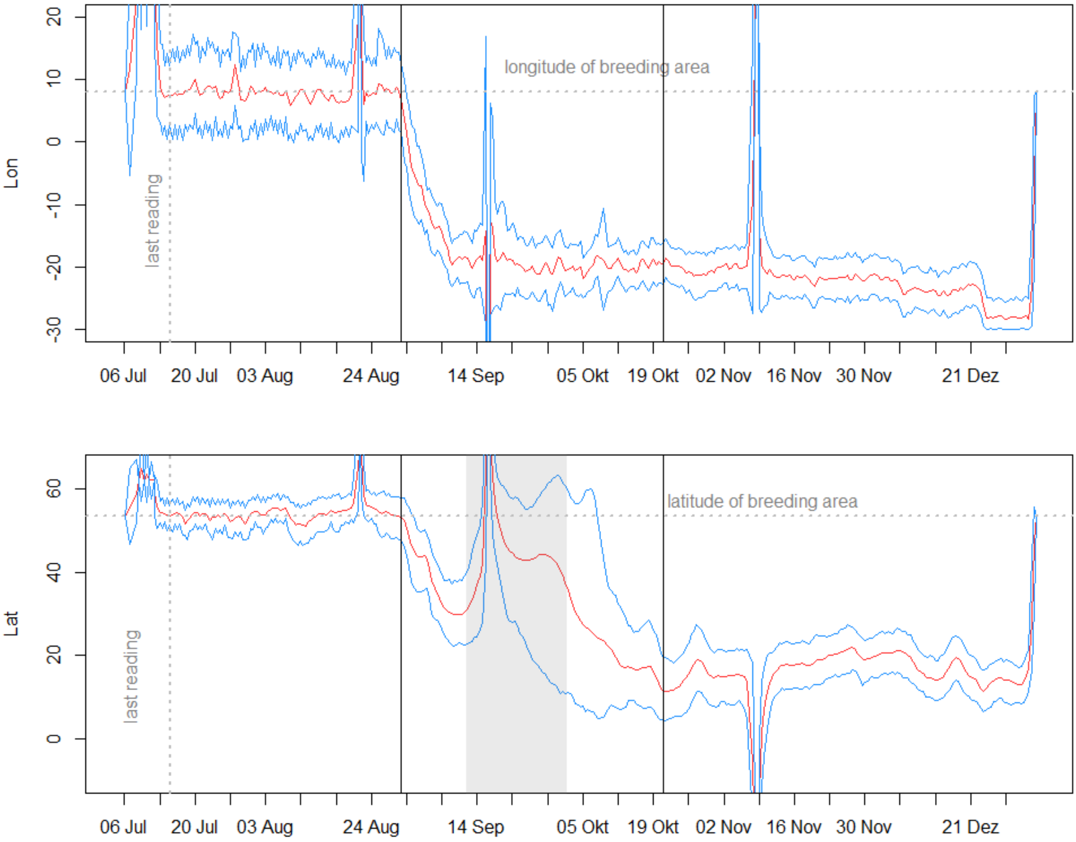


Figure S3e Geolocator number 7415 = Marianna 2009 – 2010
Only winter locations between 11th of November and 22nd of December 2009 were considered to estimate mean wintering ground. Light-level geolocator broke at the end of the year 2009

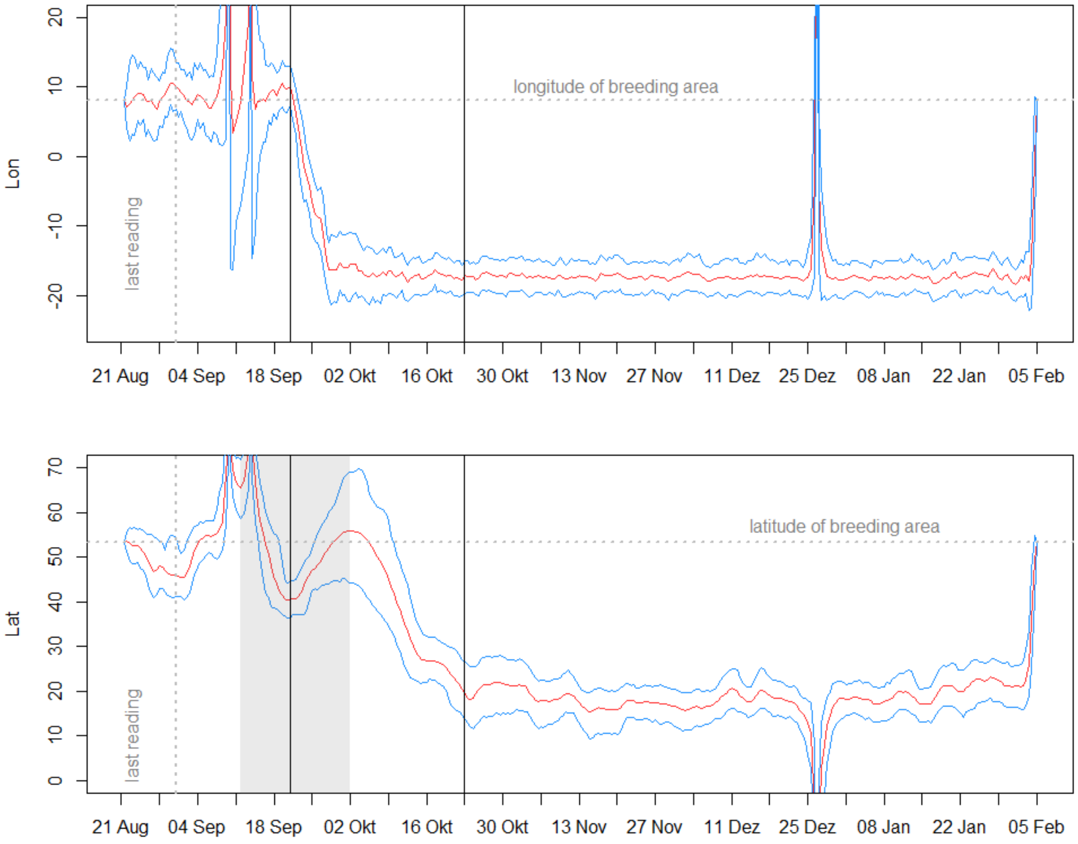


Figure S3f Geolocator number 21158001 = Joachim 2010 – 2011
Only winter locations between 1st of November 2010 and 4th of February 2011 were considered to estimate mean wintering ground. Light-level geolocator broke in the beginning of February 2011

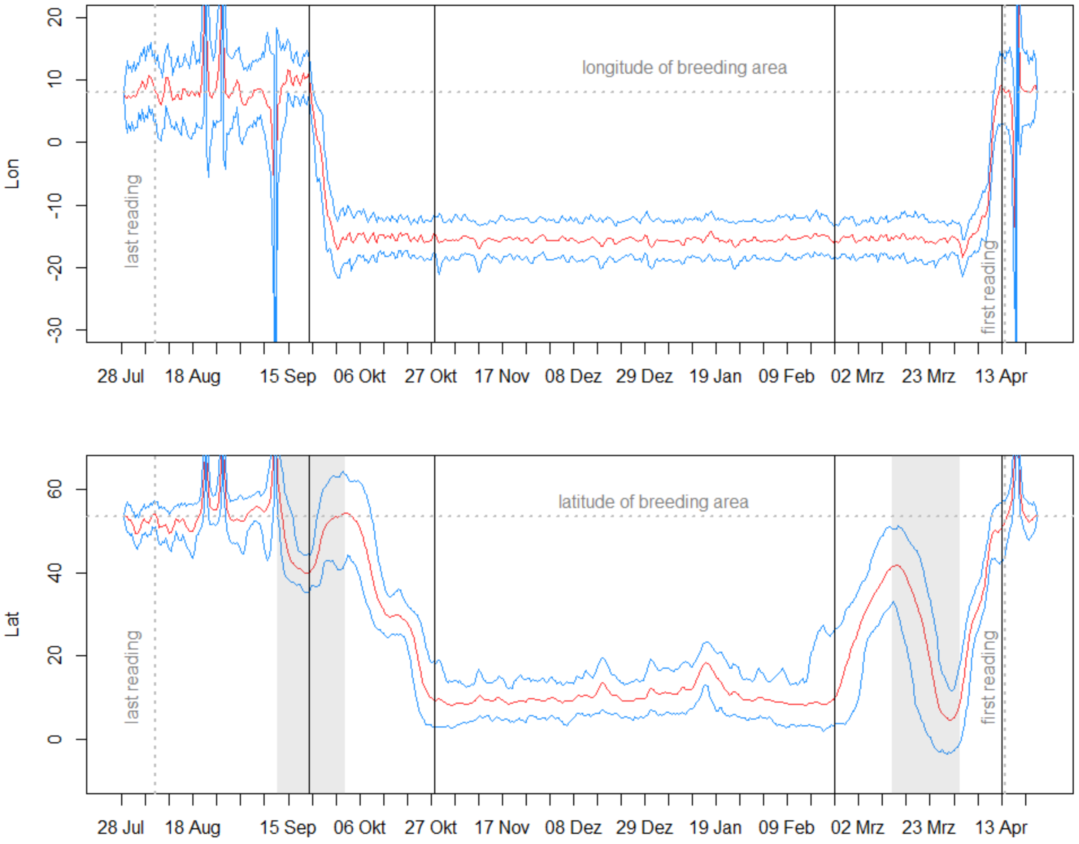


Figure S3g Geolocator number 21160001 = Ernst 2010 – 2011

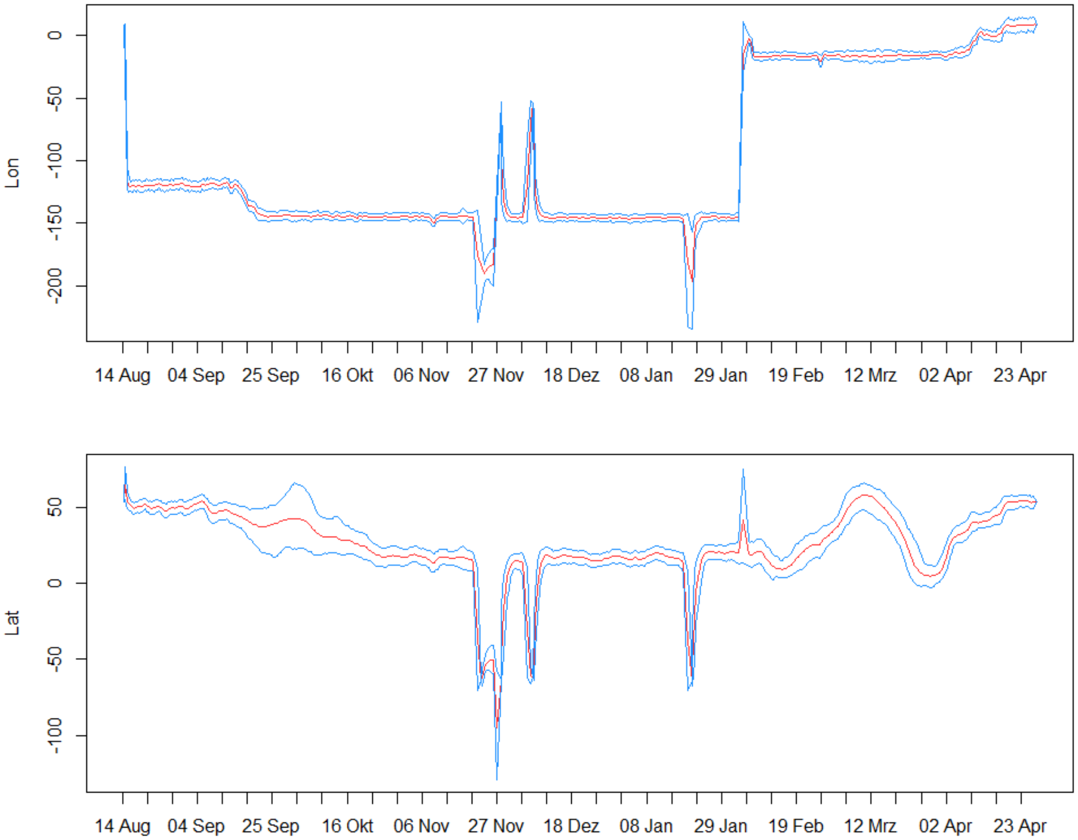


Figure S3h First figure Geolocator number 21161001 = Ayla 2010 – 2011
The internal geolocator clock drifted, see first figure of this bird. Based on the plot longitude over time, we corrected longitude estimates by adding 100°, see second figure of this bird. Data of this bird needs to be treated cautiously. Only winter locations between 10th of December 2010 and 20th of January 2011 were considered to estimate mean wintering ground

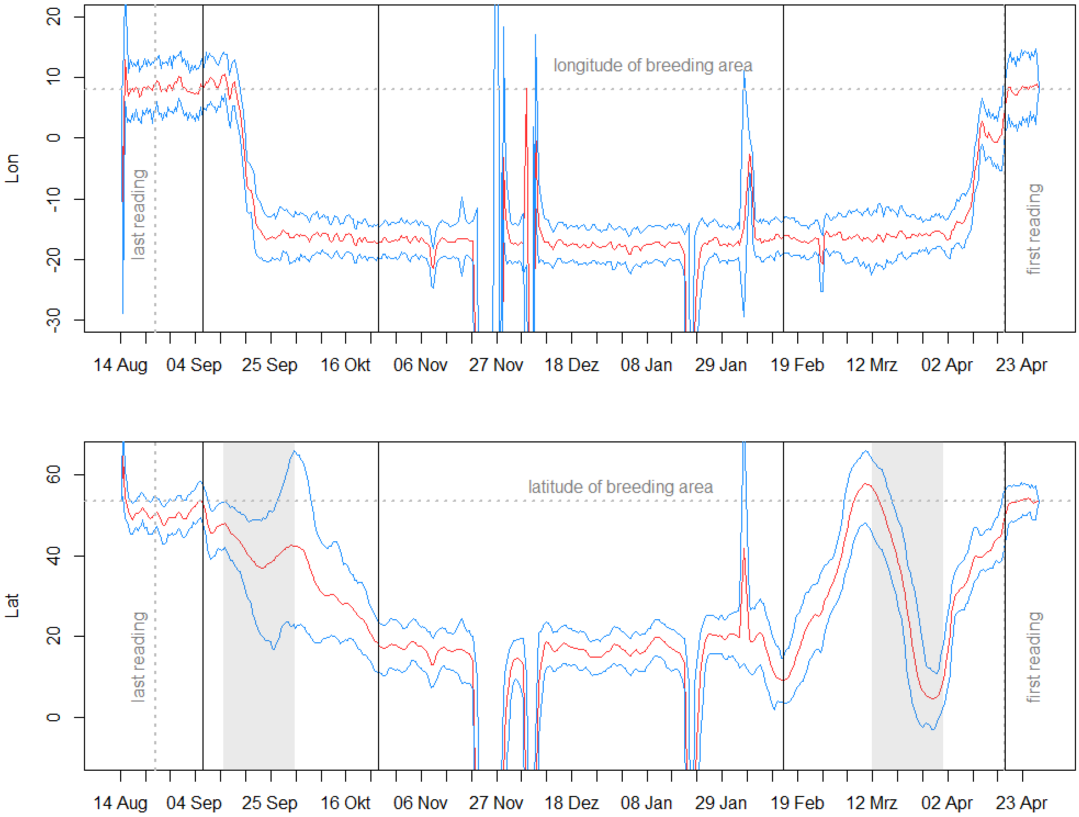


Figure S3h Second figure

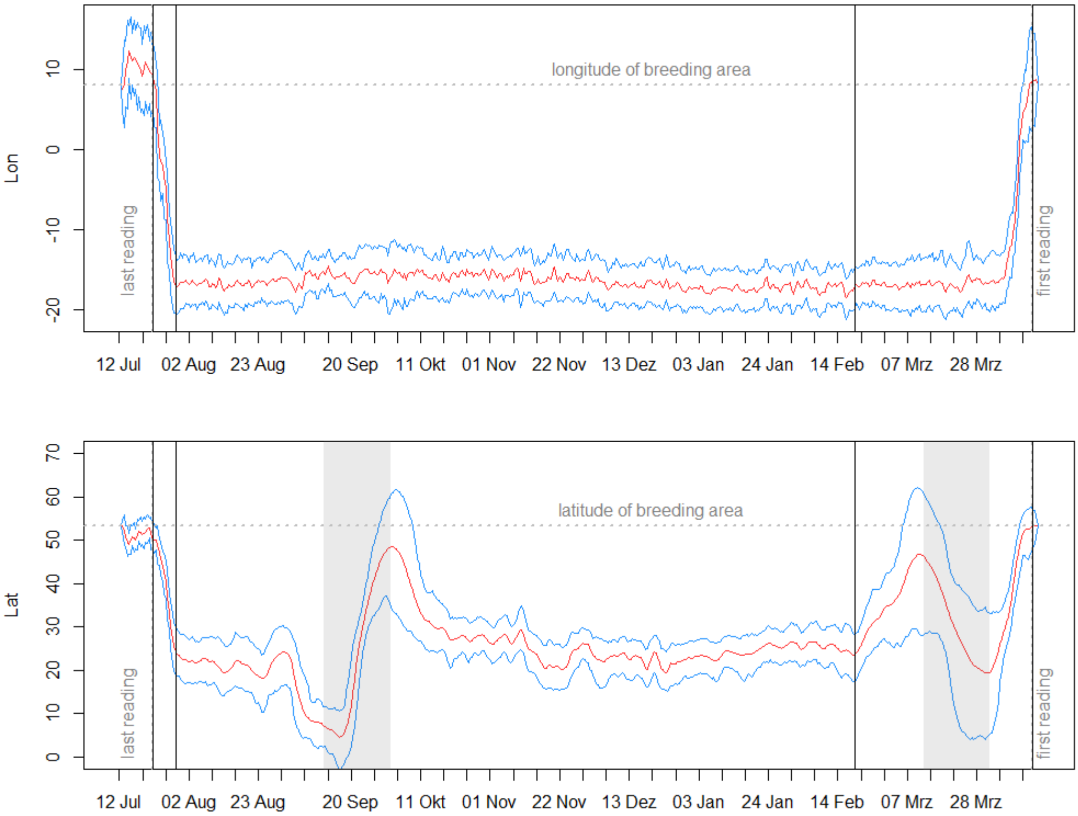


Figure S3i Geolocator number 21162001 = Cornelia 2010 – 2011

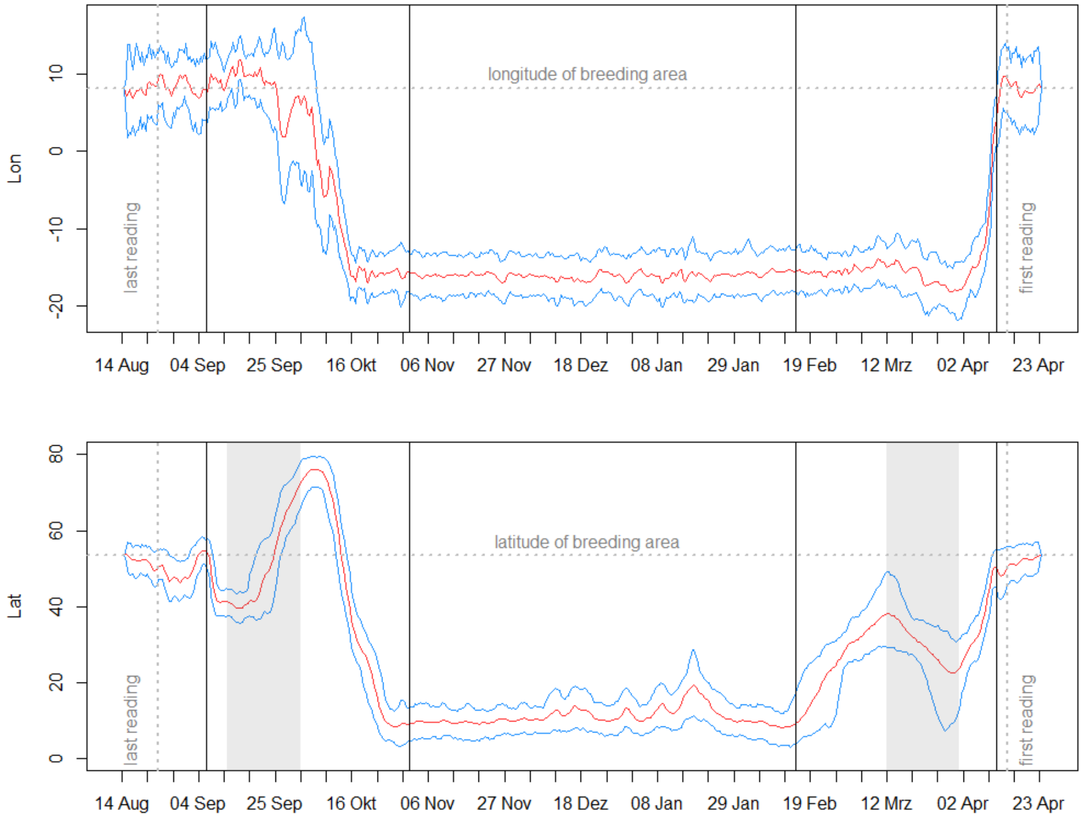


Figure S3j Geolocator number 21163001 = Heiner 2010 – 2011

Figure S3k Geolocator number 21165001 = Moses 2010 – 2011
Light-level geolocator broke in the beginning of January 2011. Last reading of the bird at the breeding colony was 12th of July 2010

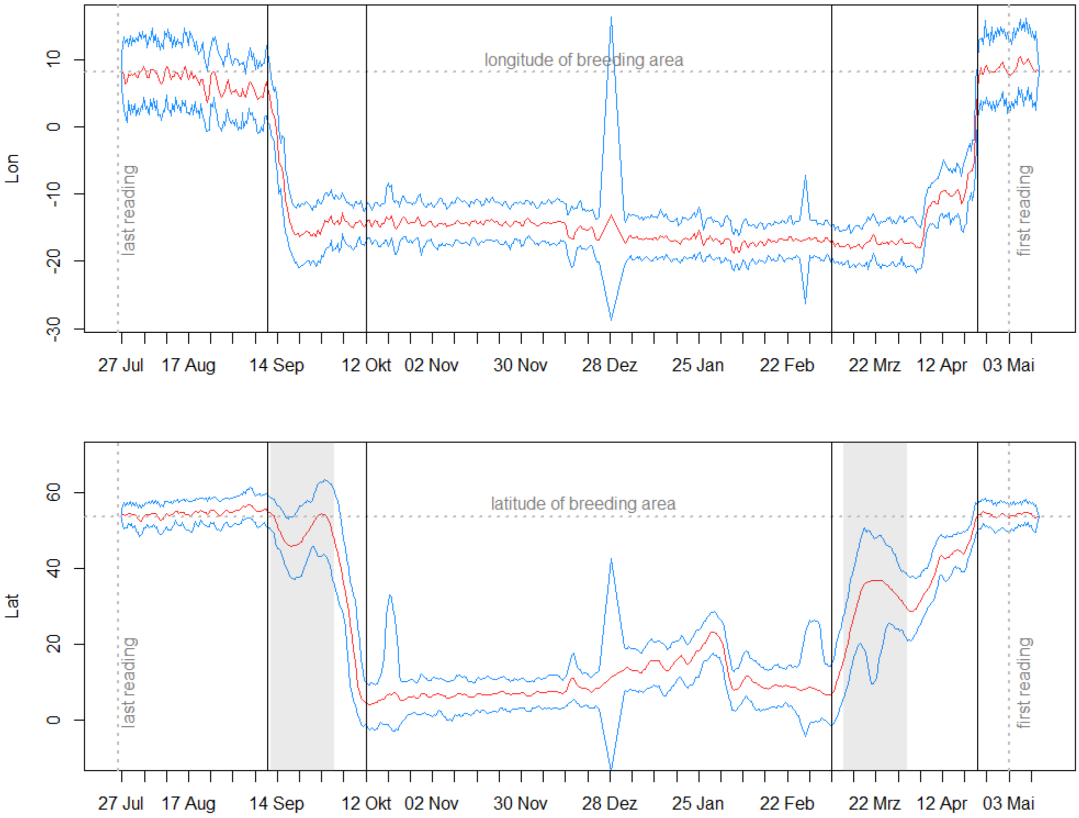


Figure S3l Geolocator number 21166001 = Wieland 2010 – 2011

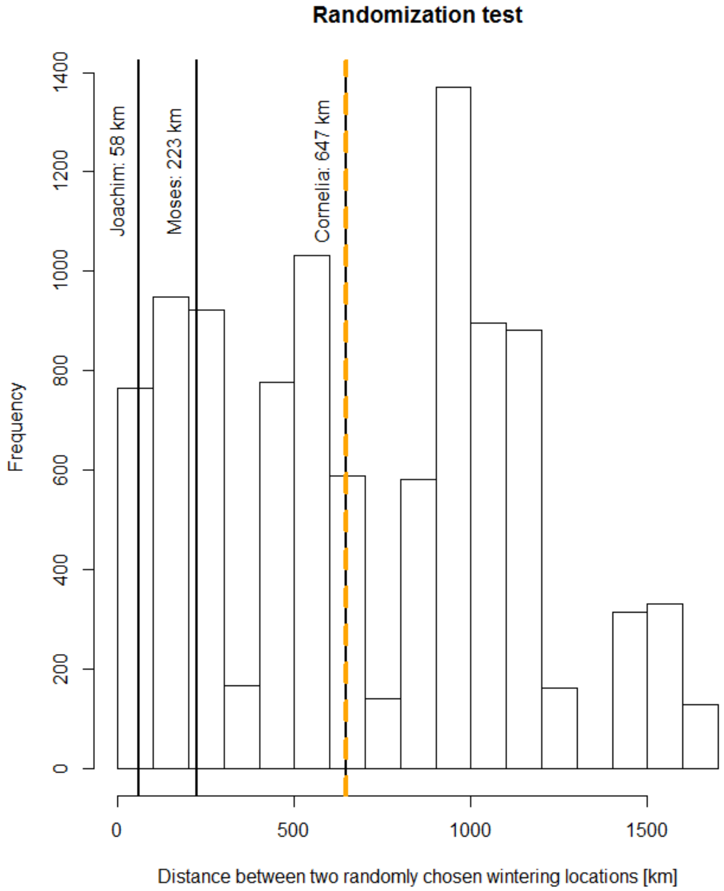


Figure S4 Frequency distribution of great circle distances between 10,000 randomly chosen wintering locations. Within-individual great circle distances between the wintering locations as estimated by light-level geolocation data for the three birds tracked during two winters (Joachim, Moses, Cornelia). Although Joachim's two wintering locations were in close vicinity to each other (58 km), 279 of the 10,000 great circle distances were closer to each other. The dashed orange line indicated the median great circle distance between the randomly chosen wintering locations

2. SUPPLEMENTARY RESULTS

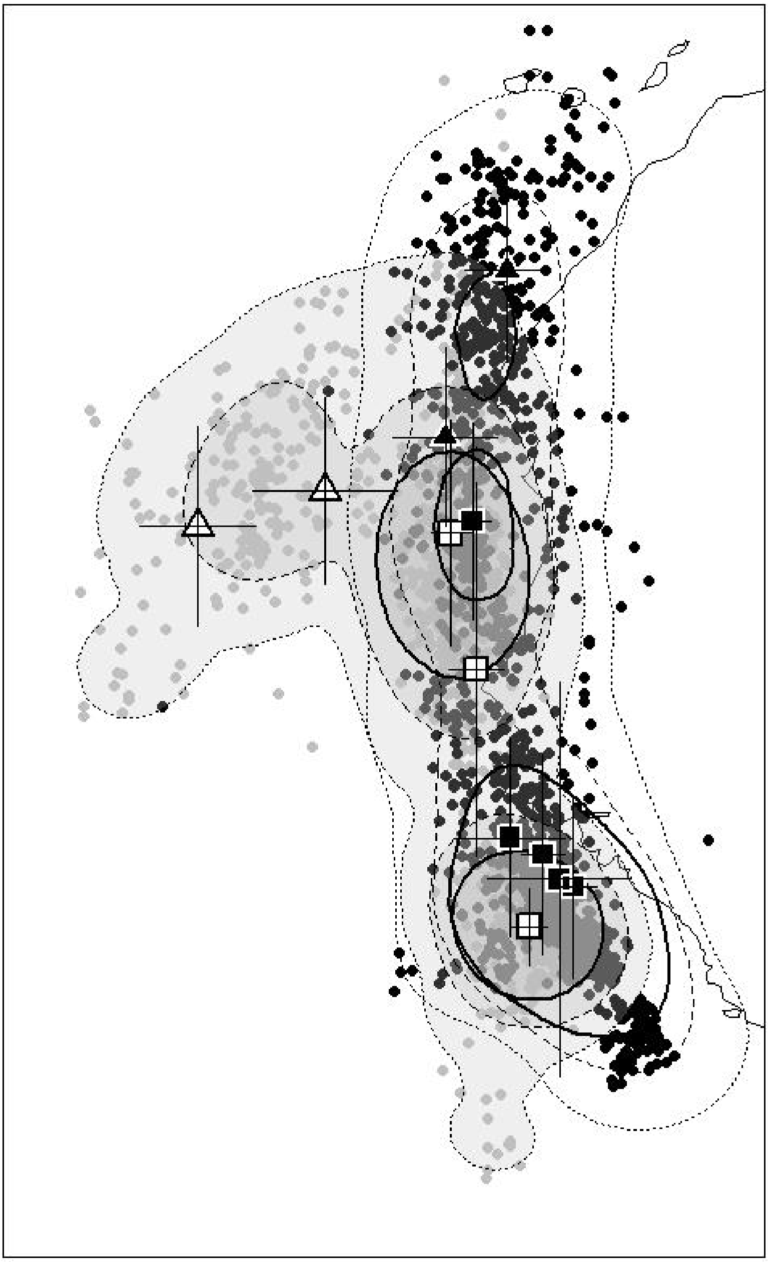


Figure S5 Differences in wintering area between years based on 12 tracks with light-level geolocators of 9 Common Terns. Grey dots = 2009/2010 data; small black dots = 2010/2011 data. Dotted lines = 95 kernel densities (highlighted in grey = 2009/2010); dashed lines 75 = kernel densities; solid lines = 45 kernel densities. Large triangles = females (filled white encircled black = 2009/2010, filled black encircled white = 2010/2011); large squares = males (filled white encircled black = 2009/2010, filled black encircled white = 2010/2011)

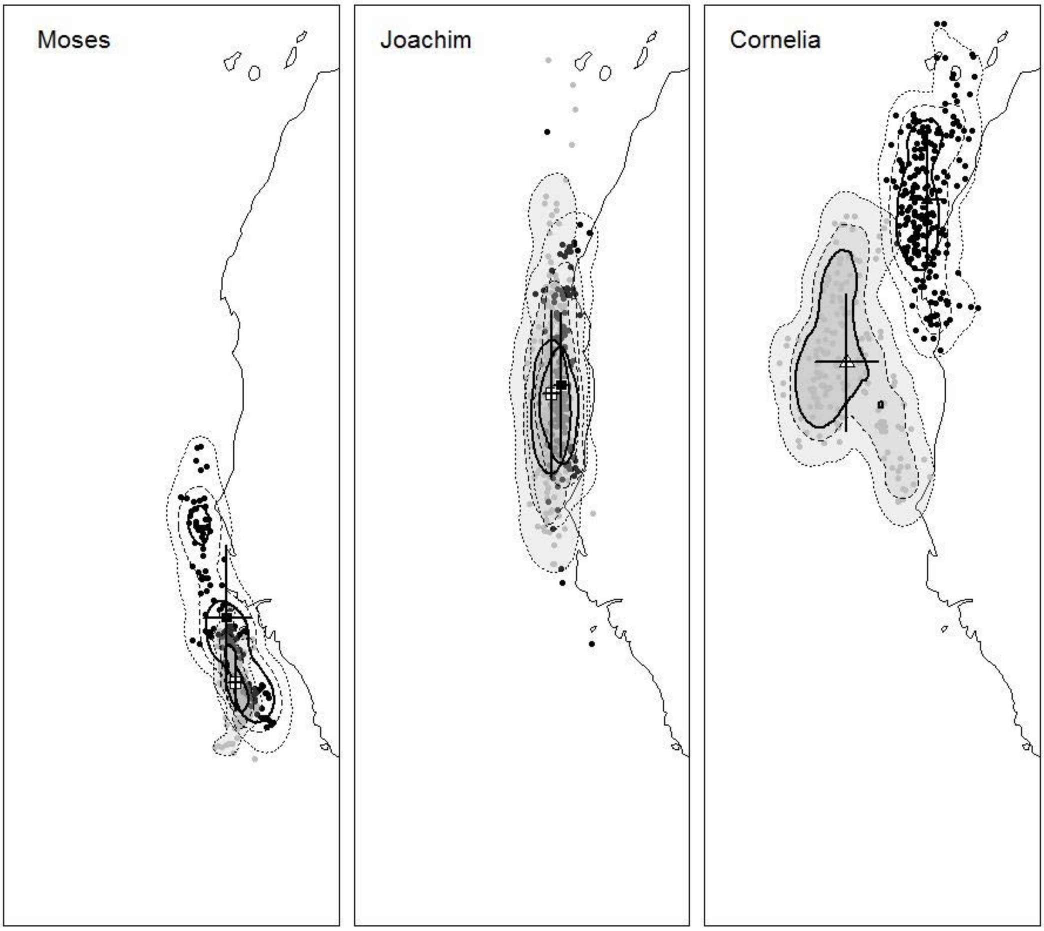


Figure S6 Wintering areas of individual Common Terns (female Cornelia, males Joachim and Moses) with two years of data. Symbols as in Fig. S5. Great circle distance between mean estimated wintering locations were 647 km (Cornelia), 58 km (Joachim), and 223 km (Moses; see also Fig. S4)

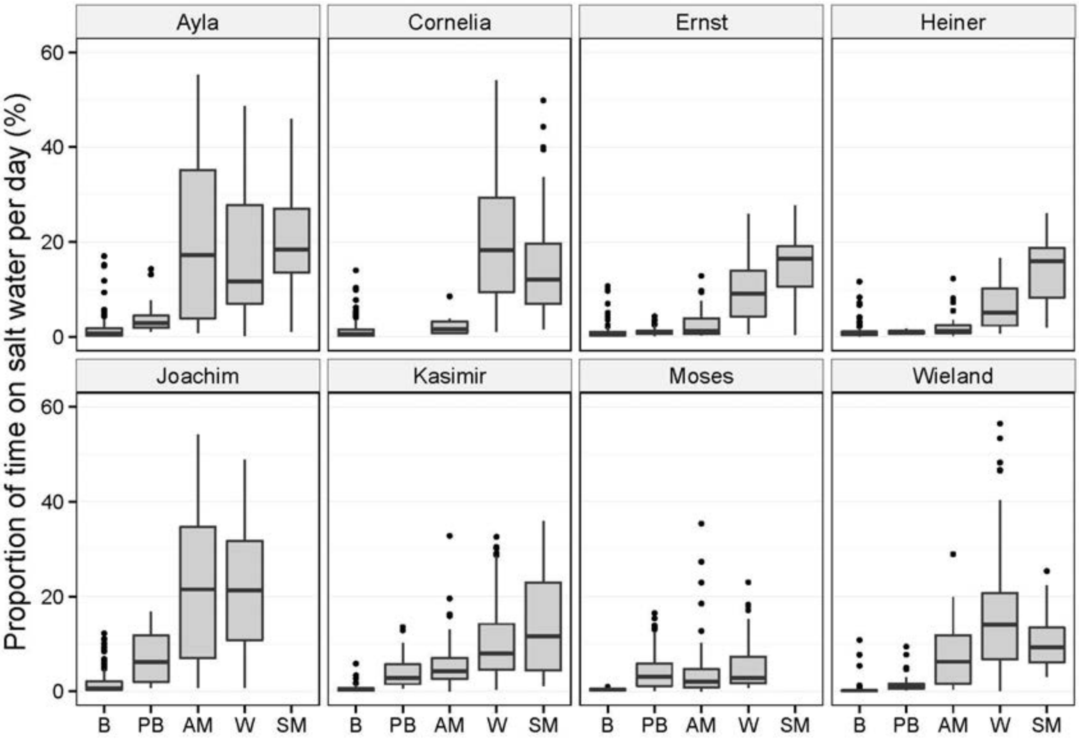


Figure S7 Seasonal variation in the temporal proportion of saltwater contact across different stages of the annual cycle. Mean daily percentage of time Common Terns had contact with salt water recorded by using saltwater immersion data from geolocators (B breeding, PB post-breeding, AM autumn migration, W wintering, SM spring migration)

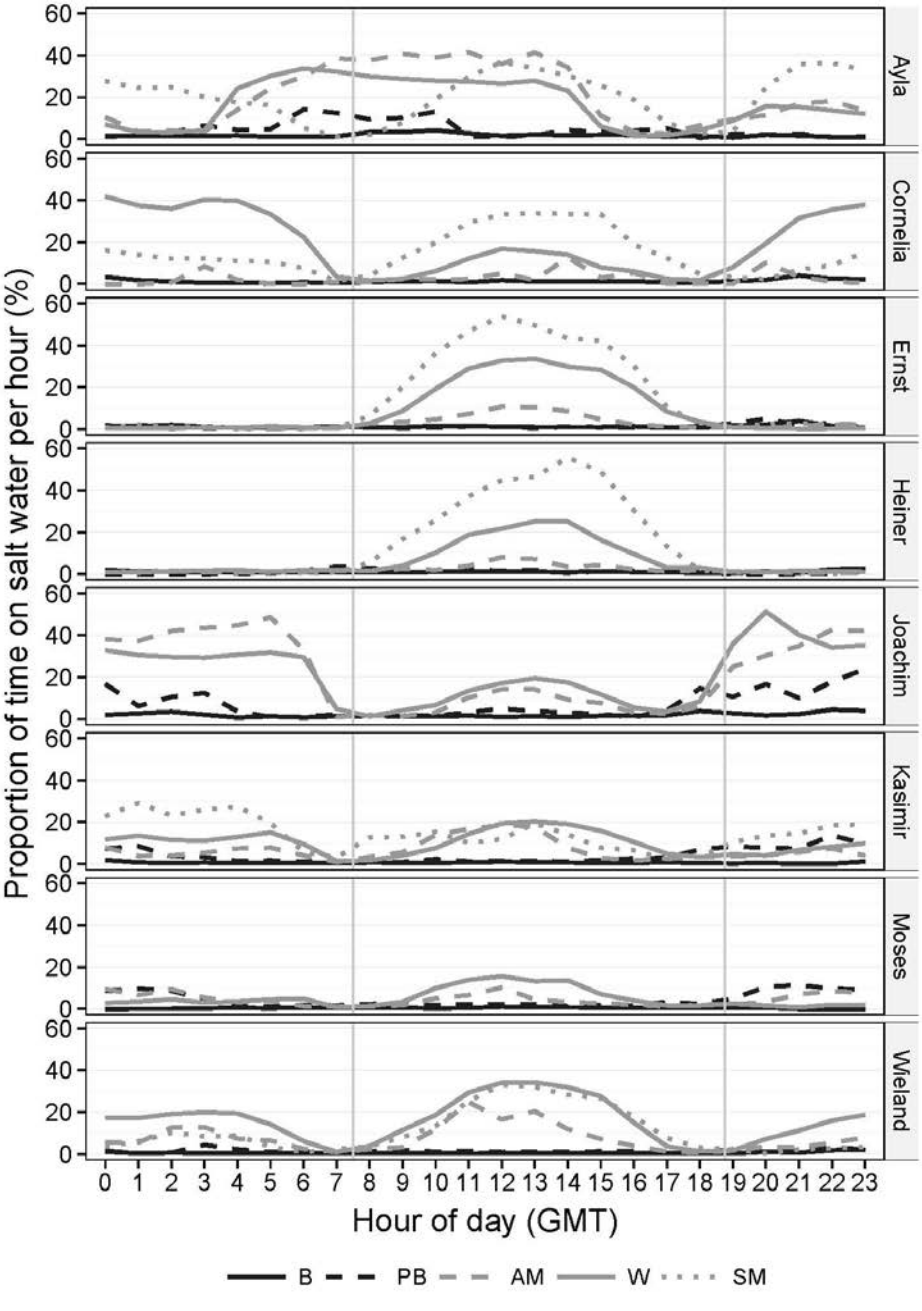


Figure S8 Diurnal at sea activity during the stages of the annual cycle, based on tracks of 8 Common Terns. The proportion of time at sea per daytime hour is presented. Vertical lines refer to mean sunrise and sunset times during wintering. (B breeding, PB post-breeding, AM autumn migration, W wintering, SM spring migration). The individual Ayla showed an internal clock shift (Fig. S3h)

Table S3 Sea water contact (hours per day ± SD, (n)) during the stages of the annual cycle, based on tracks of 8 Common Terns. Cf. Fig. 6 for daily proportions. Significant differences between stages are indicated by stage abbreviations (capitals $p<0.05$); GLMRM, n=6 individuals with data during each stage, respectively

ID	*Breeding*	*Post-breeding*	*Autumn migration*	*Wintering*	*Wintering*	*Pre-breeding*
Ayla	0.43 ± 0.77 (114)	1.12 ± 1.09 (12)	4.92 ± 4.06 (49)	4.05 ± 3.03 (112)	4.86 ± 2.51 (58)	-
Cornelia	0.35 ± 0.55 (101)	-	0.65 ± 0.68 (7)	4.75 ± 2.91 (205)	3.59 ± 2.59 (54)	-
Ernst	0.30 ± 0.52 (100)	0.30 ± 0.23 (44)	0.67 ± 0.76 (37)	2.23 ± 1.33 (118)	3.58 ± 1.56 (49)	1.16 (1)
Heiner	0.27 ± 0.40 (109)	0.24 ± 0.09 (12)	0.49 ± 0.54 (56)	1.55 ± 1.09 (106)	3.37 ± 1.51 (55)	1.22 ± 1.59 (7)
Joachim	0.47 ± 0.67 (98)	1.74 ± 1.39 (18)	5.37 ± 4.11 (32)	5.27 ± 3.22 (104)	2.00 ± 0.84 (2)	-
Kasimir	0.14 ± 0.19 (85)	0.98 ± 0.80 (61)	1.60 ± 1.71 (29)	2.41 ± 1.79 (172)	3.50 ± 2.88 (24)	-
Moses	0.10 ± 0.05 (44)	1.07 ± 1.05 (55)	1.10 ± 1.60 (52)	1.22 ± 1.22 (81)	-	-
Wieland	0.12 ± 0.37 (83)	0.36 ± 0.45 (46)	1.78 ± 1.66 (31)	3.79 ± 2.96 (147)	2.52 ± 1.32 (46)	-
Mean (n=6)	0.29 ± 0.14	0.79 ± 0.59	2.47 ± 2.13	3.21 ± 1.39	3.31 ± 0.99	-
p	*A, W,* ***S***	*A, W,* ***S***	*B, P*	*B, P*	***B****, P*	

3. ADDITIONAL INFORMATION ABOUT POTENTIAL EFFECTS OF GEOLOCATORS ON COMMON TERNS

Arrival mass

In three individuals body mass at arrival could be compared between one or more years before attachment of the geolocator and while the bird was carrying it. Average value before geolocator attachment was 125.3 ± 5.8 g (SD, n=3), and with geolocator 138.5 ± 8.7 g (n=4). Kasimir, before 122 g (2008)/with 127 g (2011); Ayla, before 122 g (2009)/with 148 g (2011); Cornelia, 1999-2002, before, on average 132 g (124-136 g)/with 140 g (138 and 141 g, 2010 and 2011, respectively). These values were within the common range of arrival mass of Common Terns at the breeding grounds, i.e.128-136g, depending on age (Limmer & Becker 2007).

Mass at catching

For 12 breeders no differences were found in mass at catching before deploying the geolocator and after retrieving it (first catch: 128.9 ± 3.3 g, second catch with geolocator: 130.4 ± 2.5 g; t = -0.848, df = 11, p = 0.415, t-test).

Arrival date

We compared arrival dates as related samples in individuals before, during, and after the geolocator attachment (Table S4; cf. Table S1). The differences were n.s. and there was no indication that arrival date was impaired by the geolocator.

Figure S9 Common Tern marked with steel ring (right leg) and geolocator attached to a plastic ring (left leg; Photo: Sabrina Weitekamp)

Table S4 Arrival dates of individuals in the year before, during or after geolocator attachment, respectively. Pairwise Wilcoxon signed-rank tests, two-tailed. Means ± SD

	Arrival Date (day of year)
Before Geoloc. Att.	113.1 ± 6.3
During Geoloc. Att.	111.9 ± 7.9
n	9
U	0.0
p	1.0
During Geoloc. Att.	107.5 ± 9.6
After Geoloc. Att.	108.8 ± 7.1
n	4
U	-0.184
p	0.854

Laying date

In five pairs with at least one mate carrying a geolocator laying date was compared before, during, and after attachment of the geolocator. Laying date (day of the year) before attachment was 133 ± 4 (SD, range 128 - 139), with geolocator 133 ± 7 (123 - 139) and after removing the geolocator 126 ± 2 (125 – 129; Friedman-test, n=5, Chi^2 = 4.800, df = 2, p = 0.091).

Reproductive success

We found no significant influence of carrying light-level geolocators on birds' reproductive success in terms of clutch size, but on hatching success, fledging success, and fledglings per pair comparing the years birds carried the light-level geolocators with adjacent years (Tables S5 and S6).

Table S5 Annual reproductive success from 2008-2011 in Common Tern pairs equipped with geolocator. In 2008, only one mate per pair was equipped (cf. Table S1). Means ± SE are given

Year	Clutch Size	Hatching Success	Fledging Success	Fledglings Pair[1]	N Pairs
2008	3.0 ± 0.0	1.00 ± 0.0	0.47 ± 0.1	1.6 ± 0.2	5
2009	2.8 ± 0.2	0.56 ± 0.2	0.06 ± 0.1	0.2 ± 0.2	6
2010	2.7 ± 0.2	0.33 ± 0.2	0.33 ± 0.2	0.5 ± 0.3	6
2011	2.7 ± 0.3	0.76 ± 0.1	0.52 ± 0.1	1.8 ± 0.3	7

Table S6 Reproductive success (means ± SE) of pairs equipped with geolocators. Pairwise comparisons between years before, during, and after geolocator attachment (Wilcoxon signed-rank test, one-tailed; hypothesis: reduced values during geolocator attachment)

	Before Geolocator Att.	**D**uring Geolocator Att.[1]	**A**fter Geolocator Att. [2]	P (n)
Cluch size	2.9 ± 0.1	2.7 ± 0.2	--	n.s. (7)
Hatching success	**0.86 ± 0.10**	**0.43 ± 0.16**	**0.89 ± 0.07**	B/D: <0.05 (7) D/A: <0.05 (6)
Fledging success	0.48 ± 0.16	0.22 ± 0.16	0.56 ± 0.06	B/D: n.s. (7) D/A: n.s. (6)
Fledglings pair-1	1.0 ± 0.4	**0.4 ± 0.3**	**1.7 ± 0.2**	B/D: n.s. (7) D/A: < 0.05 (6)
N	7	7	6	

[1] preferably from year 2010 if data from more than one year were available

[2] mainly from year 2011, after deployment of geolocator and clutch management

Figure S10 Clutch of a Common Tern pair tagged each with a geolocator. The number of fine fissures of the egg shell was increasing with incubation time and finally did cause shell breakage, clutch failure, and desertion (Photo: Peter H. Becker)

In 2009 reproductive success of the colony was very low. Beyond that in 2009 and especially in 2010, except clutch size, reproductive success of geolocator pairs was much lower than that of other experienced pairs (2009, hatching success: 0.73 ± 0.04, fledging success: 0.22 ± 0.03, fledglings pair^{-1}: 0.35 ± 0.06, n=77 pairs; 2010, hatching success: 0.84 ± 0.03; fledging success: 0.71 ± 0.03, fledglings pair^{-1}: 1.38 ± 0.09, n=99 pairs; cf. Table S3). In 2011 hatching success was increased successfully by egg exchange with dummy eggs, and incubating the eggs in an incubator for 2-6 d as far as the geolocator was deployed. An inter-annual comparison within the marked pairs showed that hatching success and fledglings pair^{-1} were significantly different between the treatments (Table S6).

Hatching success of the pairs was strongly and negatively affected by the summed no. of days the pair mates were equipped with the geolocator during the incubation period (maximum 22 d per adult; rs=-0.758, N=14, p=0.002; range = 5 – 44 d per pair and year; 2008 – 2010). Main cause of reduced hatching success was egg damage: fine fissures in the egg shell increasing with incubation time of the clutch (Fig. S7). After egg damage four pairs marked with geolocators produced a replacement clutch, one in 2009 (2 eggs), three in 2010 (3 eggs, resp.). Also these replacement clutches failed because of egg shell breakage.

Body mass and fledging age of chicks, subadult return

Maximum body mass (126.4 ± 3.8 g), fledging mass (113.0 ± 3.4 g) and fledging age (27.3 ± 0.6 d) of fledglings (n=9) reared by geolocator parents in 2008 – 2010 were in the range typical for Banter See colony, reported e.g. by Becker & Wink (2003). From these juveniles, 5 had returned as prospectors to the Banter See colony two or three years later (55%; at least one prospector from 4 of 6 pairs).


E.Ch

Chapter 3:

Spatial ecology, phenological variability and moulting patterns of the endangered Atlantic petrel, *Pterodroma incerta*

Marina Pastor-Prieto[1], Raül Ramos[1], Zuzana Zajková[1,2],
José Manuel Reyes-González[1], Manuel L. Rivas[1],
Peter G. Ryan[3] & Jacob González-Solís[1]

[1] *Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals (BEECA), Universitat de Barcelona. 08028 Barcelona, Spain*

[2] *Center for Advanced Studies of Blanes (CEAB-CSIC), 17300 Girona, Spain*

[3] *FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa*

Accepted to: Endangered Species Research, Biologging and Conservation Special issue. On 18th of September 2019.

ABSTRACT

Insights about year-round movement and behaviour of seabirds are essential to better understand their ecology and to evaluate possible threats at sea. The Atlantic petrel (*Pterodroma incerta*) is an endangered gadfly petrel endemic to the South Atlantic Ocean, with virtually the entire population breeding on Gough Island (Tristan da Cunha archipelago). We describe adult phenology, habitat preferences and at-sea activity patterns for each phenological phase of the annual cycle and refine the current knowledge about its distribution, by using light-level geolocators on 13 adults during one to three consecutive years. We also ascertain its moulting pattern through stable isotope analysis (SIA) of nitrogen and carbon in feathers from 8 carcasses. On average, adults started their post-breeding migration on 25 December, taking 10 days to reach their non-breeding areas on the South American shelf slope. The pre-breeding migration started around 11 April and took 5 days. From phenological data, we found evidence of carry-over effects between successive breeding periods. The year-round distribution generally coincided with the potential distribution obtained from habitat modelling, except during the non-breeding and pre-laying exodus periods, when birds only used the western areas of the South Atlantic. Moulting occurred during the non-breeding period, when birds spent more time on the water, and results from SIA helped us to distinguish feathers grown around Gough Island from those grown in the non-breeding area. Overall, our results bring important new insights into the spatial ecology of this threatened seabird, which should help improve conservation strategies in the South Atlantic Ocean.

1. INTRODUCTION

Seabirds are increasingly threatened worldwide, and their populations are subject to a variety of threats both on land, where they breed, and at sea, where they rest and forage throughout the year (Croxall et al. 2012, Lewison et al. 2012). Key threats affecting seabird populations include introduction of alien invasive predators to their breeding locations, pollution and habitat degradation, interactions with commercial fisheries, climate change and diseases (Lucas & MacGregor 2006, Olmos et al. 2006, Grémillet & Boulinier 2009, Hilton & Cuthbert 2010, Uhart et al. 2018, Philpot et al. 2019). Especially in the case of oceanic seabirds, their sensitive life history traits such as long life, delayed first breeding, single egg per breeding attempt, and strong mate fidelity (Warham 1996, Bried et al. 2003, Rodríguez et al. 2019), make them particularly prone to environmental and human perturbations, which contribute to their current population declines and poor conservation status (González-Solís & Shaffer 2009, Croxall et al. 2012).

In addition to long-lasting detrimental effects on population dynamics, individual life histories are also shaped by events occurring in geographically disparate places during the breeding, migration and non-breeding periods (Norris & Marra 2007). There is mounting evidence of carry-over effects (i.e. processes that influence individual performance in a subsequent season) from the breeding to the non-breeding period, suggesting that migratory, non-breeding and moulting decisions taken by individuals are influenced by their success in previous breeding attempts (Catry et al. 2013). Thus, taking into account the variability of breeding efforts within a population seems advisable when trying to define phenology and year-round distributions of long-lived species.

Gadfly petrels (*Pterodroma* spp.) are the largest genus of oceanic seabirds, with most species endemic to isolated oceanic archipelagos (Hilton & Cuthbert 2010, Croxall et al. 2012). Due to the remote location of their breeding colonies, many aspects of gadfly petrels' ecology remain poorly known (Rodríguez et al. 2019). Few novel studies have generally described their at-sea distribution, showing long-range movements across ocean basins (Rayner et al. 2008, Jodice et al. 2015, Krüger et al. 2016, Ramos et al. 2016, Clay et al. 2017, Leal et al. 2017, Ramos et al. 2017).

The Atlantic petrel (*Pterodroma incerta*) is a medium-sized procellariiform seabird (420 – 720 g), with a year-round distribution largely confined to the South Atlantic Ocean (Enticott 1991, Orgeira 2001, Cuthbert 2004). The species breeds during the austral winter; observations at the breeding islands indicate that they arrive at the colony from mid-March onwards, laying a single egg in June-July, and chicks fledge in December (Richardson 1984, Cuthbert 2004). Virtually the entire population, estimated at approximately 1 million pairs, breeds at Gough Island (40º20'S, 9º53'W) (Cuthbert 2004, Flood & Fisher 2013, Rexer-Huber et al. 2014). In the 1970s, a small remnant population bred on Tristan da Cunha, but the introduction of alien predators, in land habitat modification and hunting by islanders contributed to its presumed extinction as breeder (Richardson 1984, Cuthbert 2004, BirdLife International 2017a). A few pairs also breed on the eastern plateau of Inaccessible Island (Flood & Fisher 2013, P.G. Ryan unpubl. data). The Atlantic petrel is listed as endangered by the IUCN due to its extremely small breeding range, and the high rate of chick predation by introduced house mice (*Mus musculus*), which has caused the population decline and may even lead to its extinction, if mice are not eradicated from Gough Island (Cuthbert et al. 2013, Dilley et al. 2015, BirdLife International 2017a, Caravaggi et al. 2019).

The poor conservation status of the Atlantic petrel calls for new insights to better understand the species' ecology and guide conservation actions. Most knowledge of its distribution at sea comes from ship-based sightings (Enticott 1991, Orgeira 2001). More recently, its general phenology and distribution were summarised together with other gadfly petrels species using tracking data (Ramos et al. 2017). However, Ramos et al. (2017) did not include detailed descriptions on the phenology and spatial ecology and the factors influencing migration schedules within the population or other important aspects of its at-sea ecology, such as habitat preferences, at-sea activity patterns and moulting strategies.

This study extends our knowledge about the spatial ecology of adult Atlantic petrels. Our first aim was using geolocation-immersion data to assess in detail phenological phases, at-sea distribution, marine habitat preferences and activity patterns year-round. Second, we explored whether breeding success might lead to carry-over effects regarding phenology, behaviour or distribution, as previously found in a number of species (Catry et al. 2013, Phillips et al. 2017, Ramos et al. 2018). Since Atlantic petrels suffer high rates of breeding failure (up to 87 % rate of chick predation by introduced house mice) (Wanless et al. 2007, Cuthbert et al. 2013, Dilley et al. 2015), we expected to detect, from geolocator data, a relatively high number of birds not returning to the colony during the breeding to feed their chick, due to breeding failure. We would then expect these failed at breeding birds leaving the colony earlier than the remaining breeders to adjust their annual phenological calendar. Finally, we investigated the moulting patterns by performing stable isotope analysis (SIA) on feathers from dead specimens. We would expect feathers moulted close to the breeding grounds to show a smaller variability in the isotopic values among individuals than feathers moulted in the wintering areas, since in the latter case a larger spatial segregation of the individual wintering areas would also lead to the integration of disparate baseline isotopic levels in their feathers.

2. MATERIALS & METHODS

2.1. Tag deployment and data filtering

We deployed light-level geolocators (models Mk13, Mk14 and Mk19 from ©Biotrack) attached to a PVC ring with cable ties to the tarsus of breeding Atlantic petrels during the incubation period. Between July and August of 2010 2011 and 2012, we deployed 42 geolocators (21, 16 and 5, respectively) on 33 Atlantic petrels attending burrows near the research station at Gough Island. Sex of birds was unknown. Some individuals were tagged in more than one year. Over three years after deployment, 26 of these 33 birds were recaptured, but 5 had lost the device. From the 21 geolocators recovered, 13 provided data. Overall, we gathered tracks from 9 individuals for one year, 3 individuals for two years and 1 individual for three years, resulting in 18 year-round tracks from 13 birds. This dataset is already included in Ramos et al. (2017) to provide a general distribution and phenology of the species. Here we analyse these data in more detail, to provide information on habitat preferences, moulting strategies and activity patterns.

Geolocators measure light levels every minute and record the maximum value every 5 (model Mk19) or 10 minutes (models Mk13 and Mk14 (Afanasyev 2004)). Based on the photoperiod and sunrise and sunset times, two locations per day can be inferred (one to local midday and other to local midnight) with an average accuracy of ~186 ± 114 km (standard deviation, SD) (Phillips et al. 2004). Light level curves were supervised using TransEdit from BASTrack software (British Antarctic Survey, BAS). Geolocators were calibrated for ~1 week before deployment outside the Gough Island research station. We used calibration data to calculate sun elevation angle for each device (mean ± SD, -3.3 ± 0.44) and applied a threshold value of 20 to estimate sunrise and sunset times. We removed all locations derived from light curves presenting interferences at sunrise or sunset. Those erroneous locations inside a window of 20 days on either side of each equinox (Afanasyev 2004) were also removed, as latitude cannot be inferred by light-level geolocation for these periods. We considered locations with flying speeds higher than 55 km h^{-1} sustained over a 48 h period to be unrealistic and thus they were also removed. Final dataset for further analysis contained 67 % of all locations and is available in the Seabird Tracking Database of BirdLife International (http://www.seabirdtracking.org/) at the following address (http://seabirdtracking.org/mapper/?dataset_id=966; BirdLife International 2017b).

2.2. Phenology and spatial distribution

Phenology was determined for each year-round trip by visually inspecting filtered locations in BirdTracker software (BAS) and confirmed using conductivity data, inferred from saltwater immersion data (see below). At this step, unfiltered locations were used to inform longitudinal movements and determine phenology around the equinoxes, because longitude remains reliable (Hill 1994). Departure and arrival dates from breeding and non-breeding grounds were assessed visually. Departures were identified as the first day that any location was outside the cluster of locations from the previous 10 days that was followed by a clearly directed movement away from this area. Similarly, arrivals were assessed as the first day any location was inside the cluster of locations, preceded by a directed movement towards that area. Regarding incubation, only entire incubation periods were considered (data from 5 birds), excluding those that were not fully recorded because of the dates of deployment or recovery of devices. We defined an incubation bout as consecutive days without light and with no immersion records preceded and followed by light and immersion records. We inferred chick-rearing when birds made frequent brief visits to the colony at night, without immersion data during several hours, and characteristic of this period (Ojowski et al. 2001). Each visit took place only during night and consecutive visits were typically separated by several days with immersion records (at night and day) at sites where foraging to feed the chick presumably occurred. These sites were far enough away from the colony to consider those birds did not visit the colony on consecutive nights. We identified the onset date and duration of the following phenological phases: post-breeding migration, non-breeding, pre-breeding migration, pre-breeding (i.e. from arrival at the colony to pre-laying exodus), pre-laying exodus (i.e. period at-sea that extends from mating to egg laying), incubation and chick-rearing.

Once those events were identified, we evaluated their variability among the year-round trips recorded. A preliminary visual exploration of changes in longitude suggested the existence of two phenological groups (see Fig. S1). To typify them objectively, we applied a multivariate hierarchical clustering analysis using the function *hclust* and the method *ward.D2* from “stats” R package (R Core Team 2017). We considered seven input variables: the onset of post-breeding migration, non-breeding, pre-breeding migration, pre-breeding, pre-laying exodus, incubation (all these dates were included in statistical analyses as the number of days since January 1st), and the duration (in days) of the non-breeding period (Fig. 1A). The start of chick-rearing was not included because 3 birds performed post-breeding migration immediately after incubation, presumably because their breeding attempt failed during incubation or around hatching (many chicks are killed by mice within hours of hatching, Dilley et al. 2015). Variables were z-transformed prior to analysis. We performed a silhouette analysis, using the function *silhouette* in the R package “cluster” (Maechler et al. 2017), to evaluate within-cluster consistency, i.e. how similar each sample is to the others assigned to the same cluster (Fig. S2) (Rousseeuw 1987). Clustering results showed two well-defined phenological groups, presumably related to breeding success (Figs. 1A and 1B, but see results, Figs. S2 and S3 and discussion for the rationale of this designation), so we termed these groups successful and failed breeders. We tested for differences in phenology between these groups using a U Mann-Whitney-Wilcoxon test, applying Bonferroni correction for multiple comparisons.

Distribution at population level was determined from filtered positions for each phenological phase through kernel density estimation, using the *kernelUD* function from the “adehabitatHR” R package (Calenge 2011). We used a Lambert Azimuthal Equal Area projection centred in the centroid of all locations and a smoothing parameter equivalent to 186 km

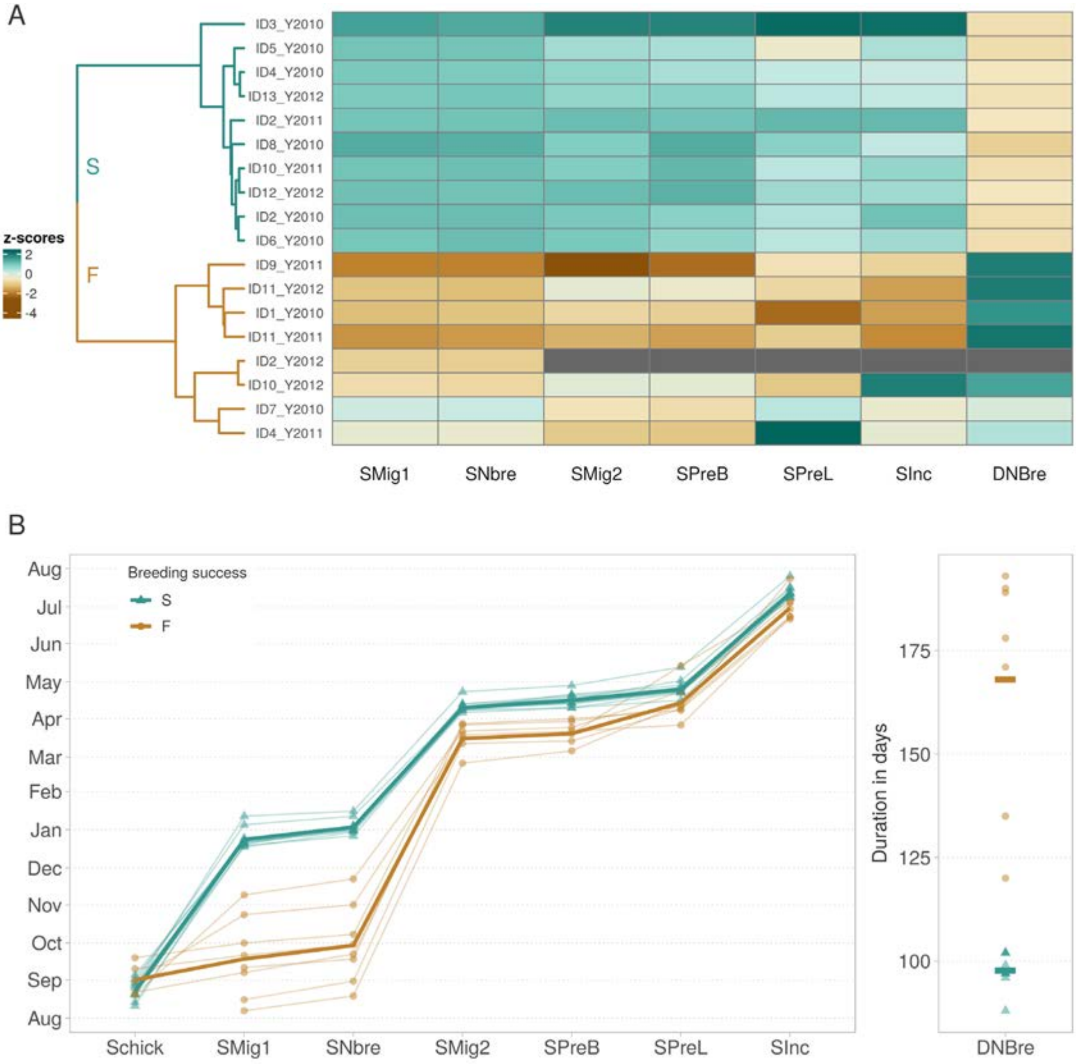


Figure 1. Hierarchical clustering analysis of seven scaled phenological variables of Atlantic petrels. (A) Two groups, assigned as successful (S, blue) and failed (F, light brown) breeders, were identified applying hierarchical clustering analysis on seven phenological variables: starting dates of post-breeding migration (SMig1), non-breeding (SNbre), pre-breeding migration (SMig2), pre-breeding (SPreB), pre-laying exodus (SPreL), incubation (SInc) and duration of non-breeding (DNBre); variables were z-transformed prior to analysis. Each row represents individual phenology identified by track ID (birdID_year), the cell colour gradient reflects the value of the z-transformed variable; dark grey shaded cells represent missing values. See Fig. S2 for the results of silhouette analysis of this hierarchical clustering. (B) Phenology of adult Atlantic petrels (successful and failed breeders separately) tracked with geolocators from Gough Island. Thick lines show mean values of each group and thin lines correspond to individual phenologies (see Fig.S3 for detailed individual phenology). Note that starting dates of chick-rearing (Schick) are detailed here, but were not included in the hierarchical clustering analysis because 3 birds performed post-breeding migration immediately after incubation, presumably because they failed either during incubation or at hatching.

(~2º, depending on latitude), in order to account for the average error in geolocation (Phillips et al. 2004). Kernel density contours of 50 and 95 % were considered to represent, respectively, the core areas of activity and the areas of active use for each period (Pinet et al. 2011a).

2.3. At-sea activity analysis

Mk13 and Mk14 geolocator models measure the conductivity in saltwater every 3 seconds and summarize the result in 10-minute blocks, with values ranging from 0 (meaning the whole block was continuously dry) to 200 (meaning the whole block was continuously wet) (Afanasyev 2004). Mk19 geolocator model provides a different data resolution, storing the time stamp when geolocator recording change from wet to dry and vice versa; data recorded with Mk19 loggers were transformed to match Mk13 and Mk14 data resolution. Saltwater immersion data can be used as a proxy to infer activity patterns of seabirds, providing insights into behavioural strategies at different temporal scales (e.g. circadian, daily or seasonal) (Mackley et al. 2011, Rayner et al. 2012, Cherel et al. 2016). Activity patterns inform whether species are mainly diurnal or nocturnal (both situations have been described in petrels, e.g. Bugoni et al. 2009, Ramos et al. 2015). This may be relevant for species inhabiting oligotrophic oceanic regions, such as gadfly petrels, where diel vertical migration of potential prey can influence seabird behaviour (Dias et al. 2012, Navarro et al. 2013). We explored the activity patterns between day and night throughout the annual cycle based on the time that every logger remained in wet mode. Sunrise and sunset times for each day were derived from geolocator transition files (files with extension "trn"). We first evaluated daily time spent on the water (in %) for successful and failed breeders at each phenological phase, and for day and night separately. For visualisation purposes only, we modelled daily activity at sea during day and night using generalized additive mixed models (GAMMs), separately for successful and failed breeders. We included Julian date as a smoothing term and bird identity as a random term. The resulting values show the proportion of day and night spent on the water, to account for the changes of day length throughout the year. We used the "mgcv" R package (Wood & Augustin 2002), based on penalized regression splines and generalized cross-validation, to select the appropriate smoothing parameters. Moonlight can influence activity patterns of petrels, particularly during the non-breeding period (e.g. Yamamoto et al. 2008, Ramos et al. 2016), so we evaluated the effect of moonlight levels on nocturnal activity during the non-breeding period. We focused on this period to avoid any constraints that breeding might have on activity patterns. We used GAMMs to estimate nocturnal time on water during the non-breeding period as a response of the number of days since November's full moon of each year (see Ramos et al. 2016 for more details of the approach) as a smoothing term. This allowed us to determine cyclicity in the time spent on water during non-breeding in relation to the lunar cycle. Finally, nocturnal time on water during the non-breeding period was regressed against moonlight levels (from 0 during a new moon, to 100 during a full moon) using locally-weighted, non-parametric regressions (Jacoby 2000).

2.4. Habitat modelling

We used MaxEnt 3.3.3k software to develop habitat suitability models (Phillips et al. 2006, Elith et al. 2011). Taking into account similar studies (Quillfeldt et al. 2013, Ramírez et al. 2013, Ramos et al. 2015), seven environmental variables were selected through jack-knife test for their possible importance for predicting Atlantic petrel distribution: seafloor depth (BAT, m), bathymetric gradient (BATG, %; estimated as proportional change of seafloor depth calculated as 100 * (maximum value - minimum value) / (maximum value)), surface chlorophyll *a* concentration (CHLA, mg m^{-3} as a proxy of biological production), distance to the colony (DCOL, km), sea surface temperature (SST, ºC), salinity (SAL, ‰) and wind speed (WIND, m s^{-1}). The environmental information layers were downloaded as monthly averages from the ERDDAP data server in raster format (Simons 2017). In order to select those environmental variables that better explain the distribution of Atlantic petrels we used the function *VariableSelection* from "MaxentVariableSelection" R package (R Core Team 2019). We first excluded those variables that contributed less than 5 % to the model (contribution threshold = 0.5) and then excluded the correlated environmental variables (Pearson correlation, correlation threshold = 0.7), keeping those with the highest contribution score. As monthly variables of BAT and BATG were correlated (Table S1), and WIND and SAL explained < 5 % of the distribution for all phenological phases, we reduced environmental predictors to four non-redundant variables: BATG, CHLA, DCOL and SST. Environmental layers were averaged for each phenological phase and resampled to a spatial resolution of 2º, in order to match the spatial error in geolocation data. With those layers, habitat suitability models for each phase were generated using 1,000 possible random locations from inside 50 % kernel density contours. Each final model was the average of 100 models and their fit was evaluated using the area under the curve (AUC) statistic, which measures the ability of model predictions to discriminate species presence from background locations.

2.5. Feather sampling and SIA

We analysed the stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C) in the 1st, 3rd, 5th, 7th and 10th primary feathers (P1, P3, P5, P7 and P10), the 13th secondary feather (S13) and the 6th tail feather (rectrix, R6) sampled from 8 dead Atlantic petrels (we cannot distinguish if immature or adults) found on Gough Island in September 2009. As feathers are metabolically inert once formed, they retain the δ^{15}N and δ^{13}C values from the bird's diet at the time of growth, when they are irrigated by blood. Therefore, stable isotopes from feathers provide information about trophic levels (δ^{15}N) and foraging areas (δ^{13}C) when feathers were growing (Hobson et al. 1994, Cherel et al. 2000). All feathers were cleaned in a 0.50M NaOH solution, rinsed twice in distilled water in order to remove any contamination and oven dried at 60ºC to constant mass. Thereafter, feathers were flash frozen with liquid nitrogen and ground using a cryogenic grinder (Spex Certiprep 6850) to obtain a fine powder. Subsamples of 0.30 – 0.32 mg were weighed and placed into tin capsules to be oxidized in a Flash EA1112 and TC/EA coupled to a stable isotope mass spectrometer Delta C through a Conflo III interface (ThermoFinnigan) in Serveis Científico-Tècnics of the University of Barcelona (Spain). Stable isotope ratios are expressed in δ conventional notation as parts per thousand (‰) according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{15}N or ^{13}C and R corresponds to ratio ^{15}N/^{14}N or ^{13}C/^{12}C related to the standard values. $R_{standard}$ for ^{15}N is atmospheric nitrogen (AIR) and for ^{13}C is Vienna Pee Dee Belemnite (VPDB). The international standards applied (IAEA N_1, IAEA N_2, USGS 34 and IAEA 600 for N; IAEA CH_7, IAEA CH_6, USGS 40 and IAEA 600 for C) were inserted every 12 feather samples to calibrate the system and compensate for any drift over time. Values of δ^{15}N and δ^{13}C were compared to those of other petrels (Procellariidae) that overlap their distribution with Atlantic petrel's non-breeding region.

2.6. Ethics statement

All work was conducted in accordance with the appropriate institutional guidelines (University of Cape Town Animal Ethics Committee: 2014/V10/PRyan and 2017/V10REV/PRyan), and with the approval of the Tristan da Cunha government. The weight of tagged birds was > 500 g and the weight of geolocator was ~ 2 g, which was well below the deleterious recommended threshold of 3 - 5 % of body weight for back-mounted devices (Phillips et al. 2003, Igual et al. 2005, Passos et al. 2010). All birds were handled in strict accordance with good animal practice; deployment and recovery of geolocators took < 5 minutes and had no visible deleterious effects on study animals.

3. RESULTS

3.1. Phenology and spatial distribution

All tracked birds remained within the South Atlantic Ocean, with most time spent west of the breeding islands. Successful and failed breeders showed similar spatial distributions in each phenological phase (Fig. 2 shows detailed distribution of each phenological group). Adults spent the non-breeding period off northern Argentina, Uruguay and southern Brazil; during the pre-laying exodus, they mainly used the waters over the edge of the South American continental shelf, whereas during incubation and chick-rearing they used two main foraging areas, one around Gough Island and another closer to the South American coast (Fig. 2).

Multivariate hierarchical clustering based on phenology identified two distinct clusters of birds (Fig. 1). The mean silhouette width, with a value of 0.59, provided reasonable support for the structure (Fig. S2). Three year-round trips presented low widths (< 0.25), which indicated low support for the classification of these sam-

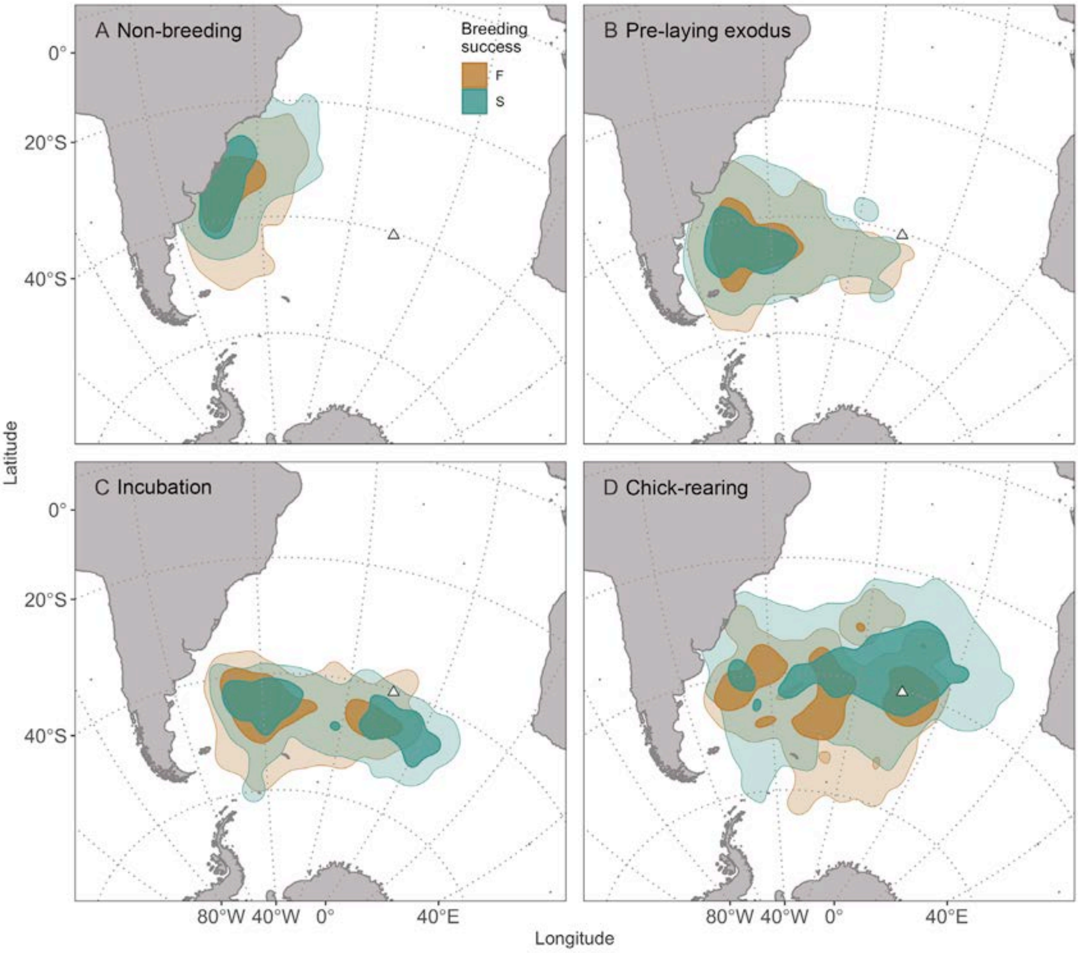


Figure 2. Year-round distributions of adult Atlantic petrels (successful and failed breeders separately). Blue for successful breeders and light brown for failed breeders. Filled contours refer to 50 % (darker polygons) and 95 % (lighter polygons) kernel UD (core areas of activity and the areas of active use, respectively) in the South Atlantic Ocean at each phenological phase. Triangle represents breeding colony at Gough Island.

Table 1. Phenology of adult Atlantic petrels detailed separately for successful and failed breeders. Starting date (day/month mean ± SD, over all years of study) corresponds to the mean date when each phenological phase or migration starts. Last column resumes results of U Mann-Whitney-Wilcox tests between successful and failed breeders phenological dates, applying Bonferroni correction for multiple comparisons. [a]Details about incubation bouts were obtained from 4 successful breeders and 1 failed breeder for which incubation period was not interrupted by deployment or recovery of the logger. This small number of birds prevents us from comparing the duration of incubation. Because only one individual of a couple was tracked, the actual length of the incubation period could be longer. [b]Duration of chick-rearing was not compared due to the small amount of data for failed breeders (3 birds performed post-breeding migration immediately after incubation).

Phenological phase	Successful (n = 10)	Failed (n = 8)	U Mann-Whitney-Wilcox Test
Post-breeding migration			
Start date	25/12 ± 8.1	19/09 ± 32.0	W = 80.0; p-value < 0.001
Duration (d)	9.6 ± 3.1	10.7 ± 3.4	W = 0.6; p-value = 0.591
Non-breeding			
Start date	04/01 ± 6.1	30/09 ± 31.1	W = 80.0; p-value < 0.001
Duration (d)	97.7 ± 4.2	168.0 ± 29.0	W = 0.0; p-value = 0.001
Pre-breeding migration			
Start date	11/04 ± 4.7	17/03 ± 10.9	W = 70.0; p-value = 0.001
Duration (d)	5.3 ± 3.0	4.1 ± 2.7	W = 0.4; p-value = 0.373
Pre-breeding			
Start date	17/04 ± 5.6	21/03 ± 9.1	W = 70.0; p-value = 0.001
Duration (d)	9.4 ± 3.8	24.6 ± 18.2	W = 0.1; p-value = 0.106
Pre-laying exodus			
Start date	26/04 ± 7.3	15/04 ± 15.1	W = 56.5; p-value = 0.039
Duration (d)	78.3 ± 4.2	77.43 ± 16.8	W = 0.5; p-value = 0.461
Incubation			
Start date	13/07 ± 5.3	01/07 ± 11.4	W = 61.0; p-value = 0.013
Duration (d)	58.0 ± 7.5[a]	82.0 ± 0.0[a]	[a]
Chick-rearing			
Start date	25/08 ± 8.1	03/09 ± 12.7	W = 14.0; p-value = 0.197
Duration (d)	122.1 ± 10.1	33.8 ± 31.4	[b]

ples, but details of their individual phenology support that their classification is more related to failed than to successful breeders (see Figs. S2 and S3 for a detailed explanation). Previous knowledge of breeding phenology based on observations on land (Cuthbert 2004) suggests that late migrants were successful breeders, whereas early migrants were failed breeders (see discussion for an extended explanation). Thus, following the clustering results, we described the phenology of the Atlantic petrels and detailed the breeding schedules separately for successful (n = 10) and failed breeders (n = 8; Table 1). Successful breeders left Gough Island at the end of December and carried out a post-breeding migration towards South America. They arrived at the non-breeding area off northern Argentina, Uruguay and southern Brazil (Fig. 2A) at the beginning of January and stayed in the area for 98 days. Successful breeders started the pre-breeding migration back to the colony in the middle of April, arriving 5 days later. In late April, at the beginning of the breeding season, they travelled to off the northern Argentinean coast and the Falkland Islands for the pre-laying exodus (Fig. 2B), returning in the middle of July to lay and incubate the egg (Fig. 2C). Detailed data about incubation (Table 1) were obtained from 4 successful breeders and 1 failed breeder for which the deployment or recovery of the logger did not interrupt the incubation period. Note however that the total length of the incubation period could be longer than recorded from the geolocator data because only one bird of each pair was tracked and its partner could have done the first or last bout. Successful breeders incubated the egg in two (3 birds) or three bouts (1 bird), with a median duration ± 95 % confidence interval of 16.0 ± 3.6 days (n = 9 bouts). One failed breeder also incubated in 3 bouts (16.0 ± 3.6 days). Chicks hatched in late August-September, when the adults foraged in the same areas used during incubation (one off the Argentinean continental shelf, and one closer to Gough Island; Figs. 2C and D). Failed breeders left for the non-breeding grounds earlier than successful breeders, had a longer non-breeding period, and returned to the colony earlier the following season (Table 1, Fig. 1B). The apparent result of failed breeders laying earlier but hatching later than successful breeders (Table 1), would not be taken in consideration because deploying and recovering of geolocators took place during incubation, thus breaking the connection between incubation and subsequent chick-rearing (i.e. the consideration as successful or failed breeders relate only to the year

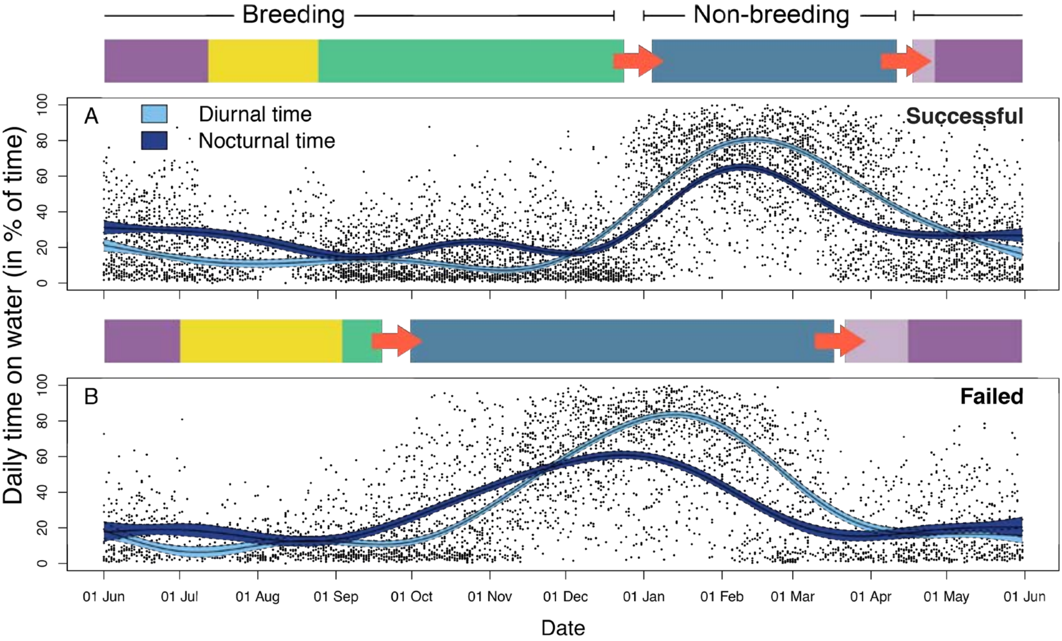


Figure 3. Year-round at-sea activity patterns of adult Atlantic petrels. Proportion of daily time spent on water (mean ± 95 % confidence interval of the slopes; estimated through generalized additive mixed models; GAMMs) during the day (light blue) and during the night (dark blue) along the annual cycle. Raw data is represented as dots on the background. Data is shown separately for the two cluster groups: (A) successful and (B) failed breeders. Horizontal bars at the top of each subplot show mean phenological dates of each cluster of birds: pre-laying exodus (dark purple), incubation (yellow), chick-rearing (green), non-breeding (blue) and pre-breeding (time from arrival at breeding grounds to pre-laying exodus; light purple). Arrows correspond to post- and pre-breeding migrations.

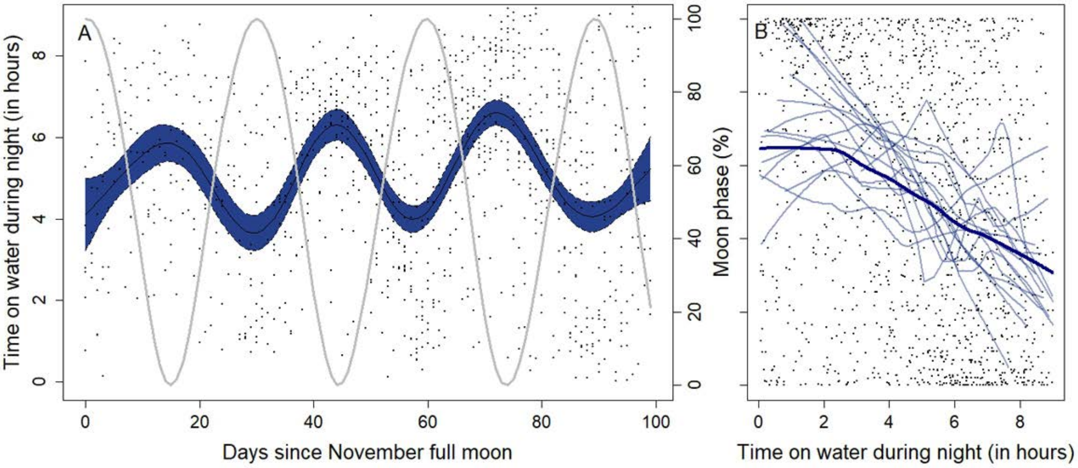


Figure 4. Effect of moonlight on non-breeding nocturnal activity of Atlantic petrels. (A) The mean of nocturnal time on water estimated through GAMMs is represented by black solid line, and the associated 95 % confidence interval of the slopes corresponds to dark blue region. To compare non-breeding data of different lunar cycles (2010 - 2013), daily hours of nocturnal time spent on water were re-scaled to the first full moon of November of each year. Moon phase is represented with a light grey wavy line (0 representing new moon and 100 full moon). (B) Nocturnal time on water during the non-breeding period as function of moonlight. Dots represent individual observations, thin lines correspond to individual locally-weighted non-parametric regressions, and the thick line corresponds to the mean of the species.

right after the logger deployment and cannot be maintained to the next year).

3.2. At-sea activity

Both successful and failed breeders spent less time on the water during the breeding period (pre-laying exodus, incubation and chick-rearing) than during the non-breeding period (Fig. 3, Table S2). Both successful and failed breeders noticeably increased the time on water during the non-breeding period, although in accordance with phenology, failed breeders clearly advanced this pattern in the calendar (Fig. 3). Despite petrels showed similar proportions of time spent on water during day and night within each phenological phase, the proportion of time on water was slightly higher during night than during day (Fig. 3), except during the non-breeding period, when nocturnal activity was clearly influenced by moonlight (Fig. 4). During this period, tracked birds spent more time on water during nights at new moon and spent more time flying on moonlit nights (Fig. 4).

3.3. Habitat modelling

The importance of each environmental variable in the MaxEnt models differed between phenological phases (Table 2, Fig. S4). The most important variables were: SST (20 - 25 ºC) in the non-breeding period; DCOL (2,500 - 4,000 km) during the pre-laying exodus; DCOL (0 - 2,500 km) and SST (0 - 7 ºC) during incubation; and DCOL (0 - 1,900 km) during chick-rearing (Fig. S4; the response curves are detailed in Fig. S5). Fig. 5 compiles the obtained habitat suitability models considering these environmental variables for each phenological phase. During non-breeding, suitable habitats outside the recorded distribution occurred in the southeast Atlantic, especially in the Benguela Upwelling region.

3.4. Stable isotope values

Atlantic petrels presented a narrower range of $\delta^{15}N$ (13.1 to 15.5 ‰) than $\delta^{13}C$ values (-19.3 to -16.1 ‰; Fig. 6, Table 3; see Table S3 for detailed values). Both isotopic ranges are wider in

Table 2. Most important environmental variables to the probability of occurrence of adult Atlantic petrels. MaxEnt modelling selected gradient of seafloor depth (BATG), chlorophyll a concentration (CHLA) as a proxy of biological production, distance to the colony (DCOL) and sea surface temperature (SST) as the most important environmental variables to predict the occurrence of adult Atlantic petrels within 50 % kernels UD (utilisation distribution) for each phenological phase. Estimates of model fit (as the area under the receiver operating characteristic curve; AUC) and relative importance (as percent contribution, in bold values over 15 %) of these environmental variables. Redundant environmental variables (BAT) and those variables explaining < 5 % of the distribution (SAL and WIND) were excluded during the modelling to reduce noise in the outputs. NA when relative importance or percent contribution < 5 %.

Phenological phase	AUC	Relative importance (%)			Percent contribution (%)				
		BATG	CHLA	DCOL	SST	BATG	CHLA	DCOL	SST
Non-breeding	0.915 ± 0.025	NA	11.9	NA	**83.6**	**22.3**	11.0	NA	**66.6**
Pre-laying exodus	0.988 ± 0.002	NA	NA	**94.0**	NA	NA	**28.7**	**59.5**	11.8
Incubation	0.991 ± 0.002	NA	NA	**66.5**	**29.9**	NA	NA	**54.4**	**28.7**
Chick-rearing	0.992 ± 0.002	NA	NA	**98.1**	NA	NA	NA	**90.7**	9.3

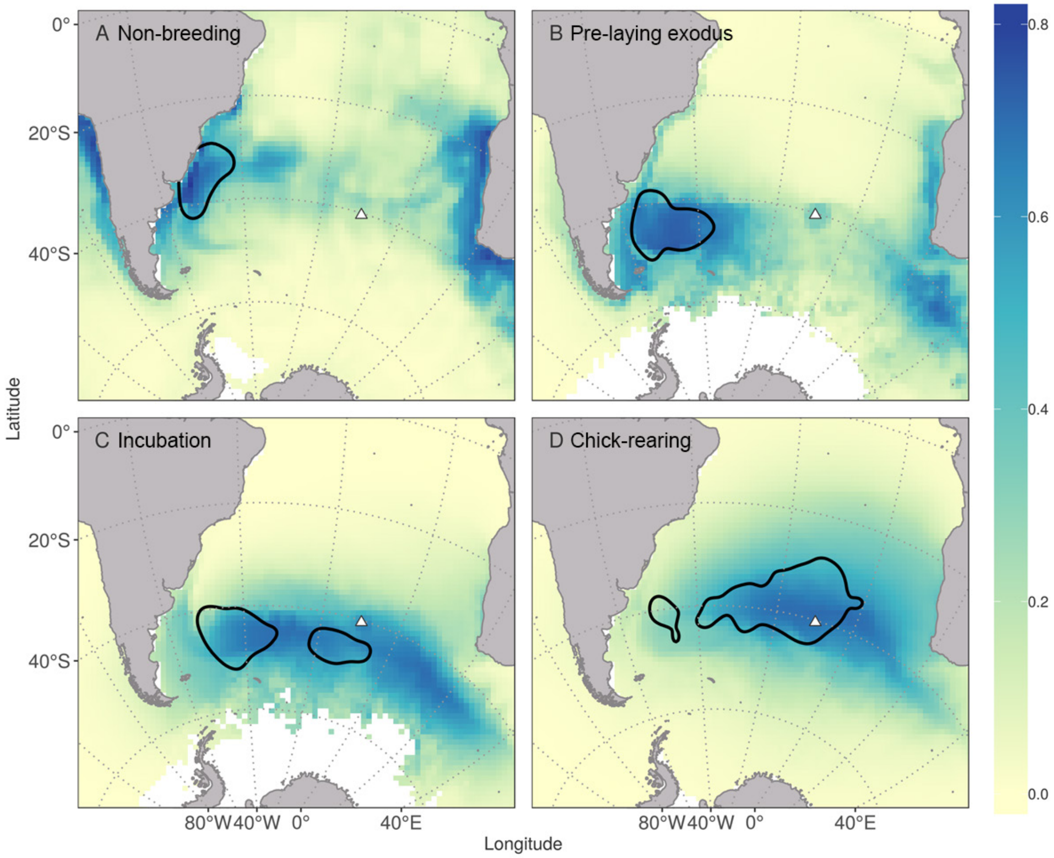


Figure 5. Habitat suitability of Atlantic petrels for every phenological phase derived from environmental modelling. Habitat suitability ranges from light yellow (less suitable habitat) to dark blue (most suitable habitat). Black contour lines indicate 50 % kernel UD of positions of both successful and failed breeders; triangle shows colony location.

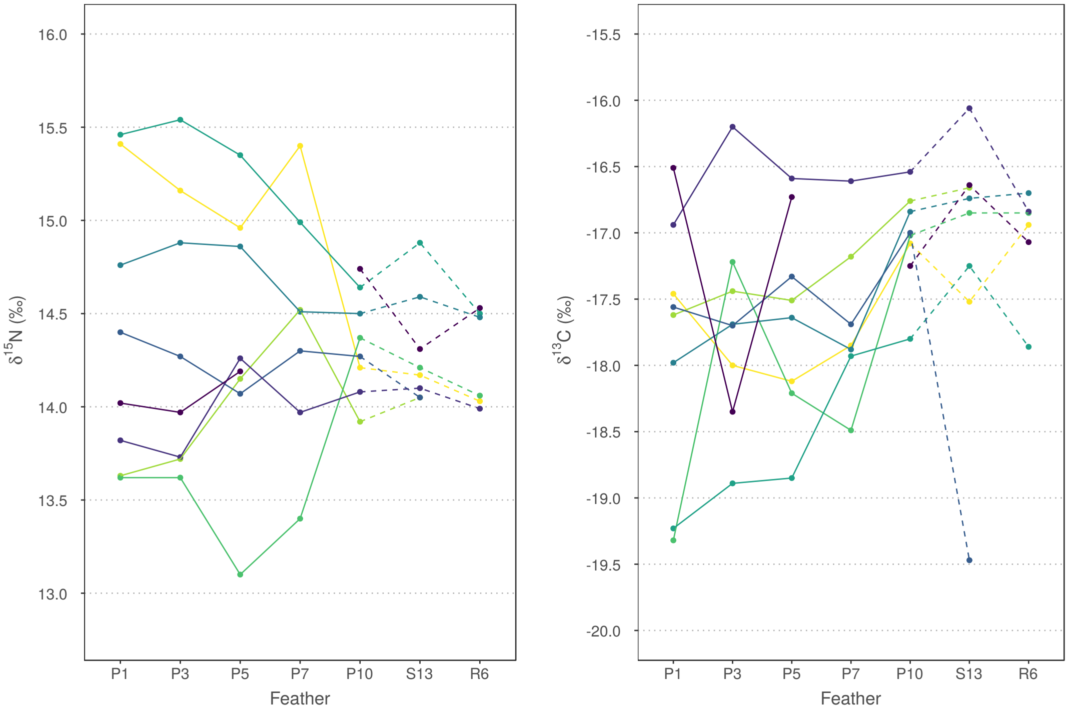


Figure 6. Stable isotope signatures (δ^{15}N and δ^{13}C) of primary, secondary and rectrix feathers of Atlantic petrels. (A) δ^{15}N and (B) δ^{13}C of 1st, 3rd, 5th, 7th and 10th primary feathers (P1, P3, P5, P7 and P10), 13th secondary (S13) and 6th rectrix (R6) feathers of Atlantic petrels (n = 8; values in Table 3). Lines connect values corresponding to feathers from the same individual, note that not all sequences are complete. Primary feather replacement is assumed to be simple and descendent in procellariiformes, starting from P1-3 and moulting sequentially towards P10. Secondary and rectrix feathers (here S13 and R6) are thought to be moulted out of the breeding season, not sequentially, as represented by dashed lines (Bridge 2006, Ramos et al. 2009).

Table 3. δ^{15}N and δ^{13}C values (mean ± SD) of feathers from several petrel and shearwater species found in the southern Atlantic Ocean. 1st, 3rd, 5th, 7th and 10th primary feathers (P1, P3, P5, P7 and P10), 13th secondary (S13) and 6th rectrix (R6) feathers of Atlantic petrels breeding on Gough Island. Feathers of Great shearwater (*Ardenna gravis*), Manx shearwater (*Puffinus puffinus*), Cory's shearwater (*Calonectris borealis*) and White-chinned petrel (*Procellaria aequinoctialis*), are known to be moulted in the Brazil-Falklands Confluence.
[a]Values excluding the outlier.

Species	Feather	n	δ^{15}N (‰)	δ^{13}C (‰)	Source
Atlantic petrel	P1	8	14.4 ± 0.7	-17.8 ± 1.0	Present study
	P3	8	14.4 ± 0.7	-17.7 ± 0.8	
	P5	8	14.4 ± 0.7	-17.6 ± 0.8	
	P7	7	14.4 ± 0.6	-17.7 ± 0.6	
	P10	8	14.3 ± 0.3	-17.0 ± 0.4	
	S13	7[a]	14.3 ± 0.3	-17.4 ± 0.5	
	R6	6	14.3 ± 0.3	-17.0 ± 0.4	
Great shearwater	P1	6	15.6 ± 1.2	-16.7 ± 1.6	T. Militão unpubl. data
Manx shearwater	R6	13	17.6 ± 1.9	-16.3 ± 0.5	T. Militão unpubl. data
Cory's shearwater	S13	4	13.9 ± 0.8	-16.4 ± 0.3	T. Militão unpubl. data
White-chinned petrel	Body feathers	8 - 10	17.6 ± 1.4	-15.5 ± 0.8	(Phillips et al. 2009)

P1-P7, showing higher isotopic variability, than within P10 feathers. Both isotopic signatures and variability of S13 and R6 showed similar values to those of P10. Compared with other petrel species moulting in the Brazil-Falklands Confluence, Atlantic petrels show lower values of δ^{15}N and δ^{13}C (Table 3).

4. DISCUSSION

Our study provides new insights into the spatial ecology of the Atlantic petrel. We report for the first time at-sea activity patterns, habitat preferences, moulting strategies, and carry-over effects over the entire annual cycle of this endangered species. Moreover, we extend previous knowledge about the timing of life-cycle events and migration schedules year-round by quantifying phenological variability that arose from presumed breeding success. We present new critical knowledge and refine previous data, providing an ensemble of relevant information for its conservation. However, the small sample size and the lack of immatures in the sample limit the general relevance of our findings.

The breeding phenology inferred in this study generally agrees with data reported in previous colony-based studies (Richardson 1984, Cuthbert 2004, Wanless et al. 2012, Dilley et al. 2015) (Table S4). However, our results highlight considerable within-population variability in phenological events. Multivariate hierarchical clustering based on phenological data allowed us to distinguish between early and late phenological groups. The group with advanced phenology dedicated, on average, about 88 days less to chick-rearing (Table 1), probably as a result of breeding failure. In recent years, a high proportion of chicks is killed by introduced house mice at Gough Island (Dilley et al. 2015). Thus, although breeding outcome was not monitored, the phenological variability found between groups likely is due to breeding success or failure. Both phenological groups differed in the starting date of post-breeding migration and the five subsequent phenological phases (Fig. 1, Table 1). The "early migrants" departed the breeding area between 7 August and 9 November (well before December, when chicks usually fledge (Cuthbert 2004)), indicating that birds showing this early post-breeding migration were likely failed breeders. The "late migrants" started their post-breeding migration in December or later, and therefore presumably, were successful breeders.

Interestingly, we found that breeding success influenced subsequent phenological phases of the species. Failed breeders not only departed to the non-breeding area earlier and stayed there longer than successful breeders, they also returned earlier to the colony at the onset of the next breeding period. These results demonstrate a carry-over effect on this species not only from the breeding to the non-breeding period, but also to the subsequent breeding period. It is likely that birds without breeding responsibilities that migrate earlier to the non-breeding grounds were able to moult and recover their body condition earlier than successful breeders, potentially improving their chances of breeding successfully in the subsequent breeding attempt (Kokko 1999). Nevertheless, despite the phenological differences between successful and failed breeders, all birds showed similar flyways and non-breeding areas, probably because of the relatively restricted and consistent non-breeding area for the entire species. This last result was also found in Cory's shearwater (*Calonectris borealis*), but their breeding success did not change their migratory schedule (Ramos et al. 2018). However, our findings contrast with previous studies also in Cory's shearwaters and Black-legged kittiwakes (*Rissa tridactyla*), where winter distribution depends on reproductive performance (Bogdanova et al. 2011, Catry et al. 2013). Among Northern gannets (*Morus bassanus*), foraging grounds also differed between failed and successful breeders (Votier et al. 2017). However, we are aware of the limitations of our sample size, and the need of an experimental design monitoring the breeding performance of every individual in order to be more conclusive on such carry-over effects (e.g. Harrison et al. 2011).

Our geolocation data confirmed that the Southwest Atlantic Ocean is the main distribution range for Atlantic petrels year-round (Ramos et al. 2017). The observed core range is more restricted to the west than traditionally considered (i.e. from east coast of South America to west coast of South Africa), but this might be a consequence of our modest sample size, and the fact that only unsexed adults were tracked in this study (Enticott 1991, Orgeira et al. 2013, Carboneras et al. 2017a). Adults were largely confined to oceanic waters of the central and western South Atlantic. The edge of the South American continental shelf, off northern Argentina, Uruguay and southern Brazil, was exploited during all phenological phases, although extension and location of core areas differed between periods (Fig. 2). In this region, the Brazil-Falklands Confluence, where warm waters from the Brazil Current mix with cold waters from the Falklands Current, creates a productive ecosystem that supports a complex community of top-predators, including many seabird species (Croxall & Wood 2002, Olmos 2002, Acha et al. 2004). Although the abundance of top-predators results in local competition, the high productivity likely explains why Atlantic petrels exploit this area. Avoidance of competition near Gough Island, where waters are less productive, and richer waters along the South American continental shelf may explain why birds commute around 3,500 km to a more distant and productive area far from the colony.

The proportion of time spent on water (both during day and night) was lower while breeding than during the non-breeding period (Fig. 3). This pattern is likely explained by moulting phenology. Although there is scant information on the timing of moult in Atlantic petrels, most petrels complete an annual primary feathers moult, starting immediately after the breeding season in order to avoid overlapping these metabolically demanding periods (breeding and moulting) (Bridge 2006). Moult typically commences with 2 - 4 inner primaries, but only 1 - 2 outer primaries are moulted at a time, because their moult has a greater impact on flight performance (Bugoni et al. 2014). The intense replacement of wing feathers during the non-breeding period (see below) decreases flight capability, forcing birds to spend more time on water (Cherel et al. 2016). The effect of moult on flight time was also observed in failed breeders that advanced both the post-breeding migration and the non-breeding period, and thus likely their moulting period (Fig. 3). Another possible contributing factor could be the move from central-place foraging while breeding (i.e. highly energy investment to meet the breeding demands) to a lower energy demand during the non-breeding period (Mackley et al. 2011, Cherel et al. 2016). To ensure breeding success, seabirds need to increase foraging effort (Lescroël et al. 2010), which likely means to perform both nocturnal and diurnal foraging to feed the chicks either more frequently or with a larger variety of prey. However during non-breeding period, compared to the breeding period, birds spent more time in flight at night (at least during periods of increased moonlight), when some species of cephalopods become more accessible near the surface due to their diel vertical migrations (DVM) (Imber 1973). As for other *Pterodroma* petrels, cephalopods are the main prey of Atlantic petrels, which may include dead or moribund squid floating at the surface during the day (Richardson 1984, Croxall & Prince 1994, Klages & Cooper 1997, Perez et al. 2019). Nocturnal activity was clearly influenced by moonlight over the non-breeding period, i.e. petrels spent more time flying with increasing levels of moonlight intensity (Fig. 4). Previous studies have found similar results in other gadfly petrel species and suggested that light intensity during full moon nights could facilitate foraging (e.g. Pinet et al. 2011b, Ramírez et al. 2013, Ramos et al. 2016). However, greater activity levels on well-lit nights may just result from DVM organisms remaining in deeper waters when moonlight is brighter, forcing Atlantic petrels to increase their search effort for prey (Benoit-Bird et al. 2009).

We observed a high individual variability in isotopic results on several primary feathers obtained from dead specimens (i.e., P1 - P7 feathers; Fig. 6, Table 3). This likely indicates that these feathers grew in different individual non-breeding grounds within the general non-breeding area (see Cherel et al. 2000, McMahon et al. 2013). By comparison, the low isotopic variability in P10, S13 and R6 among individuals possibly indicates these feathers were replaced in a common area for all birds, i.e. around the colony site after arrival from the non-breeding area between end of March and mid-April (Fig. 2). Elliot (1957) reported that birds arriving at Tristan da Cunha at the end of March were still in moult, as were birds carried inland in Brazil by hurricane Catarina in March 2004 (Bugoni et al. 2007). Although we cannot distinguish if the 8 dead specimens found at Gough Island were immature or adults, these results indicate similar phenological patterns in their migratory behaviour to those obtained through geolocator data. The isotopic gradient observed along P1 to P7 feathers could reflect a north-south gradient in isotopic baselines, with feathers with lower isotopic values moulted farther north, and those with higher isotopic values, moulted further south, in the Brazil-Falklands Confluence (Figs. 2A and 6). This north-south trend is consistent with prey isotopic data (see δ^{15}N in Table 4). However, the lack of a detailed zooplankton isoscapes for the non-breeding distribution prevented us from confirming this gradient at lower trophic levels (McMahon et al. 2013).

It is clear that the edge of the South American continental shelf is an important foraging area for Atlantic petrels year-round. Shelf slopes are important habitats for many squid species, which are caught by fishing fleets year-round along the outer shelf and upper slope off southern Brazil (Haimovici et al. 1998, Arkhipkin et al. 2015). However, we did not find an increase in isotopic values with increasing trophic levels when comparing results from flight feathers moulted in the Brazil-Falklands Confluence with those from cephalopod species sampled in the same area (e.g. Drago et al. 2015; see Table 4). This mismatch may arise from differential timing of sampling (i.e., different years and/or seasons within the same year) and from unspecified limitations of using literature isotopic data. Nevertheless, comparisons of δ^{15}N and δ^{13}C values of Atlantic petrel feathers with other shearwater species moulting in the Brazil-Falklands Confluence (e.g., Great shearwater and White-chinned petrel; Table 3) suggest a lower trophic level of the Atlantic petrel, which might reflect the limited use of fisheries discards by this species, and, thus, its lower risk of bycatch compared with other species (Barrett et al. 2007, Bugoni et al. 2008, Phillips et al. 2009, Bugoni et al. 2010).

Regarding the Atlantic petrel distribution, oceanic productivity may not be a good predic-

Table 4. δ^{15}N and δ^{13}C values (mean ± SD) of several cephalopod species (mantle muscle) in the Brazil Current and Brazil-Falklands Confluence.

Area	Prey	n	δ^{15}N (‰)	δ^{13}C (‰)	Source
Brazil Current	*Doryteuthis (Loligo) pealeii*	5	11.3 ± 0.5	-17.6 ± 0.2	(Drago et al. 2015)
	Illex argentinus	5	10.0 ± 0.5	-18.1 ± 0.2	(Drago et al. 2015)
	Loligo sanpaulensis	5	15.2 ± 0.3	-16.3 ± 0.1	(Drago et al. 2015)
	Ommastrephes bartrami / I. argentinus	8	9.3 ± 0.8	-16.7 ± 0.4	(Bugoni et al. 2010)
	All species		**11.4 ± 0.5**	**-17.2 ± 0.2**	
Brazil-Falklands Confluence	*I. argentinus*	5	14.7 ± 0.5	-17.5 ± 0.4	(Drago et al. 2015)
	I. argentinus	2	13.9 ± 0.7	-18.7 ± 0.2	(Franco-Trecu et al. 2012)
	L. sanpaulensis	5	18.6 ± 0.2	-16.7 ± 0.2	(Drago et al. 2015)
	L. sanpaulensis	2	13.7 ± 0.2	-17.9 ± 0.1	(Franco-Trecu et al. 2012)
	All species		**15.2 ± 0.4**	**-17.7 ± 0.2**	

tor of its distribution because the species relies on relatively oligotrophic waters for feeding year-round, being a truly oceanic species like most gadfly petrels (Ramos et al. 2016, Ramos et al. 2017). In general, year-round habitat suitability models based on several environmental predictors agree well with the observed species distribution (Fig. 5; Enticott 1991, Orgeira 2001, Carboneras et al. 2017a). However, during the non-breeding period, only one of the two suitable habitats, the shelf and slopes of the Brazil-Falklands Confluence, fitted well with the core range of Atlantic petrels (Fig. 5A). It is not known why Atlantic petrels are so rare in the Benguela Current region (Enticott 1991). Their distribution contrasts markedly with several other seabird species that use both areas during the non-breeding period, such as Scopoli's (*Calonectris diomedea*) and Cory's shearwaters (González-Solís et al. 2007). During the pre-laying exodus, two suitable habitats were identified, one in northern Argentina and Falkland Islands, and another south of Africa (Fig. 5B), which again was not used by any tracked birds, and is an area with few observations at sea (Enticott 1991). During incubation and chick-rearing, an apparently suitable area in the south eastern Atlantic also was not highly used by tracked birds (Figs. 5C and D), but they do occur in reasonable numbers south of Africa (38-42ºS) in November, towards the end of the chick-rearing period (P.G. Ryan pers. obs.). Apart from the small sample size, one possible explanation for these differences could be the competitive exclusion or the "ghost of past" competition with other gadfly petrels in the region (Connell 1980). The Great-winged petrel (*Pterodroma macroptera*), which shows a similar phenology and diet, is abundant off southern Africa and largely absent from the southwest Atlantic (Ridoux 1994, Brooke 2004, BirdLife International 2017a, Carboneras et al. 2017b). It breeds abundantly at islands in the Southwest Indian Ocean, and used to be common at Tristan and Gough, but has become rare in recent years due to hunting (at Tristan) and introduced predators (at both islands) (BirdLife International 2017a, Ramos et al. 2017). The smaller Soft-plumaged petrel (*Pterodroma mollis*) remains abundant at Gough and the uninhabited Tristan islands, as well as at islands in the Southwest Indian Ocean, and is the most common gadfly petrel in the southeast Atlantic, but performs the opposite phenology to the Atlantic petrel (BirdLife International 2017a, Ramos et al. 2017). In addition, the distribution and abundance of squids is poorly known in austral oceans, but commercial squid fisheries are more abundant along the South American shelf and shelf slopes than off South Africa (FAO Marine Resources Service 2005). This fact could indicate a higher abundance of the main prey for gadfly petrels off South America, where Atlantic petrels overlap with other gadfly petrels, such as the Desertas petrel (*Pterodroma deserta*; BirdLife International 2017a, Ramos et al. 2017). This area is important for fishing fleets, and the high fishing intensity may decrease prey abundance for Atlantic petrels and other seabirds (Furness 2003, Bugoni et al. 2008). It also supports large numbers of vessels with their inherent potential threats (as mortality, but also sub-lethal effects) to seabirds and marine life (Finkelstein et al. 2006, Lewison et al. 2012, Krüger et al. 2017, Rodríguez et al. 2017). Since this is the area where all tracked birds spent their non-breeding period, and as Gough Island is virtually the only breeding location for this species, a good conservation strategy for both areas is essential to ensure sustainability of the Atlantic petrel. Indeed, one Ecologically or Biologically Significant Area (EBSA) and several Important Bird Areas (IBAs) overlap with the species' non-breeding distribution. For the breeding location, one Marine Protected Area (MPA) is designated and several IBAs and MPA are proposed around Tristan da Cunha Island and Gough Island (which is part of an UNESCO World Heritage Site and also Wetlands of International Importance under the Ramsar Convention), which should help to conserve the species (BirdLife International 2017c, Convention on Biological Diversity 2017, Dias et al. 2017, Marine Conservation Institute 2017, UNESCO 2019).

5. CONCLUSIONS

In this study, we describe important aspects of the spatio-temporal ecology of Atlantic petrels. The non-breeding period of successful breeders lasted from the end of December to mid-April. Habitat preferences highlighted the South American continental shelf as an extremely important area for the species. We relate activity patterns with breeding constraints, foraging behaviour and, together with stable isotope analysis (SIA), provide new insights into the timing of wing moult. We also provide evidence of carry-over effects between consecutive breeding attempts. However, further studies tracking larger numbers of birds of different sexes and ages and monitoring their breeding performance at the colony, would provide more reliable understanding of ecological factors that determine the at-sea distribution and behaviour of this endangered seabird.

ACKNOWLEDGEMENTS

The Ministerio de Educación y Ciencia and Ministerio de Ciencia e Innovación from the Spanish Government (Projects CGL2006-01315/BOS, CGL2013-42585-P, CGL2009-11278/BOS) financially supported this study. Logistical support and financial funding during field work was provided by the South African Department of Environmental Affairs and the National Research Foundation, through the South African National Antarctic Programme, with additional support from the Royal Society for the Protection of Birds. RR, ZZ and JMR-G were supported by Spanish MINECO (Juan de la Cierva postdoctoral programme, JCI-2012-11848), Universitat de Barcelona (UB, APIF/2012) and Spanish MECD (FPU, AP2009-2163), respectively. Permission to conduct research at Gough Island was granted by the Administrator and Island Council of Tristan da Cunha, through Tristan's Conservation Department. We thank R. Ronconi for his help during field work, and the many field assistants who deployed and recovered tags at Gough Island. We thank three anonymous referees for their comments to improve an earlier version of this manuscript.

AUTHOR CONTRIBUTIONS

The study was conceptualized by RR, ZZ, JMR-G and JG-S. Data were collected by PGR and JG-S. Geolocator and isotope raw data were analysed by MP-P and MLR, respectively. Posterior data analysis were carried out by MP-P, RR, ZZ and JMR-G. The manuscript was drafted by MP-P with review and editorial contributions by RR, ZZ, JMR-G, PGR and JG-S. JG-S obtained the funding. All authors read and approved the final manuscript.

LITERATURE CITED

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. J Mar Syst 44: 83-105

Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. Memoirs of NIPR 58: 227-233

Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, Allcock L, Arguelles J, Bower JR, Castillo G, Ceriola L, Chen C-S, Chen X, Diaz-Santana M, Downey N, González AF, Amores JG, Green CP, Guerra A, Hendrickson LC, Ibáñez C, Ito K, Jereb P, Kato Y, Katugin ON, Kawano M, Kidokoro H, Kulik VV, Laptikhovsky VV, Lipinski MR, Liu B, Mariátegui L, Marin W, Medina A, Miki K, Miyahara K, Moltschaniwskyj N, Moustahfid H, Nabhitabhata J, Nanjo N, Nigmatullin CM, Ohtani T, Pecl G, Perez JAA, Piatkowski U, Saikliang P, Salinas-Zavala CA, Steer M, Tian Y, Ueta Y, Vijai D, Wakabayashi T, Yamaguchi T, Yamashiro C, Yamashita N, Zeidberg LD (2015) World Squid Fisheries. Rev Fish Sci Aquacult 23: 92-252

Barrett RT, Camphuysen KCJ, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: a review and recommendations. J Mar Sci, 64: 1675-1691

Benoit-Bird JK, Au WW, Wisdom DW (2009) Nocturnal light and lunar cycle effects on diel migration of micronekton. Limnol Oceanogr 54: 1789-1800

BirdLife International (2017a) IUCN Red List for birds. www.birdlife.org (accessed 09 Sep 2017)

BirdLife International (2017b) Seabird Tracking Database. Tracking Ocean Wanderers. http://seabirdtracking.org/mapper/?dataset_id=966 (accessed 21 Oct 2018).

BirdLife International (2017c) Marine IBA e-atlas: delivering site networks for seabird conservation. https://maps.birdlife.org/marineIBAs/default.html (accessed 4 Jun 2017)

Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. Proc R Soc B 278: 2412-2418

Bridge ES (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. Mar Ornithol 34: 7-19

Bried J, Pontier D, Jouventin P (2003) Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. Anim Behav 65: 235-246

Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

Bugoni L, Sander M, Costa ES (2007) Effects of the First Southern Atlantic Hurricane on Atlantic Petrels (*Pterodroma incerta*). Wilson J Ornithol 119: 725-729

Bugoni L, Mancini PL, Monteiro DS, Nascimento L, Neves TS (2008) Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the southwestern Atlantic Ocean. Endang Species Res 5: 137-147

Bugoni L, D'Alba L, Furness R (2009) Marine habitat use of wintering spectacled petrels *Procellaria conspicillata*, and overlap with longline fishery. Mar Ecol Prog Ser 374: 273-285

Bugoni L, McGill RAR, Furness RW (2010) The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. J Exp Mar Biol Ecol 391: 190-200

Bugoni L, Naves LC, Furness RW (2014) Moult of three Tristan da Cunha seabird species sampled at sea. Antarct Sci 27: 240-251

Calenge C (2011) Home range estimation in R: the adehabitatHR package. Office national de la classe et de la faune sauvage, Saint Benoist, Auffargis, France

Caravaggi A, Cuthbert RJ, Ryan PG, Cooper J, Bond AL (2019) The impacts of introduced House Mice on the breeding success of nesting seabirds on Gough Island. Ibis 161: 648-661.

Carboneras C, Jutglar F, Kirwan GM (2017a) Atlantic Petrel (*Pterodroma incerta*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (https://www.hbw.com/node/52525 accessed 24 Nov 2017)

Carboneras C, Jutglar F, Kirwan GM (2017b) Great-winged Petrel (*Pterodroma macroptera*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (www.hbw.com/node/52519 accessed 23 Dec 2017)

Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. Ecology 94: 1230-1235

Cherel Y, Hobson KA, Weimerskirch H (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122: 155-162.

Cherel Y, Quillfeldt P, Delord K, Weimerskirch H (2016) Combination of At-Sea Activity, Geolocation and Feather Stable Isotopes

Documents Where and When Seabirds Molt. Front Ecol Evol 4: 3 doi: 10.3389/fevo.2016.00003

Clay TA, Phillips RA, Manica A, Jackson HA, Brooke MDL (2017) Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. Mar Ecol Prog Ser 579: 139-155

Connell J (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138

Convention on Biological Diversity (2017) Ecologically or Biologically Significant Areas (EBSAs), Southern Brazilian Sea. www.cbd.int/ebsa/ (accessed 4 Jun 2017)

Croxall, JP, Prince PA (1994) Dead or alive, night or day: how do albatrosses catch squid? Antarct Sci 6: 155-162.

Croxall JP, Wood AG (2002) The importance of the Patagonian Shelf for top predator species breeding at South Georgia. Aquatic Conserv: Mar Freshw Ecosyst 12: 101-118

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22: 1-34

Cuthbert RJ (2004) Breeding biology of the Atlantic Petrel, *Pterodroma incerta*, and a population estimate of this and other burrowing petrels on Gough Island, South Atlantic Ocean. Emu 104: 221-228

Cuthbert RJ, Louw H, Lurling J, Parker G, Rexer-Huber K, Sommer E, Visser P, Ryan PG (2013) Low burrow occupancy and breeding success of burrowing petrels at Gough Island: a consequence of mouse predation. Bird Conserv Int 23: 113-124

Dias M, Granadeiro J, Catry P (2012) Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. Mar Ecol Prog Ser 467: 245-252

Dias MP, Oppel S, Bond AL, Carneiro APB, Cuthbert RJ, González-Solís J, Wanless RM, Glass T, Lascelles B, Small C, Phillips RA, Ryan PG (2017) Using globally threatened pelagic birds to identify priority sites for marine conservation in the South Atlantic Ocean. Biol Conserv 211: 76-84

Dilley B, Davies D, Bond AL, Ryan PG (2015) Effects of mouse predation on burrowing petrel chicks at Gough Island. Antarct Sci 27: 543-553

Drago M, Franco-Trecu V, Zenteno L, Szteren D, Crespo EA, Riet Sapriza FG, de Oliveira L, Machado R, Inchausti P, Cardona L (2015) Sexual foraging segregation in South American sea lions increases during the pre-breeding period in the Río de la Plata plume. Mar Ecol Prog Ser 525: 261-272

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17: 43-57

Elliott HFI (1957) A contribution to the ornithology of the Tristan da Cunha Group. Ibis 99: 545-586

Enticott JW (1991) Distribution of the Atlantic Petrel *Pterodroma incerta* at sea. Mar Ornithol 19: 49-60

FAO Marine Resources Service, Fishery Resources Division (2005) Review of the state of world marine fishery resources. In: FAO Fisheries Technical Paper, No. 457. FAO, Rome

Flood B, Fisher A (2013) Multimedia Identification Guide to North Atlantic Seabirds *Pterodroma* Petrels. Scilly Pelagics, Essex

Finkelstein M, Keitt BS, Croll DA, Tershy B, Jarman WM, Rodriguez-Pastor S, Anderson DJ, Sievert PR, Smith DR (2006) Albatross species demonstrate regional differences in North Pacific marine contamination. Ecol Appl 16: 678-686

Franco-Trecu V, Aurioles-Gamboa D, Arim M, Lima M (2012) Prepartum and postpartum trophic segregation between sympatrically breeding female *Arctocephalus australis* and *Otaria flavescens*. J Mammal 93: 514-521

Furness R (2003) Impacts of fisheries on seabird communities. Sci Mar 67: 33-45

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 6: 297-301

González-Solís J, Shaffer SA (2009) Introduction and synthesis: spatial ecology of seabirds at sea. Mar Ecol Prog Ser 391: 117-120

Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. Mar Ecol Prog Ser 391: 121-137

Haimovici M, Brunetti NE, Rodhouse PG, Csirke J, Leta RH (1998) *Illex argentinus*. In: Rodhouse PG, Dawe EG, O'Dor RK (eds) Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fisheries Technical Paper. No. 376. Rome, p 27-58

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. J Anim Ecol 80: 4-18

Hilton GM, Cuthbert RJ (2010) Review article: The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. Ibis 152: 443-458

Hill RD (1994) Theory of geolocation by light levels. Elephant Seals: Population Ecology, Behavior, and Physiology. In: Boeuf L, Burney J, Laws RM (eds) University of California Press, Berkeley

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63: 786-798

Igual JM, Forero MG, Tavecchia G, González-Solis J, Martínez-Abraín A, Hobson KA, Ruiz X, Oro D (2005) Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). Mar Biol 146: 619-624.

Imber MJ (1973) The Food of Grey-Faced Petrels (*Pterodroma macroptera gouldi* (Hutton)), with Special Reference to Diurnal Vertical Migration of their Prey. J Anim Ecol 42: 645-662

Jacoby WG (2000) Loess: a nonparametric, graphical tool for depicting relationships between variables. Elect Stud 19: 577-613

Jodice PG, Ronconi RA, Rupp E, Wallace GE, Satgé Y (2015) First satellite tracks of the Endangered black-capped petrel. Endang Species Res 29: 23-33

Klages NTW, Cooper J (1997) Diet of the Atlantic Petrel *Pterodroma incerta* during breeding at South Atlantic Gough Island. Mar Ornithol 25: 13-16

Kokko H (1999) Competition for early arrival in migratory birds. J Anim Ecol 68: 940-950

Krüger L, Paiva VH, Colabuono FI, Petry MV, Montone RC, Ramos JA (2016) Year-round spatial movements and trophic ecology of Trindade Petrels (*Pterodroma arminjoniana*). J Field Ornithol 87: 404-416

Krüger L, Ramos JA, Xavier JC, Grémillet D, González-Solís J, Kolbeinsson Y, Militão T, Navarro J, Petry MV, Phillips RA, Ramírez I, Reyes-González JM, Ryan PG, Sigurðsson IA, Van Sebille E, Wanless R, Paiva VH (2017) Identification of candidate pelagic marine protected areas through a seabird seasonal, multispecific and extinction risk-based approach. Anim Conserv 20: 409-424

Leal GR, Furness RW, McGill RA, Santos RA, Bugoni L (2017) Feeding and foraging ecology of Trindade petrels *Pterodroma arminjoniana* during the breeding period in the South Atlantic Ocean. Mar Biol 164: 211 doi: 10.1007/s00227-017-3240-8

Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG (2010) Working less to gain more: when breeding quality relates to foraging efficiency. Ecology 91: 2044-2055

Lewison R, Oro D, Godley B, Underhill L, Bearhop S, Wilson R, Ainley D, Arcos JM, Boersma PD, Borboroglu PG, Boulinier T, Frederiksen M, Genovart M, González-Solís J, Green JA, Grémillet D, Hamer KC, Hilton GM, Hyrenbach KD, Martínez-Abraín A, Montevecchi WA, Phillips RA, Ryan PG, Sagar P, Sydeman WJ, Wanless S, Watanuki Y, Weimerskirch H, Yorio P (2012) Research priorities for seabirds: Improving seabird conservation and management in the 21st century. Endang Species Res 17: 93-121

Lucas Z, MacGregor D (2006) Characterization and source of oil contamination on the beaches and seabird corpses, Sable Island, Nova Scotia, 1996–2005. Mar Pollut Bull 52: 778-789

Marine Conservation Institute (2017) MPAtlas. www.mpatlas.org (accessed 4 Jun 2017)

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58: 697-714

Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Furness RW (2011) At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia. Mar Biol 158: 429-438

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2017) Cluster: Cluster Analysis Basics and Extensions. R package version 2.0.6

Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological Segregation in Space, Time and Trophic Niche of Sympatric Planktivorous Petrels, PLoS One. 8: e62897. doi: 10.1371/journal.pone.0062897.

Norris DR, Marra PP (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. Condor 109: 535-547

Olmos F (2002) Non-breeding seabirds in Brazil: a review of band recoveries. Ararajuba - Braz J Ornithol 10: 31-42

Olmos F, Bugoni L, Neves T, Peppes F (2006) Caracterização das aves oceânicas que interagem com a pesca de espinhel no Brasil. In: Neves T, Bugoni L, Rossi-Wongtschowski CLB (eds.) Aves oceânicas e suas interações com a pesca na Região Sudeste-Sul do Brasil. Instituto Oceanográfico - USP, São Paulo, p 37–67

Ojowski U, Editmann C, Furness R, Garthe S (2001) Diet and nest attendance of incubating and chick-rearing northern fulmars (*Fulmarus glacialis*) in Shetland. Mar Biol 139:1193-1200

Orgeira JL (2001) Nuevos registros del Petrel Atlántico (*Pterodroma incerta*) en el océano Atlántico Sur y Antártida. Ornitol Neotrop 12: 165-171

Orgeira JL, Scioscia G, Torres MA, Dellabianca NA (2013) New at-sea records of pelagic seabirds in the South Atlantic Ocean and Antarctica. Polar Res 32: 18972

Passos C, Navarro J, Giudici A, González-Solís J (2010) Effects of extra mass on the pelagic behavior of a seabird. Auk 127: 100-107

Perez MS, Daudt NW, Tavares M, Ott PH, Santos RA, Fontana CS (2019) Diet of the Atlantic Petrel *Pterodroma incerta* during the non-breeding season. Mar Ornithol 47: 43-47

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk. 120: 1082–1090

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266: 265-272

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. Ecol Modell 190: 231-259

Phillips RA, Bearhop S, Mcgill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecol 160: 795-806

Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Mar Ecol Prog Ser 578: 117-150

Philpot SM, Lavers JL, Nugegoda D, Gilmour ME, Hutton I, Bond AL (2019) Trace element concentrations in feathers of seven petrels (*Pterodroma spp.*). Environ Sci Pollut Res 26: 9640-9648.

Pinet P, Jaquemet S, Pinaud D, Weimerskirch H, Phillips RA, Le Corre M (2011a) Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. Mar Ecol Prog Ser 423: 291-302

Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011b) Celestial Moderation of Tropical Seabird Behavior. PLoS One 6: e27663. doi: 10.1371/journal.pone.0027663

Quillfeldt P, Masello JF, Navarro J, Phillips RA (2013) Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. J Biogeogr 40:430-441

R Core Team (2017) R: A language and environment for statistical computing. Version 3.4.1. R Foundation for Statistical Computing, Vienna, www.R-project.org

R Core Team (2019) R: A language and environment for statistical computing. Version 3.6.0. R Foundation for Statistical Computing, Vienna, www.R-project.org

Ramírez I, Paiva VH, Menezes D, Silva I, Phillips RA, Ramos JA, Garthe S (2013) Year-round distribution and habitat preferences of the Bugio petrel. Mar Ecol Prog Ser 476: 269-284

Ramos R, González-Solís J, Ruiz X (2009) Linking isotopic and migratory patterns in a pelagic seabird. Oecol 160: 97-105

Ramos R, Sanz V, Militão T, Bried J, Neves VC, Biscoito M, Phillips RA, Zino F, González-Solís J (2015) Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). J. Biogeogr 42: 1651-1664.

Ramos R, Ramírez I, Paiva VH, Militão T, Biscoito M, Menezes D, Phillips RA, Zino F, González-Solís J (2016) Global spatial ecology of three closely-related gadfly petrels. Sci Rep 6: 23447

Ramos R, Carlile N, Madeiros J, Ramírez I, Paiva VH, Dinis H, Zino F, Biscoito M, Leal GR, Bugoni L, Jodice PGR, Ryan PG, González-Solís J (2017) It is the time for oceanic seabirds: Tracking year-round distribution of gadfly petrels across the Atlantic Ocean. Divers Distrib 23: 794-805

Ramos R, Llabrés V, Monclús L, López-Béjar M, González-Solís J (2018) Costs of breeding are rapidly buffered and do not affect migratory behavior in a long-lived bird species. Ecology 99: 2010-2024

Rayner MJ, Hauber M, Clout M, Seldon D, Van Dijken S, Bury S, Phillips R (2008) Foraging ecology of the Cook's petrel *Pterodroma cookii* during the austral breeding season: A comparison of its two populations. Mar Ecol Prog Ser 370: 271-284

Rayner MJ, Taylor GA, Gummer HD, Phillips RA, Sagar PM, Shaffer SA, Thompson DR (2012) The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). Emu 112: 107-116

Rexer-Huber K, Parker GC, Ryan PG, Cuthbert RJ (2014) Burrow occupancy and population size in the Atlantic Petrel *Pterodroma incerta*: a comparison of methods. Mar Ornithol 42: 137-141

Richardson ME (1984) Aspects of the ornithology of the Tristan da Cunha group and Gough Island 1972-1974. Cormorant 12: 123-201

Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22: 1-192

Rodríguez A, Holmes ND, Ryan PG, Wilson K, Faulquier L, Murillo Y, Raine AF, Penniman, JF, Neves V, Rodríguez B, Negro JJ, Chiaradia A, Dann P, Anderson T, Metzger B, Shirai M, Deppe L, Wheeler J, Hodum P, Gouveia C, Carmo V, Carreira GP, Delgado-Alburqueque L, Guerra-Correa C, Couzi F, Travers M, Le Corre M (2017), Seabird mortality induced by land-based artificial lights. Conserv Biol 31: 986-1001

Rodríguez A, Arcos JM, Bretagnolle V, Dias MP, Holmes ND, Louzao M, Provencher J, Raine AF, Ramírez F, Rodríguez B, Ronconi RA, Taylor RS, Bonnaud E, Borrelle SB, Cortés V, Descamps S, Friesen VL, Genovart M, Hedd A, Hodum P, Humphries GRW, Le Corre M, Lebarbenchon C, Martin R, Melvin EF, Montevecchi WA, Pinet P, Pollet IL, Ramos R, Russell JC, Ryan PG, Sanz-Aguilar A, Spatz DR, Travers M, Votier SC, Wanless RM, Woehler E, Chiaradia A (2019) Future Directions in Conservation Research on Petrels and Shearwaters. Front Mar Sci 6: 94 doi: 10.3389/fmars.2019.00094

Rousseeuw PJ (1987) Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. J Comput Appl Math 20: 53-65

Simons R. (2017) ERDDAP, Monterey, CA: NOAA/NMFS/SWFSC/ERD. https://coastwatch.pfeg.noaa.gov/erddap/index.html (accessed 15 Sep 2017).

Uhart MM, Gallo L, Quintana F (2018) Review of diseases (pathogen isolation, direct recovery and antibodies) in albatrosses and large petrels worldwide. Bird Conserv Int 28: 169-196

UNESCO (2019) World Heritage List. Gough and Inaccessible Islands. https://whc.unesco.org/en/list/740 (accessed 28 Jul 2019).

Votier SC, Fayet AL, Bearhop S, Bodey TW, Clark BL, Grecian J, Guilford T, Hamer KC, Jeglinski JWE, Morgan G, Wakefield E, Patrick SC (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proc R Soc B 284: 20171068. doi:10.1098/rspb.2017.1068

Wanless RM, Angel A, Cuthbert RJ, Hilton GM, Ryan PG (2007) Can predation by invasive mice drive seabird extinctions? Biol Lett 3: 214-244

Wanless RM, Ratcliffe N, Angel A, Bowie BC, Cita K, Hilton GM, Kritzinger P, Ryan PG, Slabber M (2012) Predation of Atlantic Petrel chicks by house mice on Gough Island. Anim Conserv 15: 472-479

Warham J (1996) The Behaviour, Population Biology and Physiology of the Petrels. Academic Press, London

Wood SN, Augustin NH (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol Modell 157: 157-177

Yamamoto T, Takahashi A, Yoda K, Katsumata N, Watanabe S, Sato K, Trathan PN (2008) The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked shearwater, *Calonectris leucomelas*, Anim Behav 76: 1647-1652

Supplementary material

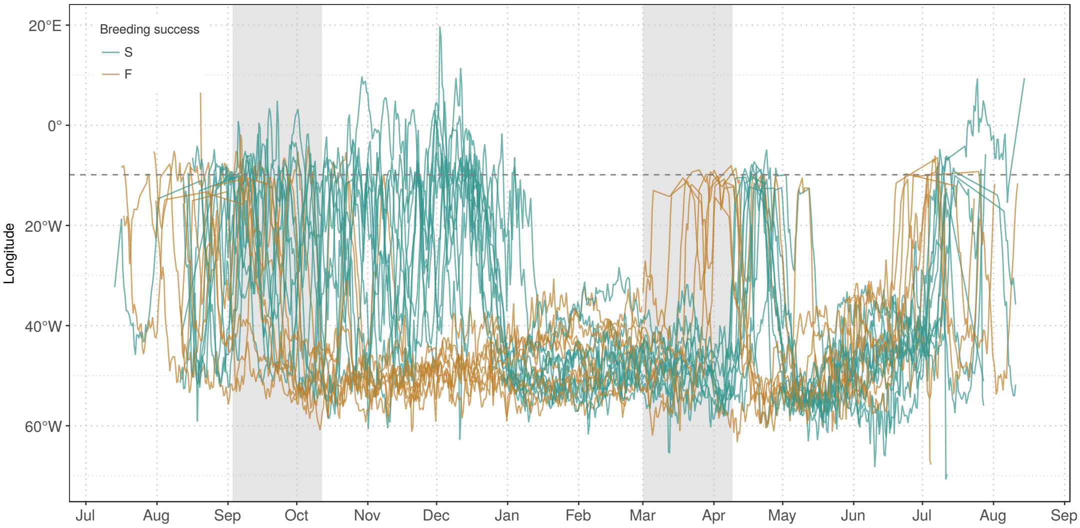


Figure S1: Changes in longitude (unfiltered locations) of Atlantic petrels throughout the year. Each line represents a different year-round trip, from a breeding episode to the next one (i.e. from July to August next year). Two phenological groups appeared to exist in the data, which led us to carry out a hierarchical clustering to statistically validate the existence of different groups (see Methods for more details). Colours correspond to two clusters obtained after applying the hierarchical clustering (successful breeders in blue; failed breeders in brown; see discussion). Grey shaded regions represent the equinoxes ± 20 days

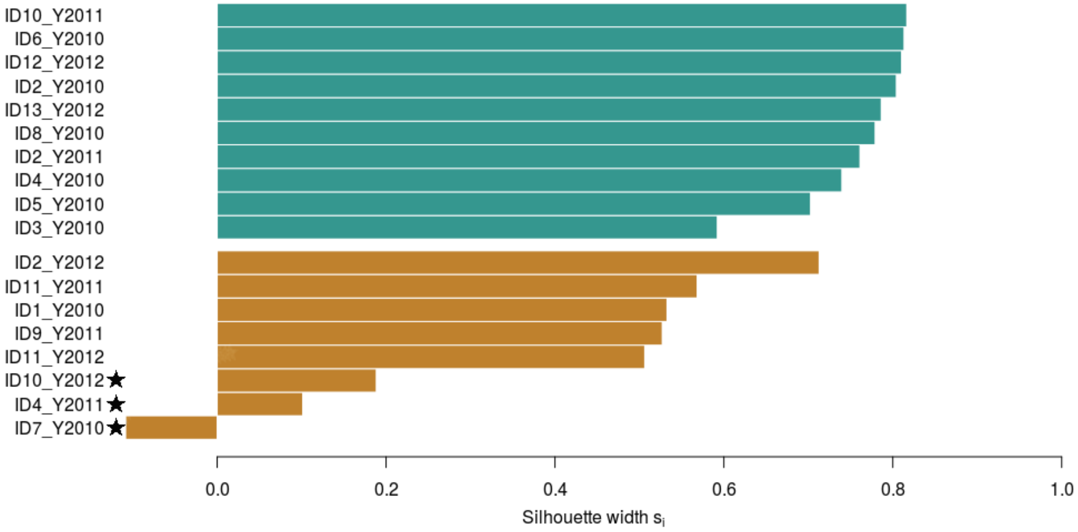


Figure S2: Silhouette analysis of hierarchical clustering performed on seven phenological variables. Hierarchical clustering analysis and phenological variables are detailed in Fig. 1. The mean silhouette width of successful breeders (Group 1, 10 birds, in blue) is 0.76. Failed breeders (Group 2, 8 birds, in light brown) have a mean silhouette width of 0.38. Mean silhouette width is 0.59 (dashed grey line). 3 individuals with low (< 0.25) silhouette widths in the failed cluster (marked with star) may indicate potentially incorrect classification. However, the individual phenology detailed in Fig. S3 shows that although these individuals performed later post-breeding migrations than most other failed breeders (and this could cause low (< 0.25) silhouette widths), their chick-rearing period was far too short for raising a chick to fledging. Each bar corresponds to a year-round trip (n = 18) identified by track ID (birdID_year) and ordered by silhouette width within each group

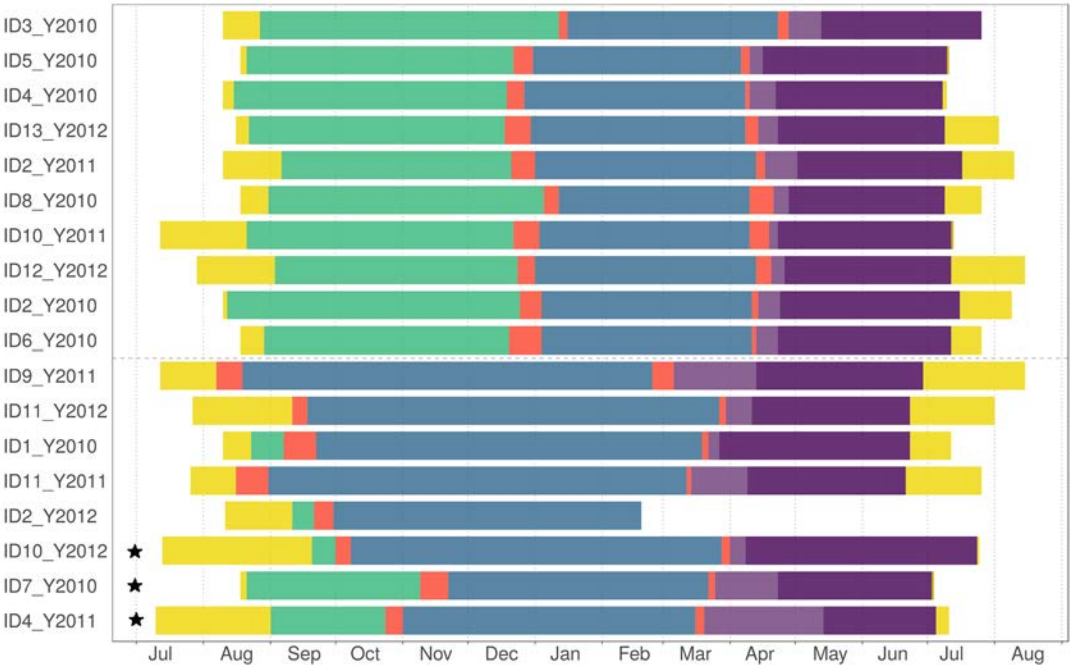


Figure S3: Individual phenologies of adult Atlantic petrels. Each bar corresponds to a year-round trip and shows phenological dates of: incubation (yellow), chick-rearing (green), post-breeding migration (red), non-breeding (blue), pre-breeding migration (red), pre-breeding (time from arrival at breeding grounds to pre-laying exodus; light purple) and pre-laying exodus (dark purple). Individual tracks (birdID_year, on the left) are in the same order as in the results of hierarchical clustering in Fig 1A. Stars indicate those individuals with low (< 0.25) silhouette widths. Dashed horizontal line separates birds classified as successful breeders (above) and those classified as failed breeders (below)

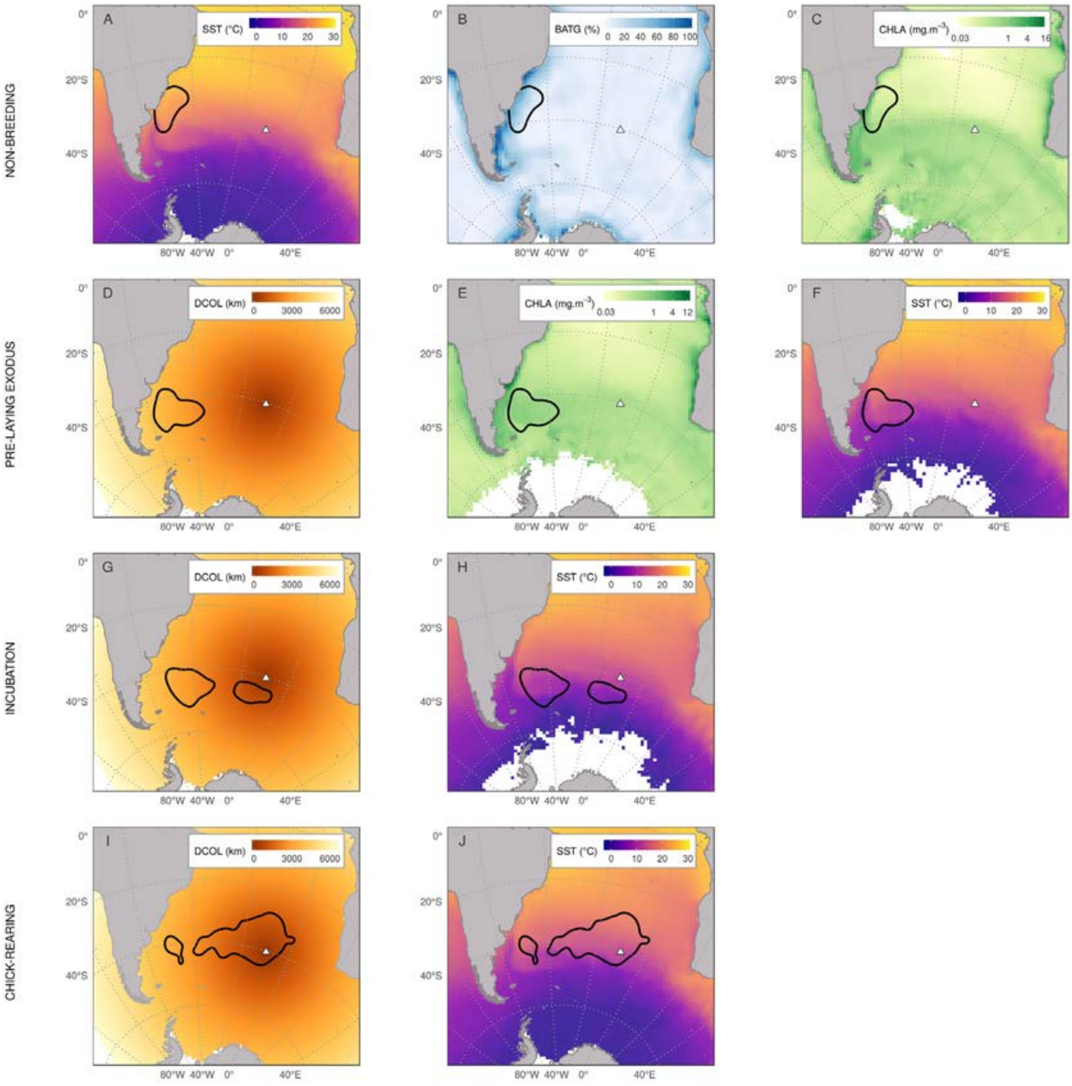


Figure S4: Important environmental variables for Atlantic petrel distribution during each phenological phase. Resulting from habitat modelling developed through MaxEnt (by percent contribution; see Table 2 for details), the environmental variables are ordered by importance and contribution to Atlantic petrel distribution (more important variables on left): gradient of seafloor depth (BATG, %), surface chlorophyll a concentration (CHLA, mg m^{-3}, as a proxy of biological production), distance to the colony (DCOL, km) and sea surface temperature (SST, ºC). 50 % kernel UD (areas of active use) of each phenological phase are represented over their important environmental variables (A-J). Triangle represents the breeding colony at Gough Island

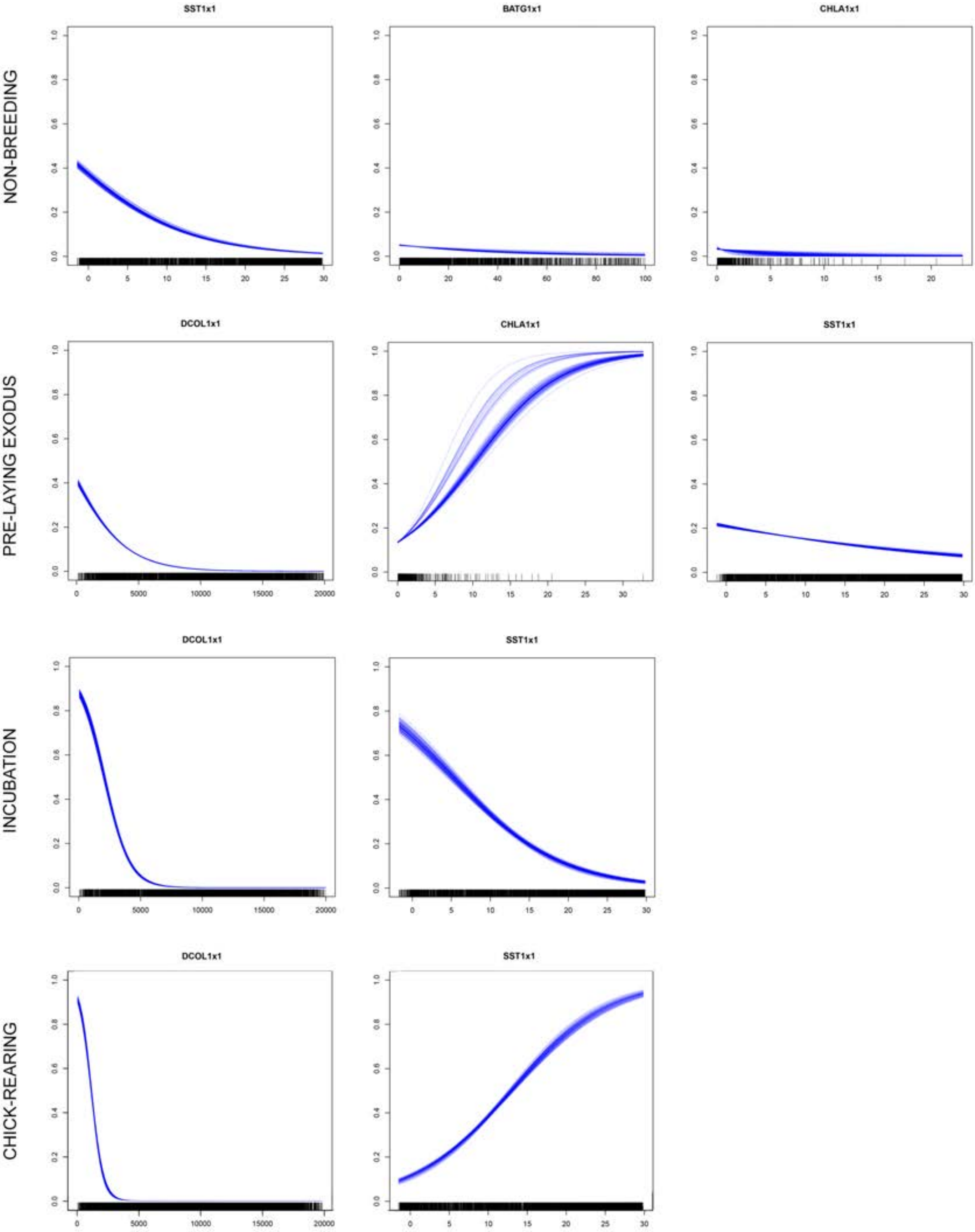


Figure S5: Response curves of most important environmental variables for Atlantic petrel distribution at each phenological phase. Probability of occurrence of Atlantic petrel (y-axis) in response to the environmental variables (x-axis), resulting from habitat modelling developed through MaxEnt. The environmental variables are: gradient of seafloor depth (BATG, %), surface chlorophyll a concentration (CHLA, mg m^{-3}, as a proxy of biological production), distance to the colony (DCOL, km) and sea surface temperature (SST, ºC)

Table S1: Pearson correlations for the environmental variables at each phenological phase. The seven environmental variables were selected at the beginning of the modelling. Note that distance to the colony (DCOL) was not selected as important during the non-breeding period. Values in bold indicate significant correlations

A Pre-laying exodus

	BAT	BATG	CHLA	DCOL	SAL	SST	WIND
BAT	1.000	**0.813**	0.404	0.121	-0.184	-0.270	-0.220
BATG		1.000	0.361	0.119	-0.190	-0.151	-0.239
CHLA			1.000	0.098	-0.120	-0.156	-0.075
DCOL				1.000	-0.207	-0.026	-0.509
SAL					1.000	0.417	-0.147
SST						1.000	-0.487
WIND							1.000

B Incubation

	BAT	BATG	CHLA	DCOL	SAL	SST	WIND
BAT	1.000	**0.813**	0.396	0.121	-0.322	-0.256	-0.290
BATG		1.000	0.356	0.119	-0.303	-0.114	-0.306
CHLA			1.000	0.104	-0.260	-0.104	-0.148
DCOL				1.000	-0.321	0.053	-0.591
SAL					1.000	0.437	0.200
SST						1.000	-0.359
WIND							1.000

C Chick-rearing

	BAT	BATG	CHLA	DCOL	SAL	SST	WIND
BAT	1.000	**0.813**	0.415	0.121	-0.350	-0.281	-0.216
BATG		1.000	0.380	0.119	-0.333	-0.176	-0.207
CHLA			1.000	0.110	-0.262	-0.152	-0.046
DCOL				1.000	-0.364	0.162	-0.257
SAL					1.000	0.389	0.094
SST						1.000	-0.456
WIND							1.000

D Non-breeding

	BAT	BATG	CHLA	SAL	SST	WIND
BAT	1.000	**0.813**	0.380	-0.216	-0.254	-0.087
BATG		1.000	0.368	-0.206	-0.213	-0.070
CHLA			1.000	-0.152	-0.170	0.018
SAL				1.000	0.473	-0.235
SST					1.000	-0.673
WIND						1.000

Table S2: Year-round at-sea activity of adult Atlantic petrels. Time spent on water (mean ± SD) during the day and night, for each phenological period, and for successful and failed breeders.

Phenological phase	n (days)		Time spent on water (% of time)			
			Day		Night	
	Succ.	Fail.	Successful	Failed	Successful	Failed
Pre-laying exodus	528	285	19.7 ± 17.0	16.4 ± 14.5	30.0 ± 17.8	23.7 ± 16.9
Incubation	62	117	13.9 ± 14.6	10.2 ± 7.9	19.6 ± 12.0	12.5 ± 9.3
Chick-rearing	536	45	11.5 ± 11.5	8.9 ± 7.5	16.7 ± 13.8	17.7 ± 14.9
Non-breeding	385	739	72.7 ± 15.9	62.6 ± 23.6	60.4 ± 22.5	53.4 ± 29.2

Table S3: Stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) of sampled feathers for each Atlantic petrel. When possible, same feathers were sampled from 8 dead Atlantic petrel individuals found at Gough Island in September 2009. These feathers were 1st, 3rd, 5th, 7th and 10th primary feathers (P1, P3, P5, P7 and P10), 13th secondary (S13) and 6th rectrix (R6). [a] Outlier not included in stable isotope mean values

ID_Sample	Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
746	P1	15.41	-17.46
746	P3	15.16	-18.00
746	P5	14.96	-18.12
746	P7	15.40	-17.85
746	P10	14.21	-17.08
746	S13	14.17	-17.52
746	R6	14.03	-16.94
747	P1	13.63	-17.62
747	P3	13.72	-17.44
747	P5	14.15	-17.51
747	P7	14.52	-17.18
747	P10	13.92	-16.76
747	S13	14.05	-16.66
748	P1	13.62	-19.32
748	P3	13.62	-17.22
748	P5	13.10	-18.21
748	P7	13.40	-18.49
748	P10	14.37	-17.02
748	S13	14.21	-16.85
748	R6	14.06	-16.85
749	P1	15.46	-19.23
749	P3	15.54	-18.89
749	P5	15.35	-18.85
749	P7	14.99	-17.93
749	P10	14.64	-17.80
749	S13	14.88	-17.25
749	R6	14.50	-17.86

ID_Sample	Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
750	P1	14.76	-17.98
750	P3	14.88	-17.69
750	P5	14.86	-17.64
750	P7	14.51	-17.88
750	P10	14.50	-16.84
750	S13	14.59	-16.74
750	R6	14.48	-16.70
751	P1	14.40	-17.56
751	P3	14.27	-17.70
751	P5	14.07	-17.33
751	P7	14.30	-17.69
751	P10	14.27	-17.00
751	S13[a]	14.05	-19.47
752	P1	13.82	-16.94
752	P3	13.73	-16.20
752	P5	14.26	-16.59
752	P7	13.97	-16.61
752	P10	14.08	-16.54
752	S13	14.10	-16.06
752	R6	13.99	-16.84
753	P1	14.02	-16.51
753	P3	13.97	-18.35
753	P5	14.19	-16.73
753	P10	14.74	-17.25
753	S13	14.31	-16.64
753	R6	14.53	-17.07

Table S4: Comparison of phenology of Atlantic petrels obtained from bibliography and current study Previous studies are based on direct evidences of the incubation and chick-rearing starting date (laying and hatching, respectively), whereas in the current study we estimated phenology based on geolocation and activity data; data included in the comparison refer to successful breeders. Mean ± SD or range values except indicated. ^{a}Since the sex of birds was unknown and only one of the parents was tracked, the entire incubation shared by both parents might be longer

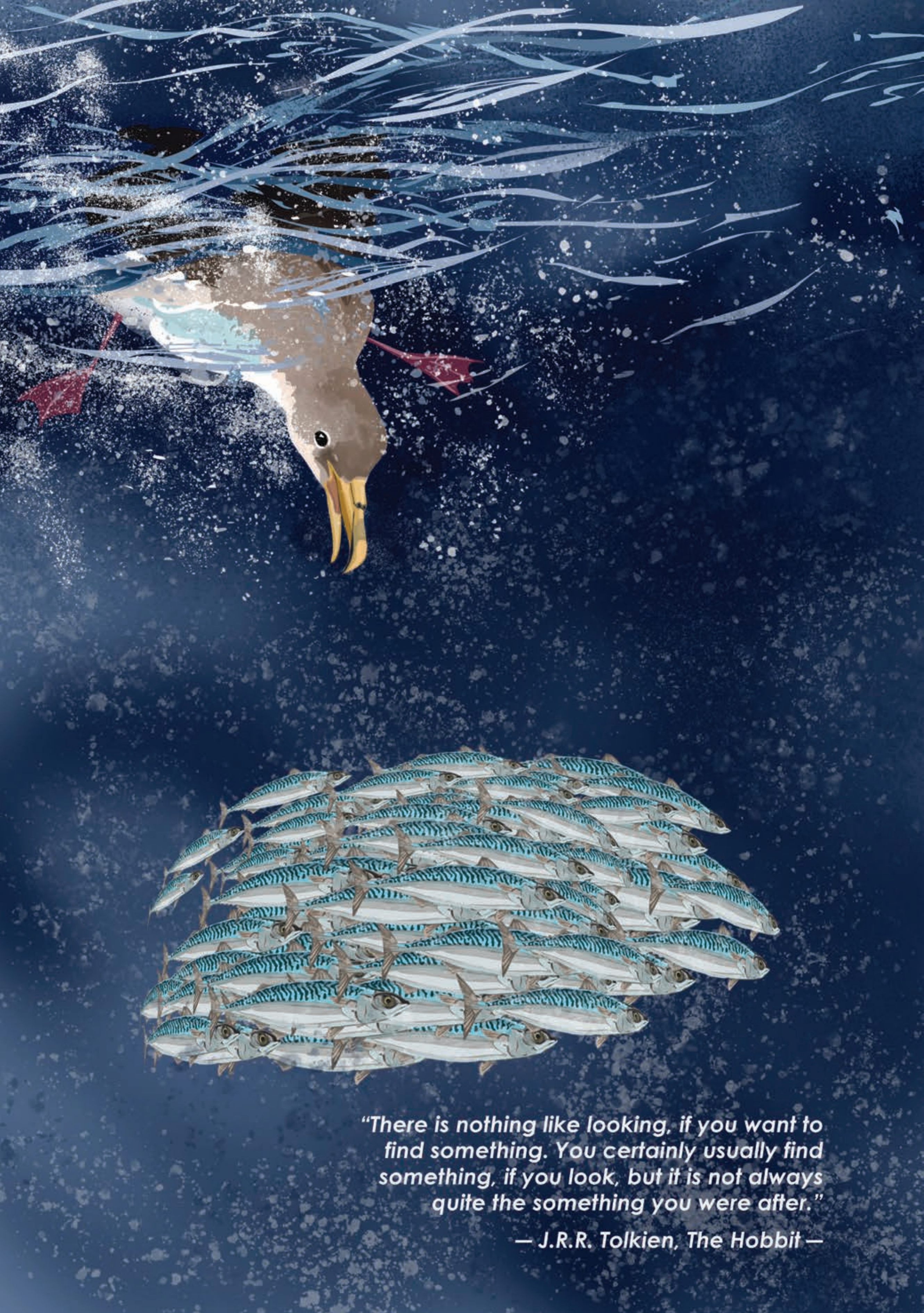
Post-breeding migration	Pre-breeding	Incubation		Chick-rearing			
Start date	Start date	Start date	Duration	Start date	Duration	Source	Study site
Mid December	Mid-March	First week of July	56	Beginning of September	106	(Richardson 1984)	Tristan da Cunha
-	-	29/06 (15/06 - 21/07)	55.5 ± 4.0	20/08 (14/08 - 10/09)	138	(Cuthbert 2004)	Gough
-	-	-	-	18/08 (06/08 - 01/09)	156	(Wanless et al. 2012)	Gough
25/12 ± 8.1	17/04 ± 5.6	13/07 ± 5.3	58.0 ± 7.5^{a}	25/08 ± 8.1	122.1 ± 10.1	Current study	Gough

LITERATURE CITED:

Cuthbert RJ (2004) Breeding biology of the Atlantic Petrel, *Pterodroma incerta*, and a population estimate of this and other burrowing petrels on Gough Island, South Atlantic Ocean. Emu 104: 221-228

Richardson ME (1984) Aspects of the ornithology of the Tristan da Cunha group and Gough Island 1972-1974. Cormorant 12: 123-201

Wanless RM, Ratcliffe N, Angel A, Bowie BC, Cita K, Hilton GM, Kritzinger P, Ryan PG, Slabber M (2012) Predation of Atlantic Petrel chicks by house mice on Gough Island. Anim Conserv 15: 472-479



> "There is nothing like looking, if you want to find something. You certainly usually find something, if you look, but it is not always quite the something you were after."
>
> — J.R.R. Tolkien, The Hobbit —

Chapter 4:

Air-water behavioural dynamics reveal complex at-sea ecology in global migratory seabirds

Zuzana Zajková[1,2], José Manuel Reyes-González [1], Teresa Militão[1], Jacob González-Solís[1], Frederic Bartumeus[2,3,4]

[1] *Institut de Recerca de la Biodiversitat (IRBio) and Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals (BEECA), Universitat de Barcelona, Barcelona, Spain*

[2] *Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Blanes, Spain*

[3] *Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Vallès, Spain*

[4] *Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain*

ABSTRACT

Characterizing the main determinants and variability of animal behaviour in the wild is a daunting task. However, to improve our efforts in the management and conservation of endangered populations it is crucial to assess the underlying sources of behavioural variability, and to identify key behavioural shifts governed by major life-history events. The recent technological revolution allows us to collect behavioural information at an unprecedented level of detail, but novel methodological protocols are required to bring biologging sensory data to amenable behavioural analyses and descriptions. Our study model, a highly-mobile migratory seabird (the Cory's shearwater) presents a complex annual cycle that involves central place foraging, ocean-basin long migratory movement and wandering in wintering areas. Our quantitative analysis, based on wet-dry data, reveals the hierarchical and modular nature of seabirds' air-water behavioural interactions, at an unprecedented level of detail. The existence of radically different behavioural contexts linked to phenology, and the need to exploit different marine environments over the year, results in different behavioural prevalences and transitions both in time and space. We uncover both flexible and structural components of the behavioural organization of Cory's shearwaters across the annual life cycle. Cory's shearwaters show complex behavioural sequences and organization during the breeding and wintering stage. On the contrary, migration restricts individual natural variability to a few dominant behavioural modes and more predictable behavioural transitions. We also observed a spatial correlation between behavioural diversity and resource hotspots (e.g. upwelling areas). Our framework paves the way for extending behavioural annotation to year-round movements of wildlife, opening new avenues to understand behavioural patterns and the seasonal timing of life-history events of animals spending most of their life out of the human's sight.

INTRODUCTION

Identifying the sources and characteristic scales of behavioural variability is an intricate task, yet it is crucial to address many fundamental questions in wildlife ecology and conservation (Krebs & Davies 2009, Berger-Tal et al. 2015). It is well known that gender, age or social status are main drivers of behavioural variability, having a strong impact on population dynamics (Nilsson et al. 2014, Lecomte et al. 2010). At the same time, major life-history events (e.g. breeding, migration, wintering) can constrain individual-level behavioural repertoire and decision-making. Identifying key behavioural shifts, and understanding the main determinants of a species behavioural organization requires covering the wide range of scales and natural conditions at which behaviour unfolds. In this context, recent advances in remote tracking and analytical tools has allowed to address fundamental behavioural questions at an unprecedented detail (Block et al. 2011, McIntyre 2014, Kays et al. 20015, Roncon et al. 2018, Harcourt et al. 2019), fostering our understanding of the adaptive potential of wildlife species to changing environments (Sih et al. 2010, Wong & Candolin 2015).

Seabirds are an ideal model to study the influence of different drivers in animal behaviour. These long-lived and highly vagile marine top-predators, nest in-land but fully rely on dynamic marine environments to accomplish most biological requirements (Gaston 2004). Individual movements and behaviour are variable but severely constrained by the seasonal timing of life-history events (Phillips et al. 2017). The changing degree of energetic demands, breeding duties and central-place foraging coupled with changes in food availability limit foraging behaviour in time and space to different extent throughout the seasons (Schreiber & Burger, 2001). Therefore, in order to maximize foraging success and fitness, individuals must adapt their behaviour over the annual cycle to face the different constraints related to intrinsic (age, sex, breeding status, breeding duties, breeding success, migration strategies, moulting strategies, etc.) and extrinsic factors (e.g. food availability, patchy resources, marine habitat, environmental stochasticity, etc.) (Weimerskirch 2007, Phillips et al. 2017). Seabirds are exposed to a changing number of threads over their annual cycle on land and at sea, making them one of the world's most rapidly declining vertebrate groups (Croxall et al. 2012). Hence, seabirds represent a particular case of interest where novel technology can revolutionize our understanding of basic behavioural knowledge, urgently needed to improve current conservation and management efforts (Lascelles et al. 2016, Dias et al. 2019).

At-sea movement of pelagic seabirds have been addressed over the last 20 years with the wide deployment of light-level geolocation loggers (global location sensor, GLS) (Burger & Shaffer 2008, Wilson & Vandenabeele 2012). GLS currently remain as the most cost-effective balanced tracking devices to get insights into the movements of pelagic seabird species over the entire annual cycle while ensuring the welfare of tagged individuals (Igual et al. 2010, Vandenabeele et al. 2011, Vandenabeele et al. 2012). Apart from the low-resolution positional data (2 positions per day), some models of GLS, usually referred as geolocation-immersion loggers, also provide high-resolution wet-dry conductivity data, which has been used as a proxy to broadly describe at-sea behaviour of seabirds (e.g. Mackley et al. 2011, Rayner et al. 2012, Gutowsky et al. 2014, Clay et al. 2017). Despite many researchers would acknowledge that the temporal sequence of wet-dry alternating states contains relevant behavioural information (i.e. landings, take-offs, sustained flight, sitting on water) (Weimerskirch et al. 1997, Lecomte et al. 2010, Shaffer 2001), wet-dry dynamics have been rarely used alone to make behavioural inferences (Guilford et al. 2009). Yet this information has been used most times as a complement in behavioural characterization approaches relying on speed and turns inferred from movement positional data (Dean et al. 2012, Freeman et al. 2013).

In this work, we aim at revealing the drivers and the behavioural complexity of a highly vagile pelagic seabird species, the Cory's shearwater *(Calonectris borealis).* We developed a novel unsupervised protocol to extract the most out of the behavioural information contained in high-resolution wet-dry geolocation-immersion data. We showed that one can make key behavioural inferences from air-water seabird interaction patterns. Based on this type of data, the behaviour of Cory's shearwaters appears to be modular and hierarchically organized, and behavioural modes differing in prevalence and transition probabilities across individuals and phenological stages (namely breeding, migration, and wintering). We analysed carefully the relationship and importance of behaviours across different scales, from individuals to population, from daily to seasonal scales, and revealed the complex and hierarchical nature of seabird behaviour over the entire annual cycle.

MATERIAL AND METHODS

Model species and fieldwork

The Cory's shearwater *Calonectris borealis* (Sangster et al. 2012) is a medium-sized free-range pelagic seabird belonging to Order Procellariiformes, which includes albatrosses and petrels. Cory's shearwaters breed in burrows on islands and islets in the North-East Atlantic Ocean. The species perform a complex migratory cycle over the year, as birds take advantage of prevailing winds in their migratory flyways, drawing an 8-shape loop over the Atlantic Ocean to move between breeding colonies and wintering areas in the South Atlantic (González-Solís et al. 2007). We studied adult breeders from the colony located at Veneguera (27° 50' 29" N, 15° 47' 29" W, Gran Canaria, Canary Islands). Birds from this colony are known to commute to the near North-west African shelf during the breeding stage to forage along the enriched cool waters of the Canary Current upwelling system (Navarro & González-Solís, 2009, Reyes-González et al. 2017).

Device deployment and data collection

We tagged 19 individuals during the breeding stage (June - July 2011) with light-level geolocation-immersion loggers (GLS hereafter). GLS model Mk19 measures light every 60 seconds and stores the information in 5-minutes blocks, allowing finally to estimate 2 low-resolution positions per day (at local midday and midnight) (Phillips et al. 2004, Fox, 2010). GLS additionally record the amount of time a tagged animal is in contact with salt-water recorded every 3 seconds (see below for more details). We also equipped birds with GPS loggers during the incubation period, deploying the devices before bird departure to a foraging trip and recovering them after bird arrival to land. Using concurrent GPS tracking we expected to have a proxy of the "ground truth" about displacements of birds during the short-term foraging trips. We programmed GPS devices to record a location every 5 minutes to ensure battery life to record complete foraging trips, which usually last several days. We mounted GLS (~ 2.4 g, Mk19 model, Biotrack Ltd ©) on a plastic ring on the leg of each bird. In the case of GPS, we attached the loggers (~ 24 g, 750 mAh battery, Perthold Engineering, Germany) to the back feathers with water-resistant TESA© tape. Body mass of tagged birds ranged from 600 to 900 g so both devices amounted to 2.5 - 3.7 % of the birds' weight, below the detrimental recommended threshold of 3-5 % (Phillips et al. 2003, Igual et al. 2005, Passos et al. 2010). All fieldwork was conducted under the license approved by the regional committee for scientific capture (Ref.Expt. 2011/0795, Consejería de Medio Ambiente del Cabildo de Gran Canaria; Oficina de Especies Migratorias - Ministry for Ecological Transition, Spain).

The final dataset involved 23 complete foraging trips of 19 individuals tracked concurrently with GLS and GPS loggers during the incubation period. Average duration of these foraging trips was 12.6 days (range: 6.9 – 16.9 days; Table S1). At the end of the incubation period, we maintained the GLS on 8 birds to record wet-dry information over the whole annual cycle.

In the following spring/summer (2012), we recovered GLS. The mean duration of year-round individual tracks recorded was 248 days (range 217 – 270 days; Table S1). For all tracks recorded (i.e. year-round and short-term foraging trips), we assigned the start and the end of the track as the moment when the animal was in contact with salt-water for the first and the last time after the logger deployment and before the recovery, respectively. Note that therefore neither GPS nor GLS tracks contained incubation stints of birds.

Year-round movements and phenology

We estimated positional data from twilight events from GLS using the probabilistic algorithm implemented in "probGLS" R package (Merkel et al. 2016). We used the function *twilight_error_estimation* to estimate twilight events from calibration of light data. The "probGLS" algorithm is based on an iterative forward step selection so for each year-round individual track a median geographic track is calculated from a cloud of weighted possible locations (at each step generated 1,000 particles). We ran 100 iterations for each of the 8 year-round individual tracks, and the particles were weighted by speed in dry (mean ± SD 50 ± 30 $m.s^{-1}$, max 95 $m.s^{-1}$) and wet state (0.5 ± 0.25 $m.s^{-1}$, max 1.7 $m.s^{-1}$) (see Orben et al. 2018 for details of this methodology). We restricted the selection of estimated locations to sea by applying a land mask. We finally obtained two locations per day, with an overall median error of 185 km during the solstice and 145 km during the equinox periods (Merkel et al. 2016).

Next, we applied the ST-DBSCAN algorithm on positional data derived from *probGLS* to objectively identify statistically coherent spatio-temporal clusters corresponding to different stages of the annual cycle along each year-round individual track. ST-DBSCAN allows clustering spatio-temporal data with arbitrary shape and does not require the predetermination of the number of clusters (see Birant & Kut 2007 for further details). We set the distance parameter to 600 km, the time window to 120 hours and a minimum number of 10 locations to consider our phenological partition, as our exploratory analysis showed this choice of parameters to conform the most meaningful figure in biological terms under Cory's shearwater expert criteria. Later, for each individual track we visually checked the assignment of each location to the different clusters. As we were interested in 3 main stages (namely breeding, migration and wintering), we identified and maintained only changes indicating the onset/end of migration and the onset/end of staging in breeding and wintering areas. In the case where stopovers were identified (i.e. a spatio-temporal cluster where an individual spent at least 5 days for refueling along the migratory path, Dias et al. 2010), we included them in the migration phase. ST-DBSCAN failed to identify a reliable spatio-temporal cluster for the breeding area in one individual that did not migrate and stayed within the Canary Current all year round. In that case we assigned the end of breeding and onset of wintering as the period from the last nocturnal visit of the nest (identified as prolonged time in dry state over the night) until the start of next breeding stage as identified by ST-DBSCAN.

Wet-dry data segmentation

The GLS model used in this work checks for the wet/dry state every 3 s, indicating whether the tagged bird was in contact with salt-water. A minimum duration of 6 s within a state is required to record a change between states. To account for natural changes in behaviour, we based our analysis on variable-time segments of the wet-dry data. Therefore, similarly to Meyer et al. (2015), we first coded the wet-dry time series data of each single track (i.e. both short-term foraging trips and year-round trips) as a binary time series, with the wet state as +1 and the dry state as -1, interpolated at 1 s time intervals (Fig. 1A). We then calculated the integrated cumulative sum of wet-dry sequences and later applied a breakpoint algorithm (*Knell & Codling 2011*). Doing so, we split the vector into homogeneous segments of different lengths with positive (prevalence of wet states) and negative (prevalence of dry states) slopes. Abrupt changes in slopes represent strong changes in wet-dry cumulative sums. The breakpoints of the wet-dry times series were obtained based on a local estimation of the slope change under an optimal running window. As smaller this running window, the more sensitive is the breakpoint algorithm in identifying changes in wet or dry states' temporal correlations, in a similar way to the "tolerance" parameter in the line-simplification algorithm (Douglas-Peucker algorithm, Thiebout & Trembley 2013). Moreover, the larger the running window size, the less jagged (smoother) is the cumulative wet/dry time series, so only large-scale consistent breakpoints are obtained (Fig. S1). Since we had no previous knowledge about the optimal time window size (TWS), we performed a coarse-graining analysis by running the algorithm with varying TWS ranging from 1 – 1440 minutes (24 h) (Fig. S1). We selected a TWS of 60 minutes (Fig. 1B and Fig. S2) because it showed the best compromise between the TWS and the number of resulting breakpoints, that is, the best compromise to obtain fine-scale segments and coarse-scale (i.e. consistent) breakpoints (i.e. elbow point in Fig. S2). Despite the optimal TWS sets an overall scale of analysis, the breakpoint analysis

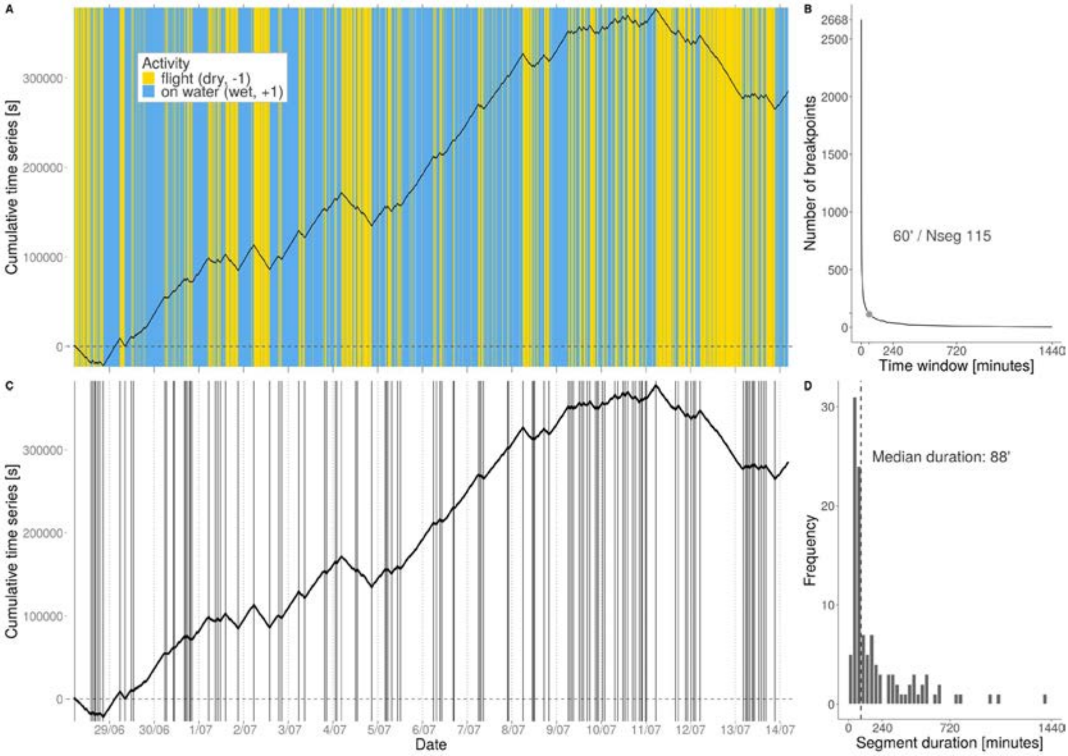


Figure 1: Segmentation of wet-dry data from geolocation-immersion loggers. Example of one individual short-term foraging trip (duration of 16 days) of Cory's shearwater tracked simultaneously with geolocation-immersion logger and GPS device. A) Original wet-dry data as two states: wet (blue) and dry (yellow). Black line represents the integrated time-series based on cumulative sum of wet (+1) and dry (-1) at 1 second resolution. This vector was used as an input to the breakpoint algorithm. B) Selecting a 60-minutes window for segmentation splits the track into 115 segments of variable lengths. C) Resulting segmentation represented by dark grey vertical lines. Dotted vertical lines represent midnights. D) Histogram of durations of segments (N=115) from the foraging trip, median duration of 88 minutes is marked as vertical dashed line.

procedure accounts much better for the multi (broad)-scale nature of behavioural dynamics reflected in a wide variation of segment durations (Fig. 1D). The fundamental assumption of this analysis is that the nature of air-water behavioural dynamics is intrinsically complex and lacks a clear characteristic scale. In other words, wet-dry dynamics, and particularly their temporal correlations, show multiple scales (from minutes to hours) which contain crucial behavioural information that is commonly missed in other approaches.

Wet-dry activity metrics

For each wet-dry segment identified previously, we calculated various descriptive activity metrics (Table 1). We generated a data matrix entailing 12 856 segments and each characterized by 11 activity metrics summarizing wet-dry patterns. We did not include the length (total duration) of the segment as input feature in our behavioural mapping and annotation protocol (see next section) to avoid multicollinearity with some other activity metrics, but we used it later to interpret our behavioural clustering output.

Inferring and building up the behavioural space

Based on the above multivariate characterization of trajectory segments (i.e. 11 variables) we built up a behavioural space. We used the unsupervised clustering protocol from the "bigMap" R package to map a two-dimensional behavioural space (Garriga & Bartumeus 2018). Data matrix refereed in the previous section (size of 12 856 x 11) was used as input in the protocol. We refer to the "bigMap" R package documentation and Garriga & Bartumeus (2018) for a detailed explanation of the protocol, therefore

Table 1: Metrics calculated from wet-dry activity data at the segment level, which were used as input features to t-SNE algorithm for behavioural annotation.

Activity metric	Abbreviation	Definition
Proportion wet	Prop.W	Duration of time on water divided by total duration of segment (range 0 - 1)
Duration wet	Dur.W	Total time in wet state (s) within segment
Duration dry	Dur.D	Total time in dry state (s) within segment
Number of changes	Nchanges	Total number of changes (transitions) between states (indifferently from wet to dry or dry to wet)
Rate of changes	Rchanges	N of changes (transitions) divided by total duration of segment (s)
Median wet duration	Median.W	Median duration (s) of wet states within segment
Median dry duration	Median.D	Median duration (s) of dry states within segment
Standard deviation wet durations	SD.W	SD of durations (s) of wet states within segment
Standard deviation dry durations	SD.D	SD of durations (s) of dry states within segment
Maximum wet duration	Max.W	Maximum duration of wet states (s) within segment
Maximum dry duration	Max.D	Maximum duration of dry states (s) within segment

here we just summarize the steps we followed. We pre-processed the data matrix by computing a principal component analysis (PCA) and a whitening of the rotated data as a standard procedure to homogenize the ranges and weights of the input features in the analysis. We then applied a parallelized and big data adjusted version of the t-stochastic neighbourhood embedding algorithm (ptSNE algorithm, function *bdm.ptsne* at “bigMap”). The t-stochastic neighbourhood embedding algorithm (t-SNE) uses an information-theoretic approach to reduce the dimensions and to embed multidimensional datasets into a 2-dimensional embedding space that represents data point similarities according to their respective features’ values (see van der Maaten & Hinton 2008 for details). A key parameter of this embedding algorithm is the so-called perplexity (ppx), which defines the neighbouring scale to measure pairwise similarity. It also sets an equilibrium between forcing a highly local analysis of similarity or a much coarse or global view of similarity involving all the points in the space. We ran the ptSNE algorithm with a broad range of perplexities and chose ppx=500 as a compromise value, since it was robust enough to maintain the same embedding space and at the same time discerned both relevant local and global features of the space (ppxs from 250 to 500 did generate statistically similar behavioural spaces). In such a 2-dimensional embedding space each data point represents a well characterized behavioral segment in terms of wet-dry activity. The segments showing similar characteristics are close together in the space, whereas faraway data points represent non-similar or clearly dissimilar segments (Fig. 2A). To better analyze the overall structure of data point distribution we applied a tailored kernel density (function *bdm.pakde* at “bigMap”; ppx=250; grid of 200 x 200 cells; Garriga & Bartumeus 2018). The kernel density clearly showed both the largest spatial concentrations of data points and the point-diluted areas in the embedding space. Over the kernel density, we applied a segmentation algorithm (function *bdm.wtt* at “bigMap”; Garriga & Bartumeus 2018; Fig. 2B) to discretize the embedding space into clusters that represent similar behavioral features across segments. Finally, we post-processed the watershed clustering output by merging the initial clusters following a signal-to-noise ratio heuristic that is applied recursively and hierarchically (function *bdm.s2nr* at “bigMap”). This coarse-graining procedure reduces the space complexity and facilitates behavioural annotation by lowering the number of clusters (Fig. 2B-C). Each of the finally obtained clusters groups wet-dry activity segments by their similitudes and would correspond to different wet-dry activity-based behavioural modes, to which we will refer hereafter as behavioural clusters (BCs).

Activity metric importance for identified BC

We used a Random Forest algorithm (RF; see Biau & Scornet 2016 for more details) to rank both the overall importance of input features to assign segments to the different BCs, and the case-wise specific importance of each feature for each different BC identified. We performed RF using the function *randomForest* from the “randomForest” R package (Liaw & Wiener 2002). We split the data set in training and testing (2/3 vs 1/3) and ensured a balanced sampling by stratified selection of equal number of samples (400) at each run. We grew 4 000 trees and selected 6 predictors randomly in each tree. The overall variable importance was measured using the mean decrease in accuracy index (MDA), which reports the MDA over all cross-validated predictions of the model when a given predictor is permuted after the training process and before prediction (Biau & Scornet, 2016). Case-wise variable importance for each BC was calculated with “LocalImp” parameter. For visualization purposes, case-wise variable importance values were rescaled to range between 0-1 within each BC. To measure accuracy of prediction, we computed the confusion matrix between observed and predicted BC, using functions from “caret” R package (Kuhn 2018).

Sources of variability in behaviour

We assessed whether observed behavioural budgets over the annual cycle were shaped by phenology or conversely, they depended more on inter-individual variability. For each BC, within-stages variability represents inter-individual variation, whereas between-stages variability represents phenological variation. If behavioural budgets were constrained by phenology, we would expect the stage means to spread out more than the inter-individual variability within each stage. For each BC, we calculated the relative amount of time allocated by individual and stage, and determined the ratio of between-stages to within-stages variances using one-way repeated-measures ANOVA F-test, setting α to 0.05. We used repeated-measures ANOVA to control pseudo-replication since same individuals were represented in the three stages.

Behavioural prevalence and transitions across phenology

To better understand changes in the behavioural space between the different stages of the annual cycle, we used the function *bdm.dMap* at "bigMap" (Garriga & Bartumeus 2018). This function allowed us to compute and visualize the distribution of behavioural segments from each stage over the 2-dimensional behavioural space. We calculated the probability of belonging to one of the three stages (breeding, migration, wintering) for each cell of the behavioural raster or grid. The visual output of the function is composed of 4 plots where the first represents the dominating stage-specific prevalence (breeding, migration, wintering) is shown. More specifically we normalized the probabilities for each stage over the behavioural space and calculated 5% contour density lines to depict the probability density for each stage. Finally, we calculated and used standardized residuals from chi-square test of independence to evaluate the association between behavioural clusters and stage.

In order to better understand behavioural strategies, we characterized the structural organization of the observed BCs using network analysis. Network topology was represented by BCs as nodes and the relations between BCs as edges. We constructed an adjacency matrix for each stage, counting the frequency of transitions between current BC at time t to next BC at $t+1$. We converted these matrices into weighted directed networks, with BCs as nodes and transitions as edges. Even though wet-dry activity patterns may be thought to represent a bipartite network structure composed of two independent sets always alternating each other (mostly wet and mostly dry segments, see Results section), we cannot treat them as bipartite because our behavioural units are the wet-dry activity segments, but our behavioural description has been statistically aggregated in the form of BCs (nodes of our network). Hence, once we use our protocol to annotate single wet-dry time-series data and later compute network edges, one may find that two consecutive segments could belong to the same BC or to a BC from the same mostly wet or dry set (though this occurs barely 1.5 % from all transitions measured). To evaluate major changes in the structural organization of behavioural modes across the 3 stages of the annual cycle, we calculated various global (i.e. network level) and local (i.e. node level) quantitative metrics (Table 2). Except for the density metric, we did not consider the weights (accounting for the frequency of transitions between BC). We used "igraph" R package for the analysis and visualization (Csardi & Nepusz 2006).

In addition, we examined transitions between BCs at each stage. To account for different duration and therefore differences in frequencies of BCs, we normalized the adjacency matrix for each stage by calculating the probability of transition between two BCs ($T_{i,j}$), conditioned by the probability of being in certain stage (S) and in certain BC (C):

$$P(T_{i,j}|C, S) = \frac{P(T_{i,j},C,S)}{(P(C|S) * P(S))}$$

By this way we obtained for each stage a matrix

Table 2: Network metrics used in the study.

Network metric	Level	Description
Size	Global	Total number of nodes in the network
Density (function *edge_density*)	Global	Ratio of the number of edges and the number of possible edges
Diameter (function *diameter*)	Global	Longest path between two nodes
Average path length (function *mean_distance*)	Global	The mean of the shortest distance between each pair of nodes in the network
Degree centrality (function *degree*)	Local	Node's in- and out-degree (being number of edges that lead into or out of node); indicates the connectivity of node
Closeness centrality (function *closeness*, normalized value)	Local	Indicates how close is the node to other nodes of the network, calculated as the reciprocal of the average length of the shortest paths to/from all other nodes in the network
Betweenness centrality (function *betweenness*)	Local	Refers to the number of shortest paths (geodesics) between two nodes that go through the node of interest

of transition probabilities between BCs, where the sum of all probabilities from BC_i equals 1. Later, we used these transition matrices to estimate entropy rate, using "ccber" R package (Vegetabile et al. 2019). We simulated 10 000 transitions for each stage using function *SimulateMarkovC*hain and used the function *CalcEntropy*Rate to obtain entropy rate for each stage.

Spatial representation of movement and behaviour

We carried out a spatially-explicit approach to visualize behavioural landscapes by identifying the most important BCs exhibited by tracked birds over their entire annual distribution range. To do so, we first merged geographical locations from GLS with wet-dry activity segments and linearly interpolated locations at the start of each segment. After that, we regularized the tracks to a location every 5 minutes, so each location had assigned the BC of the segment to which belonged. To map locations, we used R packages "sf" (Pebesma 2018), "dggridR" (Barnes 2018), and "ggplot2" (Wickham 2016). We used an Icosahedral Snyder Equal Area Projection with a cell size of approximately 70 000 km^2 and centroids of adjacent cells distanced ~260 km (varying according to latitude). Next, to get a more statistically representative map at population level in areas intensively used by several individuals, we performed 1 000 iterations of a custom-built randomization procedure to select samples, so at each run and for each grid cell, we chose randomly three-quarters of the locations and quantified the time invested in total and by BC. The final map showed for each grid cell the BC in which the most time was invested over the iterations. We also extended the concept of measuring diversity to evaluate behavioural variability in space, by creating a spatially-explicit behavioural diversity map. We calculated the Shannon diversity index (Krebs 1999) considering the number of segments belonging to each BC within each grid cell. Using a similar bootstrap procedure as before, we built up a final map that shows the average behavioural diversity for each cell. We finally explored behaviour during the breeding period, zooming into the Canary Current and using uniquely wet-dry activity segments recorded during short-term foraging trips during the incubation period, when animals were concurrently tracked with GPS loggers and thus spatial locations were accurate. To map main BCs and behavioural diversity, we applied the same bootstrap procedure on a higher resolution grid (~860 km^2 each cell and ~30 km between centroids of adjacent cells).

Data analysis

All data processing, analysis and visualization were conducted in R version 3.4.4 (R Development Core Team, 2018).

RESULTS

Movement and phenology

During the incubation period in the breeding stage, birds concurrently tagged with GPS and GLS to track their short-term foraging trips rapidly engaged in commuting flights after the trip start, heading towards the upwelling area of the Canary Current in the North-west African shelf (Fig. 9D). After the breeding, from birds tracked only with GLS year round, one individual did not migrate and remained in the vicinity of the Canary Is. year round. The rest of the birds left the breeding area and started the post-breeding migration between 2nd of November and 22nd of December, arriving to their main wintering area between 23rd of November and 4th of January. Birds spent on average 55 days (range 23 – 77 days) in one of main wintering areas located along the South African waters (Benguela and Anguhlas Currents) and the Central South Atlantic (Fig. 9A). Birds started pre-breeding migration back to the Canary archipelago between 27th of January and 2nd of March and arrived to the breeding colony between 22nd of February and 28th of March. Most birds followed an 8-shaped path to migrate over the Atlantic Ocean (Fig. 9A).

Behavioural space of Cory's shearwater at the population-level

Overall, we identified 23 clusters from wet-dry segments (Fig. 2C), which we next grouped into 10 behavioural clusters (BCs) based on their similarity (Fig. 2C), each one representing a different behavioural mode. All individuals displayed all BCs over all stages of the annual cycle.

Behavioural interpretation of clusters

BCs in the upper (BC1, BC3, BC6, BC7, BC10) and lower (BC2, BC5, BC8, BC14, BC19) regions of the behavioural space (Fig. 2) corresponded to mainly dry and mainly wet segments, respectively (Fig. S3). Within the behavioural space, more similar BCs tended to be positioned closer to each other.

Based on a joint view of the input metrics (Table 1, Fig. S4) and the temporal (Fig. S5) and spatial distribution of BCs, we proposed an interpretation to each of the BC (see Table 3 with synthesized semantics and description). We interpreted BC1 as short flights [SF], BC3 as sustained flights [StF], BC6 as transit flights with occasional landings [TFLd], BC7 as commuting flights with recurrent landings [CF], BC10 as shallow-surface diving [ShD], BC2 as short rests [SRest], BC5 as active sit-wait-dive [ActSWD], BC8 as still sit-wait-dive [StlSWD], BC14 as long sitting [Lsit] and BC19 as resting [Rest].

Dry BCs: We identified 5 flight modes, two related to ballistic displacements (BC1 [SF] and BC3 [StF]) and three presumably including foraging activities (BC6 [TFLd], BC7 [CF] and BC10 [ShD]) (Table 1, Fig. S4). Although the average median duration (~ 70 minutes) and IQR of segments assigned to BC3 [StF], BC6 [TFLd] and BC10 [ShD] were similar, we observed substantial differences in other important activity metrics defining each cluster, such as the rate of wet-dry transitions and the proportion of time in wet, leading to different behavioural interpretation of those clusters (Table 3). We interpreted BC6 [TFLd] and BC10 [ShD] as mainly related to foraging due to the high rate of air/water transitions (i.e. landings and take-offs). BC6 [TFLd] was characterized by longer flights interrupted by very short periods on water, likely related to extensive search within foraging grounds. BC10

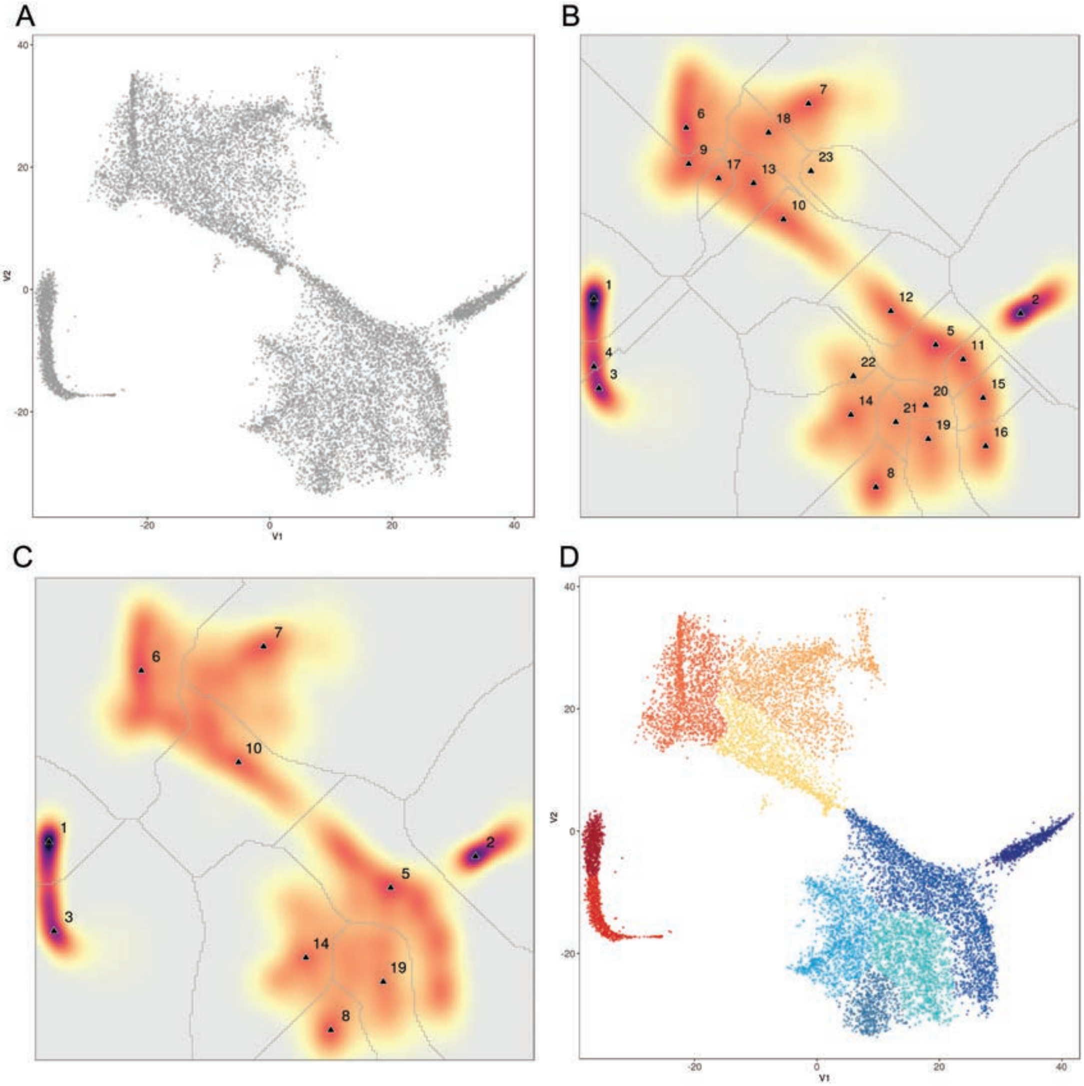


Figure 2: Behavioural space of Cory's shearwater constructed from segments of wet-dry data. (A) A multidimensional dataset (11 activity metrics and > 12 000 segments) was embedded into a 2-dimensional space resulting from the parallelized t-SNE algorithm at "bigMap" R package. Each point represents one wet-dry activity segment. (B) Probability density estimation over the 2-dimensional space (colours from light yellow to black). By a discretization algorithm the space was divided into 23 clusters; thin grey lines delimit cluster borders. (C) Original 23 clusters were merged into 10 behavioural clusters; thin grey lines delimit cluster borders. The area size of cluster region indicates the variability within the cluster. (D) Resulting behavioural space, each colour represent one of 10 main behavioural clusters. Numbers correspond to cluster identity. Black triangles represent peaks in the density.

Table 3: Description of behavioural clusters (BCs) corresponding to behavioural modes of Cory's shearwaters. Using wet-dry data obtained from geolocation-immersion loggers, we developed a protocol to build up a behavioural space composed of 10 BCs. See Material and Methods and Fig. S4 in Supplementary Material for more details. In this summary we highlight quantitative metrics that best characterize each BC, adding a description derived from interpreting BCs in different contexts (see Supplementary Material). Note that duration of segments was not used as input variable due to multi-collinearity. Values presented in the table denote median and interquartile range. CWVI indicates the most important metrics based on case-wise variable importance obtained from Random Forest (see Material and Methods and Fig. S8 in Supplementary Material for more details). Note that here we express Rate of changes (Rchanges) as wet-dry transitions h^{-1} to ease the interpretability.

BC	*Behavioural semantics*	*Wet-dry metrics*	*Behavioural mode description*
1	**Short flights [SF]**	Duration = 34 min (31 - 39) Rchanges = 0 (i.e. without any air/water transition) Prop.W = 0 CWVI: Prop.W, Dur.D	Occurred all over the day. Animals inverted less than 1% of time in this BC. Accounting for 4.9% in terms of frequency.
3	**Sustained flights [StF]**	Duration = 70 min (55 - 99) Rchanges = 0 Prop.W = 0 CWVI: Prop.W, Nchanges	Occurred all over the day. Occasionally included a limited number of very short wet states of few seconds within some segments. During the breeding stage (particularly pre-breeding stage), this BC included nocturnal visits of the colony of prolonged duration (4.7 hours on average, up to 10 hours). Individuals invested 2.8% of time in this BC. Accounting for 5.7% in terms of frequency.
6	**Transit flights with occasional landings [TFLd]**	Duration = 69 min (45 - 111) Rchanges = 3 h^{-1} (1.9 - 4.3) Median.D = 19 min (11 - 30) Median.W = 1 min (0 - 3) Prop.W = 3% (1 - 9) CWVI: Prop.W, Nchanges, Rchanges	Occurred all over the day. Includes occasional landings. Individuals invested around 5% of time in this BC on average. Accounting for 13.8% in terms of frequency.
7	**Commuting flights with recurrent landings [CF]**	Duration = 318 min (206 - 562). Rchanges = 6.7 h^{-1} (3.9 - 12) Max.D = 96 min (66 - 150) Max.W = 10 min (6 - 16) Prop.W = 9.5% (6 -15) CWVI: Dur.D, Nchanges	Occurred all over the day. Individuals engage most intensively in this BC on sunrise and sunset.–Animals invested around 25.6% of time in this BC on average, but more than 40% during the migration. Accounting for 15% in terms of frequency.

10	**Shallow-surface diving [ShD]**	Duration = 73 min (48 - 106) Rchanges = 17.7 h^{-1} (11.3 - 33.2) Median.D = 50 s (24 - 138) Median.W = 21 s (12 - 39) Max.D = 26 min (16 - 39) Max.W = 4 min (2 - 8) Prop.W = 17% (9 - 24) CWVI: Prop.W, Dur.D, Rchanges	Transit with high landing rate (the highest among all BCs). Occurred all over the day, most intensively during daylight hours. Individuals invested around 4.3% of time in this BC. Accounting for 11.3% in terms of frequency.
2	**Short rests [SRest]**	Duration = 57 min (40 - 90) Rchanges = 0 CWVI: Prop.W	Occurred all over the day, with prevalence during daylight hours. This BC occasionally included very short dry states. Individuals invested around 1.8% of time in this BC. Accounting for 5.5% in terms of frequency.
5	**Active sit-wait-dive [ActSWD]**	Duration = 85 min (51 - 147) Rchanges = 5.7 h^{-1} (2.2 - 13.6) Median.D = 22 s (12 - 63) Median.W = 11 min (2 - 31) Max.D = 2.5 min (0 - 8) Max.W = 39 min (24 - 62) Prop.W = 94% (85 - 99) CWVI: Median.W, Prop.W, SD.W	Occurred all over the day; those starting in the afternoon hours tend to last until late night hours. Time on water highly variable, and combined with short flights. Animals invested around 9.9% of time in this BC. Accounting for 19.9% in terms of frequency.
8	**Still sit-wait-dive [StlSWD]**	Duration = 615 min (473 - 786) Rchanges = 4.5 h^{-1} (3.1 - 7) Median.D = 18 s (12 - 28) Median.W = 105 s (48 - 280) Max.W = 270 min (212 - 367) Prop.W = 95% (92 - 97) CWVI: Max.W	The longest median duration among all BCs. Generally including long wet state and various dry and wet short states of variable durations. Occurred all over the day, with prevalence to start in the afternoon/dusk, long over the night and finishing before the dawn. Individuals invested around 11.8% of time in this BC. Accounting for 4.5% in terms of frequency.
14	**Long sitting [LSit]**	Duration = 567 min (393 - 846) Rchanges = 5.2 h^{-1} (3.3 - 10.5) Median.D = 18 s (12 - 33) MedianW = 4 min (1 - 12) Max.D = 15 min (9 - 21) Prop.W = 92% (88 - 95) CWVI: Dur.W, Nchanges	Occurred all over the day, with prevalence of the start after the sunrise and before sunset. Individuals invested around 27.8% of time in this BC. Accounting for 9.4% in terms of frequency. Includes segments with up to 127 min of continuously wet.
19	**Resting [Rest]**	Duration = 232 min (149 - 336) Rchanges = 3.4 h^{-1} (2.1 - 5.5) Median.D = 21 s (12 - 51) Median.W = 6 min (2 - 15) Max.D = 6 min (1 - 14) Max.W = 115 min (87 - 165) Prop.W = 95.5% (90 - 99) CWVI: Max.W, SD.W, Prop.W	Occurred all over the day, except time around sunrise. With prevalence to start in the afternoon/dusk, long over the night (nocturnal resting) and finishing before the dawn. Individuals invested around 10.5% of time in this BC. Accounting for 10% in terms of frequency.

[ShD] encompassed segments with the highest rate of transitions per hour, indicating high foraging activity, probably related to active area-restricted search within foraging patches, including short shallow dives to catch prey near the surface. We interpreted BC7 [CF] as commuting flights. The long continuous duration of dry state (~ 100 minutes) and rate of changes clearly indicated relocation movements. Indeed, concurrent GPS tracking during incubation pinpointed BC7 to be mainly restricted to commuting corridors between the breeding colony and the main foraging grounds in the North-west African shelf (Fig. 6). Year-round GLS tracking also supported BC7 as commuting, as it was prevalent in most part of the migratory routes between breeding and wintering sites (Fig. 7, Fig. S7). However, a small sub-cluster of segments within the BC7 [CF] corresponding to the pre-breeding and chick-rearing presumably included prolonged nocturnal visits to the colony (Fig. S5). Similarly, within the BC3 [StF] during the pre-breeding stage, we identified segments of prolonged duration of several hours during the night (Fig. S5), which we assumed to correspond also with visits to the colony.

Wet BCs: Segments in these other 5 BCs are characterized by high proportion of time spent on water (> 90% of segment duration on average). Based on short duration and any take-offs/landings, we interpreted BC2 as short rests [Srest]. We propose BC5 to correspond to active sit-wait-dive behaviour [ActSWD], characterized by a high rate of wet-dry transitions, high variability in duration of wet states and short flights. This BC might be related to intense local feeding in patches with abundant prey, where birds sit on water and dive to capture prey within birds' reach (i.e. fish schools near the surface). Generally, segments in BC8 [StlSWD], BC14 [LSit] and BC19 [Rest] were longer (> 3.5 hours on average) than the other BCs, indicating that once in wet state, birds tended to persist in it. These BCs likely included periods of rafting/drifting when birds siting on the sea surface are passively carried by ocean currents and seldom interrupted by short periods of flights. BC8 [StlSWD] was characterized by long durations and by containing at least one long wet state lasting several hours, presumably related to nocturnal resting, though surface-foraging events during those long bouts should not be discarded.

Variable importance in behavioural classification

We obtained an overall accuracy of 97% of prediction of BC based on the 11 activity metrics using RF. Metrics that mostly contributed to the accuracy of the classification of BCs were those reflecting the wet-dry activity variability at the segment level (e.g. number and rate of changes), together with the total durations of wet and dry states and proportion of wet (Fig. S6A). At the cluster level, case-wise variable importance varied between BCs, being proportion of wet the most important for five BC (Table 3, Fig. S6B).

Changes in the behavioural space over the annual cycle

Computation of density maps by stage confirmed a different prevalence of BCs per stage (Fig. 3A-C). The time budget allocated to each BC (Fig. 5A) and a significant statistical association between certain BC and stages (Supplementary Material, Fig. S7) also support this result. Essentially, different regions of the behavioural space, involving different BCs, were dominant at the different stages (Fig. 3A-C, Fig. S8). During the breeding period BC1 [SF], BC2 [SRest] and BC3 [StF] dominated the behavioural space, alongside with BC5 [ActSWD], BC6 [TFLd] and BC14 [LSit]. During the migration, BC5 [ActSWD] and BC7 [CF] emerged as most dominant, although BC1 [SF], BC2 [SRest] and BC3 [StF] maintained their dominance. During the wintering, BC6 [TFLd], BC10 [ShD] and BC8 [StlSWD] were dominant. Moreover, we observed that even within the same BC region, different parts of the area were dominant in different stages (e.g. BC5 [ActSWD], BC10 [ShD]) (Fig. 3).

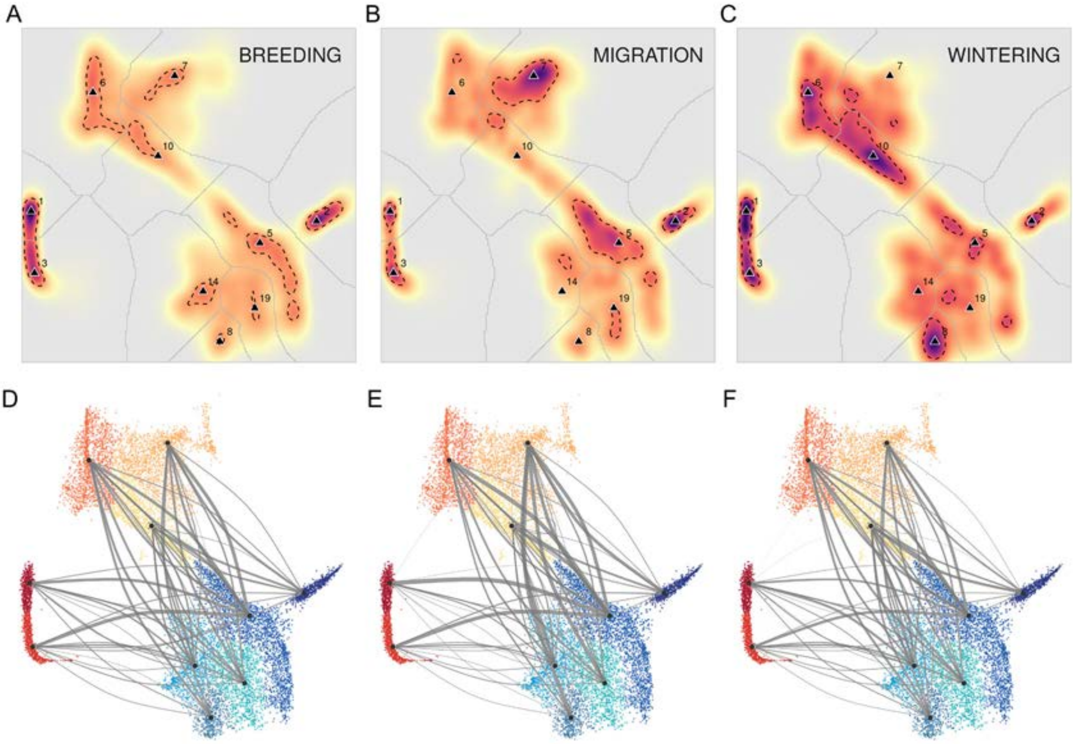


Figure 3: Changes in the behavioural space of Cory's shearwater over the annual cycle. Probability density estimation over the behavioural space for separated stages: A) breeding, B) migration and C) wintering. Dashed lines represent 5% contours. Peaks correspond to dominant behavioural clusters (BCs) after grouping to 10 clusters. D-F) Transition probability rates between behavioural clusters for separated stages: D) breeding, E) migration and F) wintering. Layout of nodes reflect the 10 peaks of BCs in the behavioural space. Grey lines represent connections between BCs, the width of line is relative to the transition probability between BCs. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

Behavioural networks

At global level, we did not find differences in network metrics (Table S2), indicating similar global network structure in the three stages of the annual cycle (Fig. 4). At local (node) level, mostly dry BC6 [TFLd], BC7 [CF] and BC10 [ShD] were the most important BCs in all three stages, as they were directly connected to the majority of BCs (see in- and out-degree centrality values, Table S2). In contrast, mostly wet BC2 [SRest], BC5 [ActSWD], BC8 [StlSWD], BC14 [Lsit] and BC19 [Rest] had less connections (i.e. lowest in- and out-degree centrality values). All BCs were closely connected regardless of the stage. BC10 [ShD], BC7 [CF], BC6 [TFLd] and BC3 [StF] were the most important in terms of closeness centrality as shortest paths connected them to other BCs (Table S2). Conversely, BCs with lower closeness centrality values (mostly wet BCs) needed longer paths to connect to other BCs (Table S2). Two BCs acted as major "hubs" in the networks: BC10 [ShD] was the most central node in terms of betweenness centrality during the breeding (high betweenness centrality), but during wintering both BC10 [ShD] and BC7 [CF] had equal importance. During the migration, however, BC7 [CF] was the most central node (Table S2, Fig. 4D-F). In terms of transition probabilities between BCs (Fig. 4, Fig. S9), especially during the migration there was a high probability of

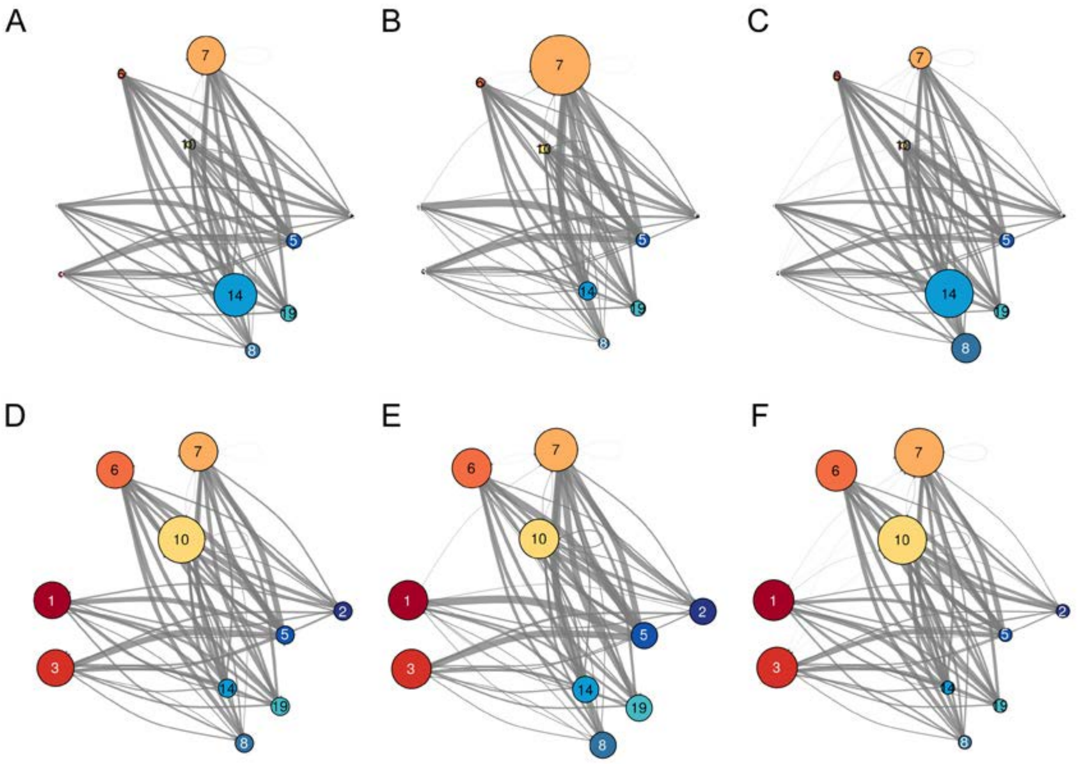


Figure 4: Behavioural networks of Cory's shearwaters at the three different phenological stages over the annual cycle. Each column, from left to right, correspond to breeding, migration and wintering. The layout reflects the 10 peaks in the behavioural space. Grey lines represent connections between BCs. The width of these lines is relative to the transition probability between BCs. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest. A-C) Average time invested in each behavioural cluster (BC) is represented by the size of the point, for separated stages: D-F) Betweenness centrality metric on node level represented by the size of the point. Two BCs, BC10 and BC7, acted as main "hubs" over all stages.

mostly dry BCs to transit to BC5 [ActSWD] (range of transition probabilities 0.36-0.54) and mostly wet clusters to transit to BC7 [CF] (range 0.40-0.49). During the breeding and the wintering, these transitions were more evenly distributed (see transition matrices in Supplementary Material, Fig. S9). During wintering BC8 [StlSWD] gained importance compared to breeding and migration (transition probabilities ranged between 0.11-0.17 in wintering whereas was < 0.1 in breeding and migration). Finally, estimated entropy rate was the lowest for the migration stage, but values in breeding and wintering were only slightly above (breeding: 2.21, migration: 2.09, wintering: 2.23; see Table S2).

Sources of variability in behavior

We found between-stage variance significantly greater than within-stage variance in BC3 [StF], BC7 [CF], BC8 [StlSWD] and BC14 [Lsit] (BC3: $F_{2,13} = 7.4$, $p = 0.007$; BC7: $F_{2,13} = 18.49$, $p < 0.001$; BC8: $F_{2,13} = 9.46$, $p = 0.003$; BC14: $F_{2,13} = 11.33$, $p = 0.001$), indicating that between-stage behavioural variability was greater than inter-individual variability in those BCs (Fig. 5, Table S3). Birds were constrained in the amount of time invested in each BC particularly during the migration, when the amount of time in BC7 [CF] increased and time in BC14 [Lsit] decreased in all individuals, comparing to breeding and wintering. We observed a gradual decrease in time invested in BC3 [StF] from breeding through migration to wintering, and contrarily, an increase in time invested in BC8 [StlSWD] from breeding to wintering for all individuals. Conversely, in the rest of BCs inter-individual variability was high across stages (Fig. 5, Table S3). The amount of time invested in these BCs (BC1 [SF], BC2 [SRest], BC5 [ActSWD], BC6 [TFLd], BC10 [ShD] and BC19 [Rest]) indicated higher flexibility of birds in time allocation for these behaviours and thus likely not so constrained by stages of the annual life cycle.

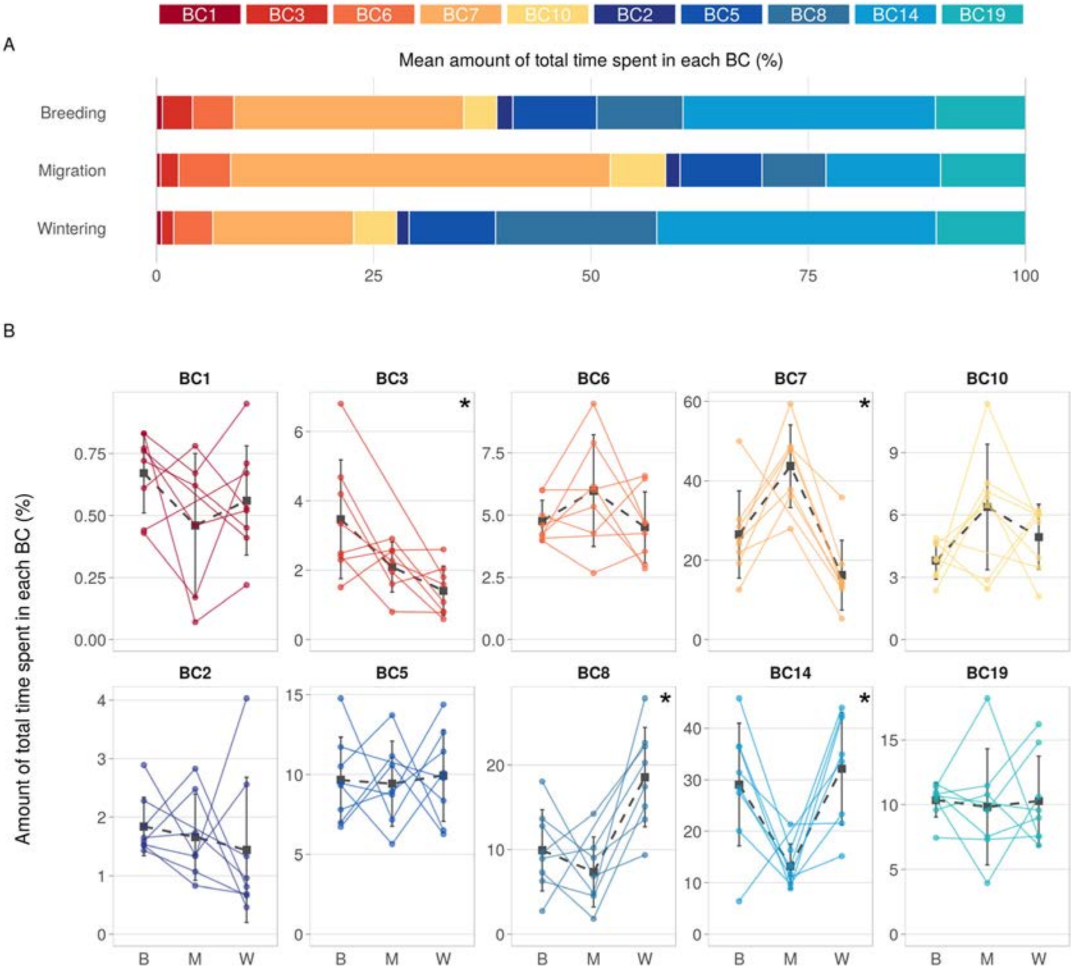


Figure 5: Changes in the amount of time invested in each behavioural cluster (BC) over the annual cycle of Cory's shearwater derived from wet-dry data. A) Mean proportion of time invested in each BC of 8 individuals in three stages. B) Individual variability in the amount of time invested in each BC. Points refer to individual proportions. Solid lines connect individual values over stages (B=breeding, M=migration, W=wintering). Black squares and solid vertical lines refer to mean ± SD values; dashed lines connect mean values over stages. Colours refer to BCs. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest. Note the variable scales on y-axis. Asterisks in the upper right corner identify BCs where between-stage variability was significantly greater than inter-individual variability.

Behavioural space of Cory's shearwater at the individual-level

We showed that changes in time allocation to BCs varied between stages and individuals on a coarse-scale. We also visually evaluated the interpretation of BCs and time allocation at individual level, at various spatial and temporal scales. For visualization purposes, all subsequent figures refer to a single individual (ID: 6175726; Fig. 6, Fig. 7 and Fig. 8)). During the foraging trip of 13 days, the tagged bird tracked with GPS (Fig. 6), was involved in BC7 [CF] on the outward and inward commuting flights to foraging grounds over the African shelf. Both during the day and night bird was involved in foraging behaviours BC5 [ActSWD], BC6 [TFLd], BC10 [ShD] and sustained flights BC3 [StF]. Resting behaviours BC8 [StlSWD] and BC14 [LSit] dominated during the night, but BC 19 [Rest] during the day. Year-round track over the whole breeding cycle from GLS (Fig. 7) reveals that, for example, on southward migration to wintering grounds the tagged bird was involved mostly in BC7 [CF] during the day and rested during the night, more engaged in BC14 [Lsit] and BC19 [Rest]. However, on the northward migration to the breeding grounds in Canary Islands the tagged bird was involved in BC7 [CF] also during the night, since earlier arrival to breeding sites is advantageous for males to defend the nest. We present an actogram plot of a selected example (Fig. 8, see also Fig. S10 for other individual actograms). We can observe some clear circadian rhythms in shearwater's behaviour, also adjusted over the

Figure 6: Movement and behaviour of one individual of Cory's shearwater over one short-term foraging trip to the North-west African shelf. The plot illustrates a GPS track of 13 days of duration, composed of 117 behavioural segments of variable durations. Each point on the map, representing a GPS position, is coloured by the corresponding behavioural mode (i.e. behavioural cluster, BC) identified from unsupervised clustering of wet-dry data. In the zoom to a foraging area on the left, the positions are split into day (white border of the point), twilight (grey border) and night (black border). Note, for example, that animal was engaged in foraging BCs (BC10, BC6, BC5) mostly during the day, and in resting BCs during the night (BC14, BC8), although not exclusively. Black star indicates the breeding colony. Grey arrows indicate the direction of the commuting flights. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

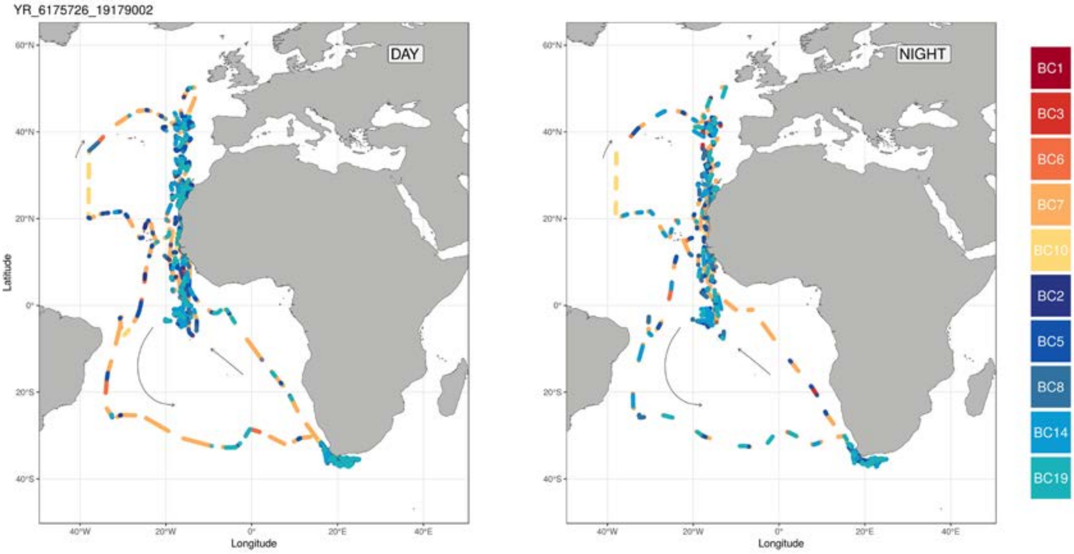


Figure 7: Movement and behaviour of Cory's shearwater derived from GLS and wet-dry data over the year-round annual cycle. Plots show an example of one individual year-round track. For illustration purposes, positions were linearly interpolated from 2 daily GLS positions to the start of each behavioural segment and later at 5-minutes intervals until the start of next behavioural segment, therefore should be treated with caution. Positions are split into day (left) and night (right). Each colour represents the behavioural mode (i.e. behavioural cluster, BC) identified from unsupervised clustering of wet-dry data from GLS. Grey arrows indicate the direction of the migratory flyway. Note, for example, active flight (BC7) during the night while engaged the pre-breeding migration to the colony (right panel), when the animal is likely pressured to arrive to the colony to defend the nest and start mating. Code on the top indicates individual and track identity. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

year-round cycle. For example, several behaviours tended to be more diurnal (BC6 [TFLd], BC10 [ShD], BC5 [ActSWD]), although not exclusively. At the end of the breeding season (mid-September), this tagged bird was involved in mostly wet BCs, particularly BC14 [Lsit]. BC7 [CF] and BC3 [StF] presented bimodal pattern: while during the migration and wintering stage these BCs were mostly restricted to daylight hours, during breeding they occurred also during the night, likely representing nocturnal visits to the nest. We can observe a clear shift in the circadian rhythm during the wintering spent in the South-African coast (Fig. 8), when the bird adjusted behaviour to earlier sunrise and sunset. Especially at the beginning of the breeding season (March), before entering the breeding colony after the sunset, bird was engaged in wet BCs, particularly BC5 [ActSWD] and BC19 [Rest].

Spatial and temporal distribution of behaviours

At global scale, mostly "wet" BCs [Srest, ActSWD, StlSWD, Lsit, DRest] predominated within the wintering areas (Fig. 9B). BC14 [LSit] dominated in the southernmost part of the Canary Current, west Gulf of Guinea, Namibia off-shore and Agulhas Current. However, in the wintering area of the Mozambique Channel, BC8 [StlSWD] was dominant. In the wintering area located in the pelagic zone of the South Atlantic BC8 and BC19 were similarly dominant. Mostly "dry" BCs [SF, StF, TFLd, CF, ShD] predominated along the migratory

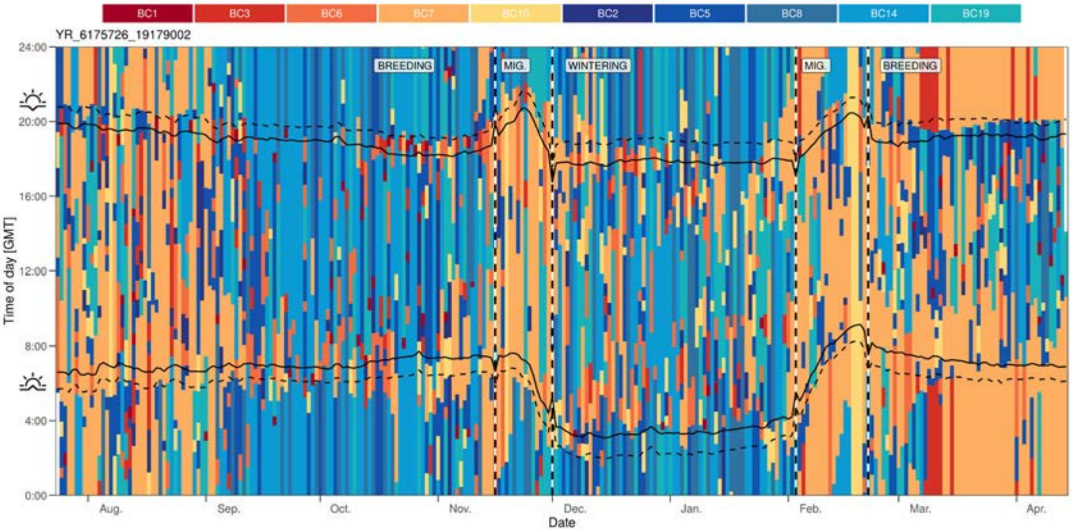
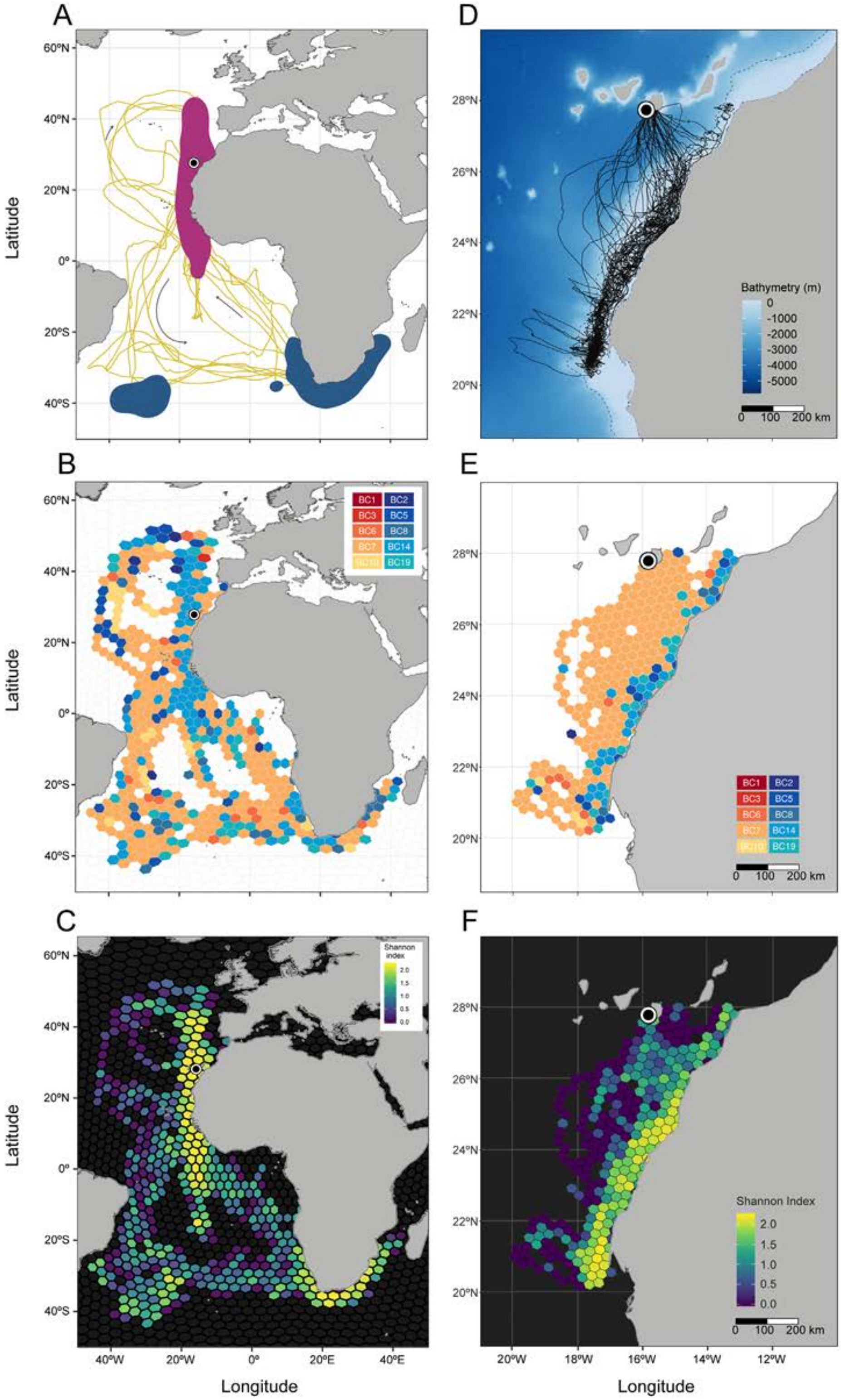


Figure 8: Individual actogram of year-round behaviour of a Cory's. Each coloured segment, of variable length, represents the behavioural mode (i.e. behavioural cluster, BC) identified from unsupervised clustering of wet-dry data from GLS. Each column represents one single day (0-24h). On the x-axis data starts on the day of deployment of the logger and ends on the day of recovery the next year. Black horizontal solid and dashed lines refer to time of local sunrise/sunset and nautical twilight at bird location, respectively. Vertical black-white lines delimit stages of annual life cycle: onset of post-breeding migration, arrival to the main wintering area, onset of pre-breeding migration and arrival to the breeding area, respectively. Note, for example, a clear shift in the circadian rhythm during the wintering spent in the South-African coast, when the bird adjusted behaviour to earlier sunrise and sunset. Code on the top indicates individual and track identity. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

flyway, particularly the BC7 [CF]. Though wet BCs were dominant in the northernmost part of the flyway in the North Atlantic. Regarding behavioural diversity, maximum values of Shannon index rose up in the breeding and the wintering areas were animals spent most of the time over the annual cycle (Fig. 9B). Intermediate diversity was maintained in the pelagic wintering area of the South Atlantic and also along the southern section of the migratory 8-shape loop flyway. However, lowest values were in the northwest section of the 8-shape loop. Focusing in the Canary Current during the incubation period, mostly wet BCs were dominant, especially BC14 [Lsit] over the neritic domain of the African continental shelf (Fig. 9D-F). In

Figure 9 (next page): Spatially-explicit behavioural landscapes of Cory's shearwaters tracked with GLS (A-C) and concurrently with GPS and GLS (D-F). A) Year-round movements and distribution of 8 individuals tracked with GLS across the Atlantic Ocean, all individuals pooled together. Blue areas represent main wintering areas in the central South Atlantic and South African coast (wintering area of a resident individual around Canary Is. is ex-cluded for clarity). Purple area represents the distribution during the breeding stage according to GLS positional data. Yellow lines represent migratory flyway; grey arrows indicate the direction of the trip. D) Short-term foraging trips (n=23) of 19 individuals tracked concurrently with GPS and GLS during the breeding period. Black dashed line delimits the continental shelf. B and E) Main behavioural modes inferred from wet-dry data. Each grid cell shows the BC in which birds invested most of the time. C and F) Map of behavioural diversity based on Shannon Index. Black point refers to the breeding colony. See Material and Methods for details. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.


A
B
C
D
E
F
60ºN
40ºN
20ºN
0º
20ºS
40ºS
Latitude
40ºW
20ºW
0º
20ºE
40ºE
Longitude
BC1
BC2
BC3
BC5
BC6
BC8
BC7
BC14
BC10
BC19
Shannon index
2.0
1.5
1.0
0.5
0.0
28ºN
26ºN
24ºN
22ºN
20ºN
20ºW
18ºW
16ºW
14ºW
12ºW
Bathymetry (m)
0
-1000
-2000
-3000
-4000
-5000
0 100 200 km
Shannon Index

contrast, BC7 [CF] was largely predominant in the pelagic domain out of the continental shelf. Behavioural diversity reached the highest values over the continental shelf, especially in the southernmost region visited, whereas intermediate values were reached in the commuting flyways connecting the foraging grounds with the breeding colony in Gran Canaria Is. The lowest diversity values were located out of the commuting flyways and the continental shelf.

DISCUSSION

Based on wet-dry data, we uncovered both flexible and structural components of the behavioural organization of Cory's shearwaters across the annual life cycle. Our study model, a highly-mobile migratory bird, presents a complex annual cycle that involves central place foraging, ocean-basin long migratory movement, and wandering in wintering areas. The existence of radically different behavioural contexts linked to phenology, and the need to exploit different marine environments over the year, results in different behavioural prevalence and transitions both in time and space.

A multi-scale wet-dry behavioural dynamics

Wet-dry data (i.e. GLS wet-dry dynamics) have high behavioural content of at-sea movement behaviour, spanning scales from elementary motion patterns (e.g. minutes, hours) to complex ecological interactions (e.g. seasonality, annual life cycle). However, the majority of studies using wet-dry data rely on fixed-time segments (e. g. 10s, 10 minutes, 1 hour, etc.), depending on the sampling and aggregation time-scale of the logger. The time-scale is optimized by manufacturers or researchers, mainly as a trade-off between memory storage capacity and battery life (Johnson et al. 2017). Moreover, these values are traditionally aggregated and activity budgets are reported as the proportion of total time spent on water/in flight or splitting into day and night (Phalan et. 2007, Mackley et al. 2010, Dias et al. 2012a).

The fixed-time approach ignores the natural dynamics and transitions between potentially different behavioural modes, limiting the behavioural representation of wet-dry patterns (Bom et al. 2014). Despite some GLS loggers can store continuous data by registering each change and duration of a wet-dry state, analyses of these time-series have been limited to calculation of flight durations and number of landings/take-offs over different time periods (Catry et al. 2004, Shaffer et al. 2001). Indeed, only few studies have accounted for continuous transitions in order to split wet-dry data and identify foraging bouts (Dias et al. 2012b, Gutowsky et al. 2014, Ponchon et al. 2019). In this study, we revealed the presence of strong disruptions on wet-dry cumulative dynamics, and we used this as the basis of our behavioural segmentation and our quantitative description. We suggest this is a better way to capture the inherent multi-scale character of air-water behavioural dynamics in seabirds, ranging from minutes to many hours. More generally, the behavioural mapping protocol used in this work, namely (i) breakpoint analysis to segment wet-dry time-series, (ii) multidimensional characterization of the segments, (iii) unsupervised classification and embedding based on wet-dry metrics similarity, and (iv) interpretation of clusters as behavioural modes, goes much beyond the standard analysis of wet-dry activity data and opens the door to obtain further behavioural information from biologging.

A rich wet-dry behavioural space

Our quantitative analysis reveals the hierarchical and modular nature of seabirds' air-water behavioural dynamics at an unprecedented level of detail. The resulting behavioural space covers a wide range of behavioural scales and can be analysed at different levels of coarse-graining. In this work we identified 10 statistically significant behavioural clusters (BCs) for Cory's shearwaters corresponding to 10 behavioural modes, a number fairly greater than reported in previous studies using wet-dry data for any seabird species (Guilford et al. 2009, Dean et al. 2013, Gutowsky et al. 2014, Conners et al. 2015), yet low enough to ease interpretability.

Two large regions emerged in the behavioural space containing mostly wet and mostly dry behavioural modes, respectively (Fig. 2). Based on the activity metrics measured we were able to distinguish 5 modes within each region.

Dry BCs: BC1 [SF] and BC3 [StF] involved essentially short flight displacements, whereas BC6 [TFLd], BC10 [ShD], and BC7 [CF] involved different types of foraging strategies. Whether covering more extensive areas (BC6 [TFLd]) or showing more intense and localized activity (shallow-surface diving in high-resource patches (BC10 [ShD]), foraging behaviour can be identified by high air-water transitions rates (i.e. landings and take-offs). BC10 [ShD] is likely related to active area-restricted search within foraging patches, including pursuit diving and short shallow-surface dives to catch prey near the surface (Cianchetti-Benedetti et al., 2017). Large distance commuting flights from the breeding colony to foraging grounds or during migration also incorporate short wet periods to rest or forage (BC7 [CF]). This observation is in line with the previously reported ‘‘fly-and-forage’’ strategy of Cory’s shearwaters during migration (Dias et al. 2012b), also found in related species such as Grey-headed albatross or Manx shearwater (Catry et al. 2004, Dean et al. 2013). The median of the maximum duration of continuous flight state in BC7[CF] was about 100 minutes, which is close to flight bout durations described previously for *Calonectris* species (Dias et al. 2012b, Yoda et al. 2017).

Despite in our analysis we omitted incubation behaviour, “dry” states include not only the periods of flight, but also visits to the colony for mating and nest attendance while breeding. We identified prolonged nocturnal visits to the colony in BC3 [StF] and BC7 [CF]. The duration and aim of these visits may be related to different breeding duties according to the date along the breeding stage, from nest defence and matting to brood-guarding and food-provisioning of the chick (Navarro et al. 2007).

Wet BCs: In wet BCs birds spent most of the time on water (> 90% of segment duration on average). While on water, seabirds can show a wide spectrum of behaviours, from feeding to rafting/drifting, resting, bathing and plumage maintenance (Catry et al. 2004, Weimerskirch et al. 2010, Carter et al. 2016, Johnson et al. 2017, Granadeiro et al. 2018). Prey capture, handling, ingestion and digestion also occur in water (Harper 1987) and differences in wet BCs may reflect different feeding strategies according to the ecology and behaviour of targeted prey (Elliot et al. 2008, Weimerskirch 1997, Davoren 2000). Except for BC2 [SRest] that we interpret as short resting periods on water, the rest of wet BCs can be related to (i) surface-foraging strategies (sit-wait-and-dive, surface seizing), e.g. BC5 [ActSWD], BC8 [StlSWD], where birds target prey while sitting on the sea surface (Weimerskirch et al. 1997), or (ii) resting behaviour, e.g. BC14 [LSit] and BC19 [Rest], when birds sit on the sea surface for long times but seldom interrupted by short flights.

Sit-wait-dive activity can be characterized by high wet-dry transitions rates and variable wet state durations (classified as “active”, BC5 [ActSWD]) or else, by low wet-dry transition rates and more regular wet state durations (classified as “still”, BC8 [StlSWD]). BC5[ActSWD] suggests active fishing by sitting on water in patches with abundant prey. Moreover, as observed in individual actograms, BC5 [ActSWD] occurred frequently at dusk, particularly during the breeding season (March-April), indicating also rafting behaviour of shearwaters in the vicinity of the breeding colony, before entering the nest. Rafting has been previously described for other seabird species (Wilson et al. 2008, Weimerskirch et al. 2010, Rubolini et al. 2015) and thus pointed out the importance of waters nearby the colony for seabirds (Carter et al. 2016, Granadeiro et al. 2017).

BC8 [StlSWD] suggests less active or sporadic fishing and may include also night foraging behaviour combined with resting. This type of behaviour has been recorded using biologging techniques in several albatross species that feed during the night on small-sized prey (Catry et al. 2004, Louzao et al. 2014).

Long periods sitting on water (BC14 [LSit]) both during daylight and darkness (Fig. 8, Fig. S10, Fig. S5) suggest important constraints forcing birds to reduce energy expenditure. Moulting is a high-energetically demanding process for birds since it alters flight capability and requires energy allocation to feathers replacement (Bridge et al. 2006, Ramos et al. 2009, Cherel et al. 2016). In Cory's shearwater, moulting of primary feathers starts at the end of the breeding stage (mid-September, Alonso et al. 2008, Ramos et al. 2018) and ends in the wintering area (Camphuysen & Van Der Meer 2001). We found many birds intensively engaged in BC14 [LSit] in the southern-most part of the Canary Current from mid-September to mid-November (Fig. 8, Fig. S10), then migrating to the wintering area (engaged mostly in BC7 [CF]) and then again spending most of the time in BC14 [LSit] upon arrival. This finding suggests that BC14 may be related to active moulting of flight feathers, when birds are forced to sit on the water for prolonged periods of time, and that birds may interrupt moulting to account migration and restart it after arrival to the wintering area.

Behavioural space use: changes in behavioural strategies, organization and complexity

Animals need to cope with different biological constrains over the different stages of the annual cycle, which can lead to a different arrangement of activity budgets (Maclkey et al. 2011, Rayner et al. 2012, Gutowsky et al. 2014, Clay et al. 2017). Moreover, changes of behavioural organization may also reflect environmental and habitat conditions that animals faced (Perón et al. 2010, Freeman et al. 2013).

Despite all BCs appeared in all stages of the annual cycle, we found the relative prevalence was markedly different, and some BCs were dominant at breeding (BC1 [SF], BC2 [SRest], BC3 [StF], BC5 [ActSWD], BC6 [TFLd], BC14 [LSit]), at migration (BC7 [CF] and BC5 [ActSWD]), or at wintering (BC8 [StlSWD], BC6 [TFLd], BC10 [ShD]). Our results are consistent with the idea that during breeding most activity has to do with different feeding strategies and complex high air-water transition rates, whereas during migration birds spent more than 40% of their time in flight (BC7 [CF]) but refill their energy on stopover sites (Dias et al. 2012b, Freeman et al. 2013). Wintering period is important to adult seabirds, especially to restore energy after the breeding and migration and to prepare for the next breeding season. Hence, a generalized decrease in flight and an increase in drifting on water surface are probably related to the stronger biological constrains while wintering (Perón et al. 2010, Mackley et al. 2011, Rayner et al. 2012, Gutowsky et al. 2014, Clay et al. 2017), including the energetically-costly moulting process (Ramos et al. 2009, 2018). These results are clearly observed in our network analysis, which suggests that the behavioural strategy observed during the breeding stage, where animals combine flight and water activity in relatively similar proportions (e.g. time invested in BC7 [CF] and BC14 [LSit], respectively, Fig. 4A-C), is clearly a 'mixture' of the behavioural strategies observed during the migration and wintering periods.

Cory's shearwaters showed more complex behavioural sequences and organization during the breeding and wintering stage, as the larger the entropy rate the larger the behavioural complexity. Migration forces shearwaters to restrict their behavioural organization to sequences between several dominant behavioural modes, mainly dry BC7 [CF] alternated by some wet BC (foraging/resting in stopovers). Transitions between behaviours became more frequent and predictable than during breeding and wintering, as seen by stronger fluxes in our network analysis, and larger values of betweenness centrality of mostly wet BCs (i.e. BC2, BC5, BC8, BC14 and BC19). The latter BCs become relevant during migration as transitions between other BCs pass systematically through them, see Fig. 4).

When evaluating the potential sources of behavioural variability in each BC, we showed that the phenology shapes the variability of the most dominant BCs (BC7, BC14, BC8, and also

BC3) over the annual cycle, yet for non-dominant BCs inter-individual variability is larger compared to the variability introduced by the phenological stages. Our results suggest a multi-level (i.e. individual vs. population) and complex behavioural response of seabirds to both intrinsic and extrinsic (environmental) signals, which expand over a wide range of scales, from daily to seasonal scales.

Global spatially-explicit behavioural landscapes

The construction of spatially-explicit behavioural maps allowed us to reveal differences in the prevalence and diversity of BCs over different areas. Both at global (year-round trips) and local (short-term foraging trips) scales we found the highest behavioural diversity to overlap with upwelling regions of the Atlantic, both during breeding (Canary Current) and wintering (Benguela and Agulhas Currents), This result suggests a positive correlation between hotspots of behavioural diversity and important foraging grounds, so that wet-dry data alone can be used to identify major feeding areas for the species. Contrarily, areas related to migratory routes and transits to foraging grounds showed low behavioural diversity. More generally, these findings indicate a positive correlation between behavioural complexity and habitat complexity, but further investigations are needed to confirm this result with more data and refined spatial statistical methodologies.

Actograms: revealing individual daily and seasonal behavioural patterns

As far as we know, this is the first study showing detailed year-round behaviour of seabird at such detail inferred uniquely from wet-dry data. Actograms (Bäckman et al. 2017) allows for detailed examination of time allocated to the different behavioural modes simultaneously on both daily and seasonal scales. From inspecting temporal changes in behavioural modes we can infer the timing of major annual life cycle events, such as migration (e.g. increase in BC7 [CF]), wintering (prevalence of mostly wet BCs) and return to breeding grounds (nocturnal visits to the colony, e.g. BC7 [CF] and BC3 [StF]). Our protocol combined with the use of actograms may also assist to evaluate the existence of carry-over effects (i.e. processes that influence individual performance in a subsequent season) since deviation from common timing of phenological events and associated changes in behavioural budgets may be expected when individuals fail to success in events such as breeding (Harrison et al. 2011, Catry et al. 2013, Fayet et al. 2016). For example, actograms can easily allow us to infer breeding failure according to time budget allocated to behavioural modes related to nest attendance (BC7 [CF] and BC3 [StF]). Indeed, they can even help to detect an advancement of the moulting period, presumably due to breeding failure (Ramos et al. 2018), when prevalence of the behavioural mode likely related to moult (BC14 [LSit]) advances in the calendar. Therefore, our protocol to decipher behavioural modes combined with appropriated data visualization, such as actograms, provide a powerful tool to depict the timing and time allocation of behaviours over the entire annual cycle.

Framework transferability: applicability on biologging data

Despite we develop our framework with wet-dry data from geolocator-immersion loggers, it could be suited for different tracking data. As a multi-step process, the whole or part of the protocol can be applied on multiple sources of biologging data. Steps of segmentation, dimensionality reduction and clustering carried out to build up a behavioural space and discretize behavioural complexity into interpretable units allows for analysing multidimensional data, such as data recorded by multi-sensor devices. Moreover, functions provided by the "bigMap" R package that we applied here (Garriga & Bartumeus 2018) are especially designed to work with big data, as such generated with multi-sensor devices equipped with accelerometer and able to work for prolonged periods of time.

CONCLUDING REMARKS

In this work we provided a novel framework for behavioural annotation based on wet-dry data from geolocator-immersion loggers, which allows for exploring behavioural organization and diversity in behavioural repertoires at several scales of complexity, from daily to annual scale and from individual to population level. We illustrated the protocol analysing behavioural complexity over the annual cycle of a long-range migratory seabird species tracked with geolocator-immersion sensors, yet the multi-step protocol may be suited to other different sources of biologging data. This framework paves the way for extending behavioural annotation to year-round movements of wildlife, opening new avenues to understand behavioural patterns and the seasonal timing of life-history events of animals spending most of their life out of the human's sight.

AUTHORS' CONTRIBUTION

ZZ, JMRG and FB developed the conceptual framework and design of the study. ZZ analysed data and developed visualizations. JMRG analysed data and developed behavioural landscapes visualization. TM analysed GLS raw data. JGS provided funding for fieldwork and FB for computational resources (Computational Biology Lab, CEAB-CSIC). TM and JMRG carried out the fieldwork. ZZ, JMRG and FB wrote the first version of the manuscript, with later contributions of JGS. All authors revised the last version of this manuscript.

AKNOWLEDGEMENTS

We are thankful to Joan Garriga, the developer of the "bigMap" R package, for the guidance and recommendations on the use of specific functions and parameter selection along the analytical framework.

BIBLIOGRAPHY

Alonso, H., Matias, R., Granadeiro, J.P. & Catry, P. (2009) Moult strategies of Cory's Shearwaters Calonectris diomedea borealis: the influence of colony location, sex and individual breeding status. *Journal of Ornithology*, 150(2): 329-337.

Anderson, D.J. & Perona, P. (2014) Toward a science of computational ethology. *Neuron*, 84(1): 18-31.

Bäckman, J., Andersson, A., Pedersen, L., Sjöberg, S., Tøttrup, A.P. & Alerstam, T. (2017) Actogram analysis of free-flying migratory birds: new perspectives based on acceleration logging. *Journal of Comparative Physiology A*, 203(6-7): 543-564.

Barnes, R. (2018) *dggridR: Discrete Global Grids*. R package version 2.0.3.

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M. K., Smith, F.A. & Lawler, J.J. (2017) Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, 15(6): 299-308.

Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S. L., Owen, M.A., Saltz, D., Cassady, C. & Swaisgood, R.R. (2016) A systematic survey of the integration of animal behavior into conservation. *Conservation Biology*, 30(4): 744-753.

Berman, G.J., Bialek, W. & Shaevitz, J.W. (2016) Predictability and hierarchy in Drosophila behavior. *Proceedings of the National Academy of Sciences*, 113(42): 11943-11948.

Berman, G.J., Choi, D.M., Bialek, W. & Shaevitz, J.W. (2014) Mapping the stereotyped behaviour of freely moving fruit flies. *Journal of The Royal Society Interface*, 11(99): 20140672.

Biau, G. & Scornet, E. (2016) A random forest guided tour. *Test*, 25(2): 197-227.

Birant, D. & Kut, A. (2007) ST-DBSCAN: An algorithm for clustering spatial–temporal data. *Data & Knowledge Engineering*, 60(1): 208-221.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J. et al. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475(7354): 86.

Bom, R.A., Bouten, W., Piersma, T., Oosterbeek, K. & van Gils, J.A. (2014) Optimizing acceleration-based ethograms: the use of variable-time versus fixed-time segmentation. Movement ecology, 2(1): 6.

Bridge, E.S. (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. *Marine Ornithology*, 34: 7-19.

Burger, A.E. & Shaffer, S.A. (2008) Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *The Auk*, 125(2): 253-264.

Camphuysen, C.J. & Van Deer Meer, J.A. (2001) Pelagic distribution, moult and (sub-) specific status of Cory's Shearwaters *Calonectris [d.] diomedea/borealis* wintering off southern Africa. *Marine Ornithology*, 29: 89-96.

Carter, M.I., Cox, S.L., Scales, K.L., Bicknell, A.W., Nicholson, M.D., Atkins, K.M., Morgan, G. Morgan, L. Grecian, J.W., Patrick, S. & Votier, S.C. (2016) GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): implications for foraging ecology and conservation, *Bird Study*, 63(1): 83-95.

Catry, P., Dias, M.P., Phillips, R.A. & Granadeiro, J.P. (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology*, 94(6): 1230-1235.

Catry, P., Granadeiro, J.P., Ramos, J., Phillips, R.A. & Oliveira, P. (2011) Either taking it easy or feeling too tired: old Cory's Shearwaters display reduced activity levels while at sea. *Journal of Ornithology*, 152(3): 549-555.

Catry, P., Phillips, R. A., Phalan, B., Silk, J.R. & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses Thalassarche chrysostoma: integration of movements, activity and feeding events. *Marine Ecology Progress Series*, 280: 261-273.

Cherel, Y., Quillfeldt, P., Delord, K. & Weimerskirch, H. (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution*, 4: 3.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J. & Scott, B.E. (2016) The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecology and Evolution*, 6(3): 727–741.

Cianchetti-Benedetti, M., Catoni, C., Kato, A., Massa, B. & Quillfeldt, P. (2017) A new algorithm for the identification of dives reveals the foraging ecology of a shallow-diving seabird using accelerometer data. *Marine Biology*, 164(4): 77.

Clay, T., Phillips, R.A., Manica, A., Jackson, H. & Brooke, M. (2017) Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Marine Ecology Progress Series*, 579, 139-155.

Conners, M.G., Hazen, E.L., Costa, D.P. & Shaffer, S.A. (2015) Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. *Movement Ecology*, 3(1): 28.

Croxall, J.P., Butchart, S.H., Lascelles, B.E.N., Stattersfield, A.J., Sullivan, B.E.N., Symes, A. & Taylor, P.H.I.L. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, 22(1): 1-34.

Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research, *InterJournal*, *Complex Systems*, 1695(5): 1-9.

Davoren, G.K. (2000) Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Marine Ecology Progress Series*, 198: 283-291.

Dean, B., Freeman, R., Kirk, H., Leonard, K, Phillips, R.A., Perrins, C.M. & Guilford, T. (2013) Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society Interface*, 10(78): 20120570.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2012a) Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. *Marine Ecology Progress Series*, 467: 245-252.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2012b) Do seabirds differ from other migrants in their travel arrangements? On route strategies of Cory's shearwater during its trans-equatorial journey. *PLoS One*, 7(11): e49376.

Dias, M.P., Granadeiro, J.P., Phillips, R.A., Alonso, H. & Catry, P. (2010) Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society B: Biological Sciences*, 278(1713): 1786-1793.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C. Phillips, R.A., Yates, O., Lascelles, B., Garcia Borboroglu, P. & Croxall, J.P. (2019) Threats to seabirds: A global assessment. *Biological Conservation*, 237: 525-537.

Dominoni, D.M., Åkesson, S., Klaassen, R., Spoelstra, K. & Bulla (2017) Methods in field chronobiology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734): 20160247.

Egnor, S.R., & Branson, K. (2016) Computational analysis of behavior. *Annual Review of Neuroscience*, 39: 217-236.

Elliott, K.H., Woo, K., Gaston, A.J., Benvenuti, S., Dall'Antonia, L. & Davoren, G. K. (2008) Seabird foraging behaviour indicates prey type. *Marine Ecology Progress Series*, 354: 289-303.

Fayet, A.L., Freeman, R., Shoji, A., Kirk, H.L., Padget, O., Perrins, C.M. & Guilford, T. (2016) Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, 85(6): 1516-1527.

Fox, J. W. (2010) Geolocator manual v8. British Antarctic Survey, Cambridge.

Freeman, R., Dean, B., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M. & Guilford, T. (2013) Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx Shearwater. *Journal of the Royal Society Interface*, 10(84): 20130279.

Garriga, J. & Bartumeus, F. (2018) bigMap: Big Data Mapping with parallelized t-SNE. *arXiv preprint*, arXiv: 1812.09869.

Gaston, A.J. (2004) *Seabirds: a natural history*. Yale University Press.

González-Solís, J., Croxall, J.P., Oro, D. & Ruiz, X. (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment*, 5(6): 297-301.

Granadeiro, J. P., Campioni, L. & Catry, P. (2018) Albatrosses bathe before departing on a foraging trip: implications for risk assessments and marine spatial planning. *Bird Conservation International*, 28(2): 208-215.

Guilford, T., Meade, J., Willis, J., Phillips, R.A., Boyle, D., Roberts, S., Collett, M., Freeman, R. & Perrins, C.M (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning. *Proceedings of the Royal Society B: Biological Sciences*, 276(1660): 1215-1223.

Gutowsky, S.E., Gutowsky, L.F., Jonsen, I.D., Leonard, M.L., Naughton, M.B., Romano, M.D. & Shaffer, S.A. (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. *Movement Ecology*, 2(1): 23.

Han, S., Taralova, E., Dupre, C. & Yuste, R. (2018) Comprehensive machine learning analysis of Hydra behavior reveals a stable basal behavioral repertoire. *eLife*, 7: e32605.

Harcourt, R., Sequeira, A.M.M., Zhang, X., Roquet, F., Komatsu, K., Heupel, M. et al. (2019) Animal-Borne Telemetry: An Integral Component of the Ocean Observing Toolkit. *Frontiers in Marine Science*, 6:326.

Harper, P. C. (1987) Feeding behaviour and other notes on 20 species of procellariiformes at sea. *Notornis*, 34: 169-192.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R & Bearhop, S. (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80(1): 4-18.

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T. & Bloch, G. (2017) Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734): 20160246.

Hill, R.D. & Braun, M.J. (2001) Geolocation by light level, electronic tagging and tracking in marine fisheries. *Proceedings of the symposium on tagging and tracking marine fish with electronic devices*. East-West Center. University of Hawaii. Berlin: Springer. pp. 315–330.

Igual, J.M., Forero, M.G., Tavecchia, G., González-Solís, J., Martínez-Abraín, A., Hobson, K.A., Ruiz, X. & Oro, D. (2005) Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Marine Biology*, 146(3): 619-624.

Johnson, L.R., Boersch-Supan, P.H., Phillips, R.A. & Ryan, S.J. (2017) Changing measurements or changing movements? Sampling scale and movement model identifiability across generations of biologging technology. *Ecology and Evolution*. 7(22): 9257-9266.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240): aaa2478.

Knell, A.S. & Codling, E.A. (2011) Classifying area-restricted search (ARS) using a partial sum approach. *Theoretical Ecology*, 5: 325-339.

Krebs, C.J. (1999) *Ecological Methodology*. Addison-Wesley.

Krebs, J. R. & Davies, N. B. (2009) *Behavioural ecology: an evolutionary approach*. John Wiley & Sons.

Kuhn M. et al. (2018) *caret: Classification and Regression Training*. R package version 6.0-79.

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S. et al. (2016) Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, 22(4): 422-431.

Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouvé, C., Besson, D., Chastel, O. & Weimerskirch, H. (2010) Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America*, 107(14): 6370–6375.

Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R news*, 2(3): 18-22.

Louzao, M., Wiegand, T., Bartumeus, F. & Weimerskirch, H. (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Movement Ecology*, 2(1): 8.

Mackley, E.K., Phillips, R.A., Silk, J.R., Wakefield, E.D., Afanasyev, V., Fox, J.W. & Furness, R.W. (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Marine Ecology Progress Series*, 406, 291-303.

Mackley, E.K., Phillips, R.A., Silk, J.R., Wakefield, E.D., Afanasyev, V. & Furness, R.W. (2011) At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia. *Marine Biology*, 158(2): 429-438.

Marques, J.C., Lackner, S., Félix, R.L. & Orger, M.B. (2018) Structure of the Zebrafish Locomotor Repertoire Revealed with Unsupervised Behavioral Clustering. *Current Biology*, 28: 181-195.e5.

McIntyre, T. (2014) Trends in tagging of marine mammals: a review of marine mammal biologging studies. *African Journal of Marine Science*, 36(4): 409-422.

Merkel, B., Phillips, R.A., Descamps, S., Yoccoz, N. G., Moe, B. & Strøm, H. (2016) A probabilistic algorithm to process geolocation data. *Movement Ecology*, 4(1): 26.

Meyer, X., MacIntosh, A.J., Kato, A., Chiaradia, A. & Ropert-Coudert, Y. (2015) Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species. *Animal Biotelemetry*, 3(1): 25.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49): 19052-19059.

Navarro, J. & González-Solís, J. (2009) Environmental determinants of foraging strategies in Cory's shearwaters *Calonectris diomedea*. *Marine Ecology Progress Series*, 378: 259-267.

Navarro, J., González-Solís, J. & Viscor, G. (2007) Nutritional and feeding ecology in Cory's shearwater *Calonectris diomedea* during breeding. *Marine Ecology Progress Series*, 351: 261-271.

Nilsson, J.Å., Bronmark, C., Hansson, L.A. & Chapman, B.B. (2014) Individuality in movement: The role of animal personality. In: Hansson et al. (Eds.) *Animal Movement Across Scales*, Oxford university press.

Norris, K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology*, 41: 413-426.

Orben, R. A., Kokubun, N., Fleishman, A. B., Will, A. P., Yamamoto, T., Shaffer, S. A., Paredes, R., Takahashi, A. & Kitaysky, A. S. (2018) Persistent annual migration patterns of a specialist seabird. *Marine Ecology Progress Series*, 593: 231-245.

Passos, C., Navarro, J., Giudici, A. & González-Solís, J. (2010) Effects of extra mass on the pelagic behavior of a seabird. *The Auk*, 127(1): 100-107.

Pebesma, E. (2018) Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10 (1): 439-446.

Péron, C., Delord, K., Phillips, R.A., Charbonnier, Y., Marteau, C., Louzao, M. & Weimerskirch, H. (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Marine Ecology Progress Series*, 416: 267-284.

Phalan, B., Phillips, R.A., Silk, J. R., Afanasyev, V., Fukuda, A., Fox, J., Catry, P., Higuchi, H. & Croxall, J. P. (2007) Foraging behaviour of four albatross species by night and day. *Marine Ecology Progress Series*, 340: 271-286.

Phillips, R.A., Lewis, S., González-Solís, J. & Daunt, F. (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series*, 578: 117-150.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. (2004) Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series*, 266: 265-272.

Phillips, R.A., Xavier, J. C. & Croxall, J.P. (2003) Effects of satellite transmitters on albatrosses and petrels. *The Auk*, 120(4): 1082-1090.

Ponchon, A., Cornulier, T., Hedd, A., Granadeiro, J.P. & Catry, P. (2019) Effect of breeding performance on the distribution and activity budgets of a predominantly resident population of black-browed albatrosses. *Ecology and Evolution*, 9(15): 8702-8713.

R Core Team (2019) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ramos, R., Llabrés, V., Monclús, L., López-Béjar, M. & González-Solís, J. (2018) Costs of breeding are rapidly buffered and do not affect migratory behavior in a long-lived bird species. *Ecology*, 99(9): 2010-2024.

Ramos, R., Militão, T. González-Solís, J. & Ruiz, X. (2009) Moulting strategies of a long-distance migratory seabird, the Mediterranean Cory's Shearwater *Calonectris diomedea diomedea*. *Ibis*, 151:151–159.

Rayner, M.J., Taylor, G.A., Gummer, H.D., Phillips, R.A., Sagar, P.M., Shaffer, S.A. & Thompson, D.R. (2012) The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (Pterodroma axillaris). *Emu - Austral Ornithology*, 112(2): 107-116.

Reyes-González, J. M., Zajková, Z., Morera-Pujol, V., De Felipe, F., Militão, T., Dell'Ariccia, G., Ramos, R., Igual, J. M., Arcos, J. M. & González-Solís, J. (2017) *Migración y ecología espacial de las poblaciones españolas de pardela cenicienta. Monografía n.º 3 del programa Migra*. SEO/BirdLife. Madrid.

Roncon, G., Bestley, S., McMahon, C.R., Wienecke, B. & Hindell, M.A. (2018) View from below: inferring behavior and physiology of Southern Ocean marine predators from dive telemetry. *Frontiers in Marine Science*, 5: 1-23.

Rubolini, D., Maggini, I., Ambrosini, R., Imperio, S., Paiva, V.H., Gaibani, G., Saino, N. & Cecere, J.G. (2015) The effect of moonlight on Scopoli's Shearwater *Calonectris diomedea* colony attendance patterns and nocturnal foraging: a test of the foraging efficiency hypothesis. *Ethology*, 121(3): 284-299.

Sánchez-Román, A., Gómez-Navarro, L., Fablet, R., Oro, D., Mason, E., Arcos, J.M., Ruiz, S. & Pascual, A. (2019) Rafting behaviour of seabirds as a proxy to describe surface ocean currents in the Balearic Sea. *Scientific Reports*, 9(1): 17775.

Sangster, G., Collinson, J.M. Crochet, P.A., Knox, A.G., Parkin, D.T. & Votier, S.C. (2012) Taxonomic recommendations for British birds: eighth report. *Ibis*, 154: 874-883.

Schreiber, E.A. & Burger, J. (2001) *Biology of marine birds*. CRC press.

Shaffer, S.A., Costa, D.P. & Weimerskirch, H. (2001) Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology*, 70: 864-874.

Shamoun-Baranes, J., Bouten, W., Camphuysen, C.J. & Baaij, E. (2011) Riding the tide: intriguing observations of gulls resting at sea during breeding. *Ibis*, 153: 411-415.

Sih, A., Stamps, J., Yang, L.H., McElreath, R. & Ramenofsky, M. (2010) Behavior as a key component of integrative biology in a human-altered world. *Integrative and comparative biology*, 50(6): 934-944.

Thiebault, A. & Tremblay, Y. (2013) Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird. *Behavioral Ecology and Sociobiology*, 67(6): 1013-1026.

Todd, J.G., Kain, J.S. & Bivort, B.L. (2017) Systematic exploration of unsupervised methods for mapping behavior. *Physical Biology*, 14(1): 015002.

van der Maaten, L. & Hinton, G. (2008). Visualizing data using t-sne. *Journal of Machine Learning Research*, 9: 2579-2605.

Vandenabeele, S.P., Shepard, E.L., Grogan, A. & Wilson, R.P. (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology*, 159(1): 1-14.

Vandenabeele, S.P., Wilson, R.P. & Grogan, A. (2011) Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare-The UFAW Journal*, 20(4): 559.

Vegetabile, B. G., Stout-Oswald, S.A., Davis, E.P., Baram, T.Z. & Stern, H.S. (2019) Estimating the entropy rate of Finite Markov Chains with application to behavior studies. *Journal of Educational and Behavioral Statistics*, 44(3): 282-308.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(3-4): 211-223.

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J.C. & Goya, E. (2010) Use of social information in seabirds: compass rafts indicate the heading of food patches. *PloS one*, 5(3): e9928.

Weimerskirch, H., Wilson, R.P. & Lys, P. (1997) Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series*, 151: 245-254.

Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, 2016.

Wilson, L.J., McSorley, C.A., Gray, C.M., Dean, B.J., Dunn, T. E., Webb, A. & Reid, J. B. (2008) Rafting behaviour of Manx Shearwaters *Puffinus puffinus*. *Seabird*, 21: 85-92.

Wilson, R.P. & Vandenabeele, S.P. (2012) Technological innovation in archival tags used in seabird research. *Marine Ecology Progress Series*, 451: 245-262.

Wong, B. & Candolin, U. (2015) Behavioral responses to changing environments. Behavioral Ecology, 26(3): 665-673.

Yoda, K., Shiomi, K. & Sato, K. (2014) Foraging spots of streaked shearwaters in relation to ocean surface currents as identified using their drift movements. *Progress in Oceanography*, 122: 54-64.

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M. & Yamamoto, M. (2017) Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology*, 27(21): R1152-R1153.

Supplementary material

SUPPLEMENTARY FIGURES

Fig S1: Segmentation of wet-dry data applying different time windows
Fig S2: Selection of time window
Fig S3: Values of activity variables mapped on the behavioural landscape
Fig S4: Summary metrics plot per wet-dry activity metrics
Fig S5: Temporal distribution of behaviours.
Fig S6: Random forest variable importance
Fig S7: Association between BCs and phonological stage (Pearson's residuals of chi-square test of independence)
Fig S8: Changes in the behavioural landscape of Cory's shearwater over the breeding cycle: fuzzy clustering of pixels per stages
Fig S9: Transition prob. Matrices
Fig. 10: Individual actograms of year-round behavior of 8 Cory's shearwater

SUPPLEMENTARY TABLES

Table S1: Tracking details and deployments
Table S2: Summary table of network metrics results for each stage.
Table S3: Results from the one-way repeated-measures ANOVA to test the effect of stage on amount of time invested in each behavioral cluster (BC)

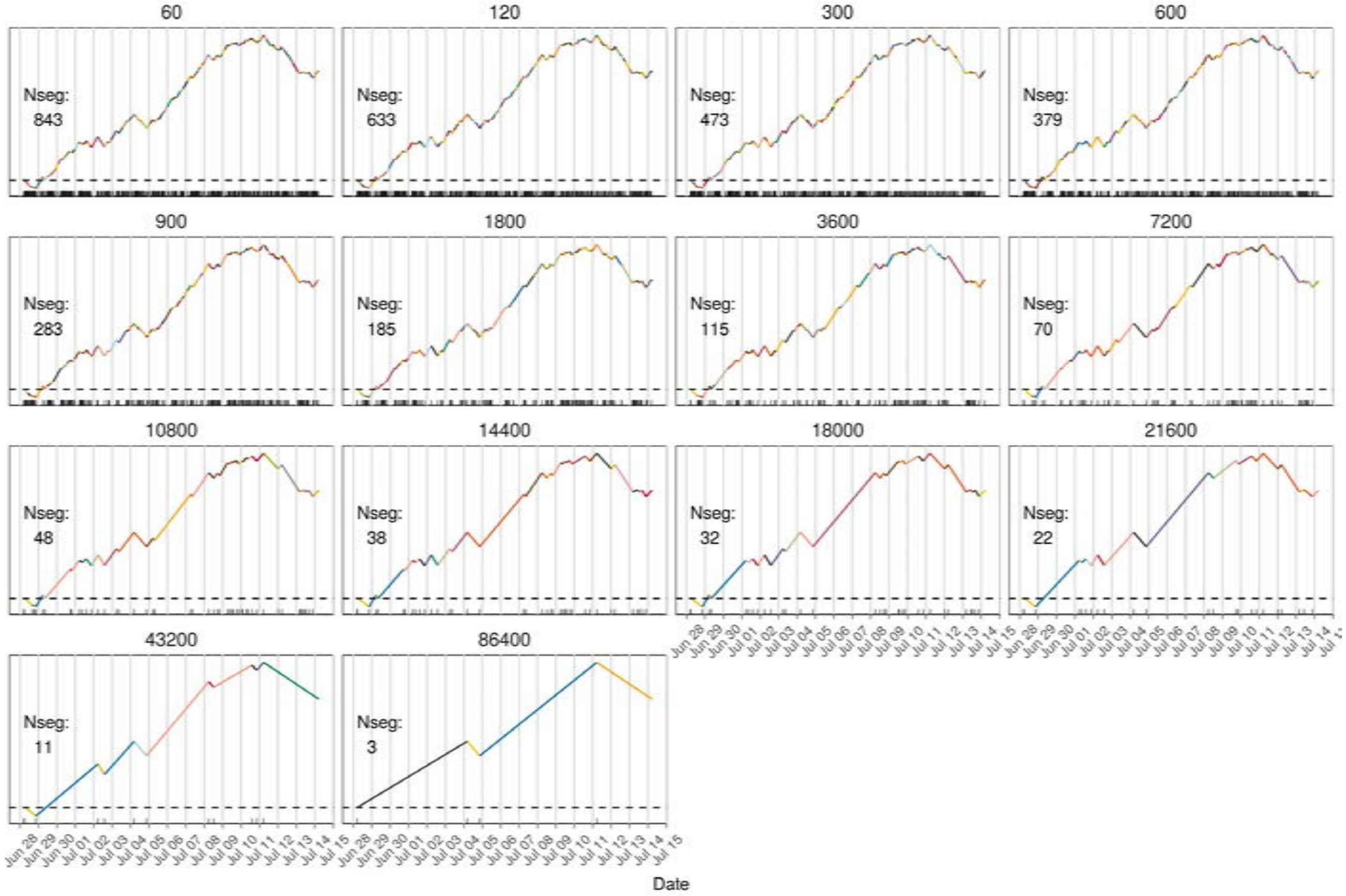


Fig S1: Effect of time window selection on segmentation of wet-dry data from Cory's shearwater, showed on example of one foraging trip of 17 days of duration (see Fig. 1a in the main text). Each facet represents segmentation using the time window showed above (in seconds), from 1 min to 24 h. Smaller time window results in higher number of segments (Nseg. on the left side of the plot). The rug lines on the bottom refer to the location of breakpoints between segments on the time axis. The lightgrey vertical lines represent division between days. For analysis presented in this work we chose the time window of 60 min (3600 s). To facilitate the distinction of segments, they are colour-coded randomly.

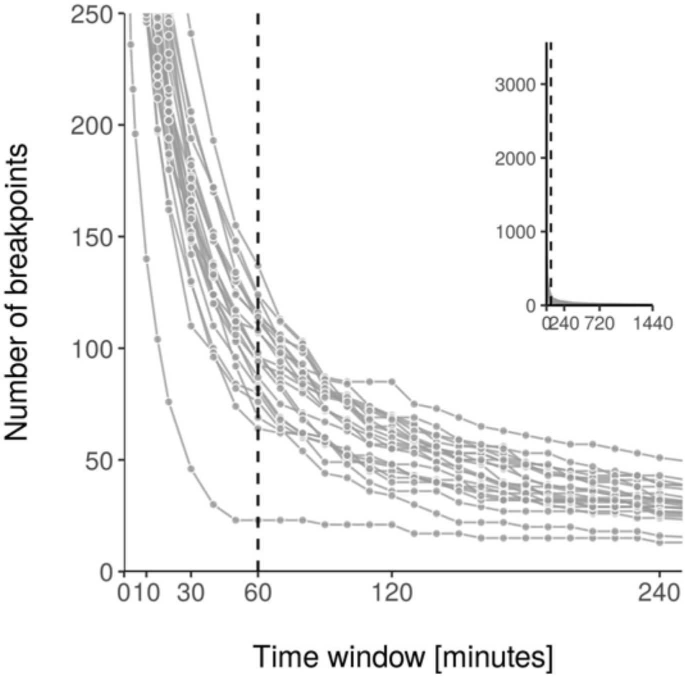


Figure S2: Selection of time window used for segmentation of wet-dry cumulative time series. Each line represents one track, GLS and GPS tracks pooled together. We used various time windows (from 1 min up to 24 h, see Fig. S1) to study the relation between the time window size applied and resulting number of breakpoints. Inset represent whole range of values. For simplicity of the presented approach, after visual examination we used 60 min time window to segment all tracks (darkgrey vertical dashed line in the plot).

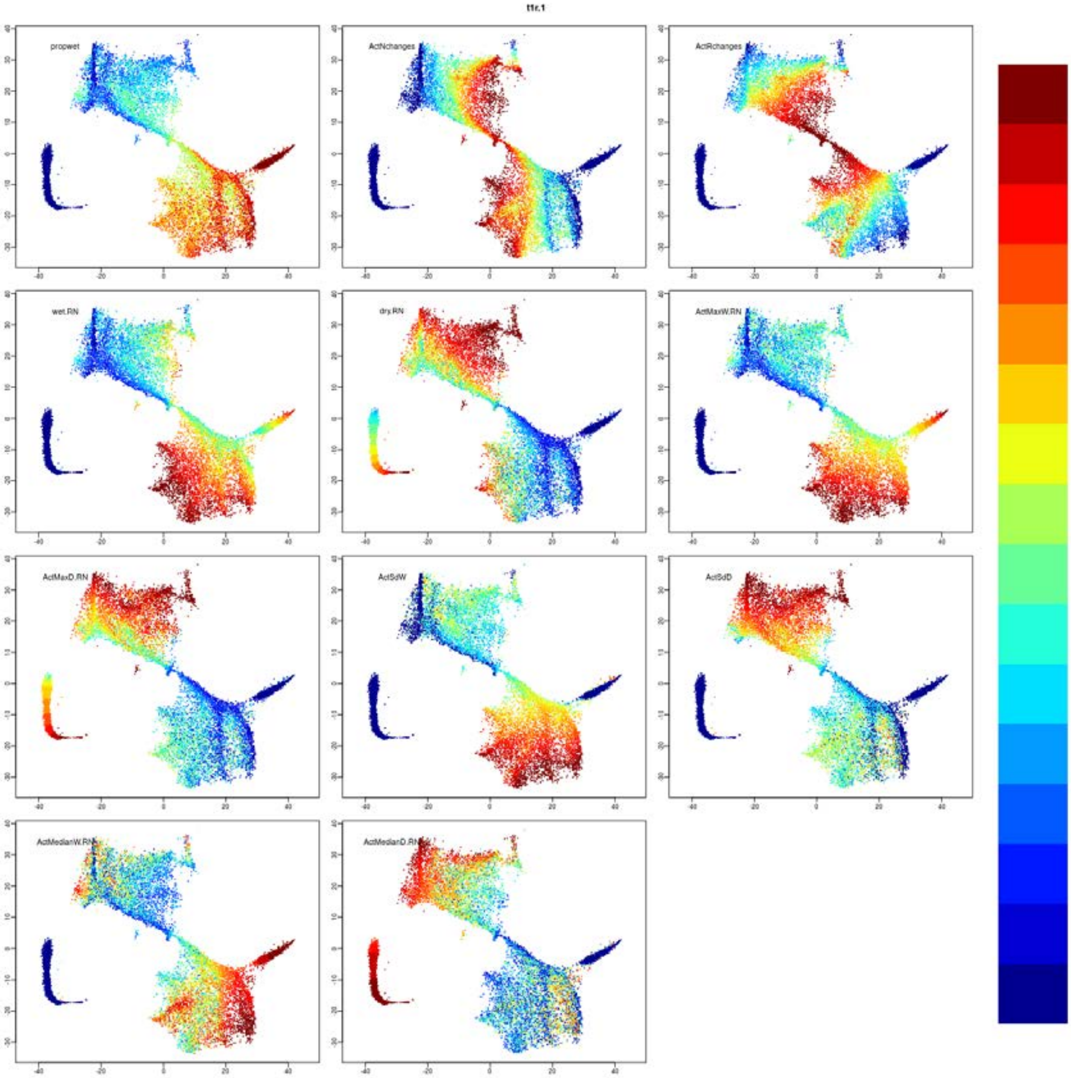


Figure S3: Values of activity variables mapped on the behavioural space, as default output from the “bigMap” R package. Each point represents a segment obtained from wet-dry behavioural dynamics data. Values of each variable are scaled to range from low (blue) to high values (red). Activity metrics: Prop.W = proportion wet, Dur.W = duration wet, Dur.D = duration dry, Nchanges = number of changes, Rchanges = rate of changes, Median.W = median wet duration, Median.D = median dry duration, SD.W = standard deviation wet durations, SD.D = standard deviation dry durations, Max.W = maximum wet duration, Max.D = maximum dry duration.

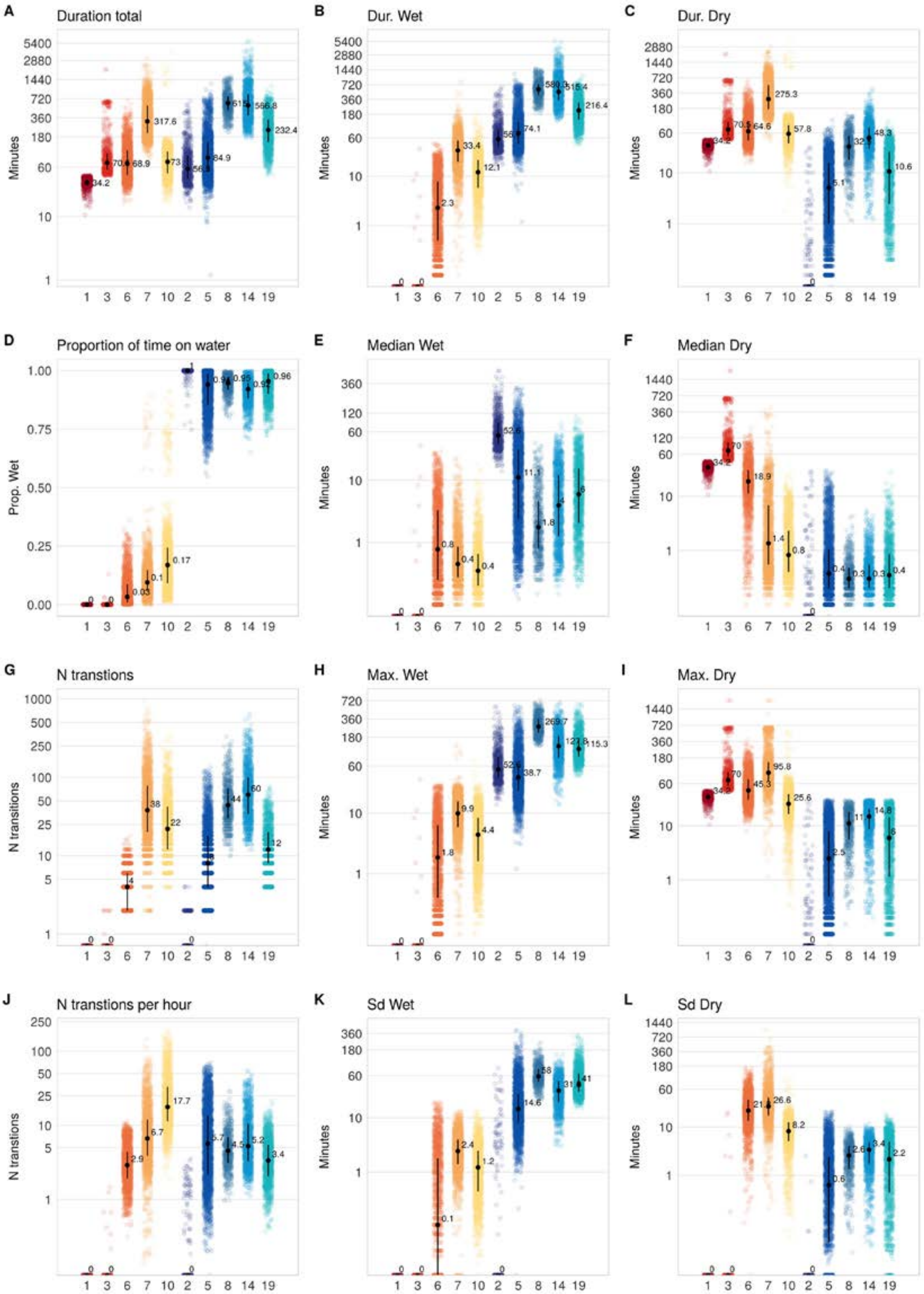

A
Duration total
Minutes
5400
2880
1440
720
360
180
60
10
1
34.2
70
68.9
317.6
73
56.3
84.9
615
566.8
232.4
1 3 6 7 10 2 5 8 14 19
B
Dur. Wet
Minutes
5400
2880
1440
720
360
180
60
10
1
0
0
2.3
33.4
12.1
56
74.1
580.3
515.4
216.4
1 3 6 7 10 2 5 8 14 19
C
Dur. Dry
Minutes
2880
1440
720
360
180
60
10
1
34.2
70.5
64.6
275.3
57.8
0
5.1
32
48.3
10.6
1 3 6 7 10 2 5 8 14 19
D
Proportion of time on water
Prop. Wet
1.00
0.75
0.50
0.25
0.00
0
0
0.03
0.1
0.17
1
0.94
0.95
0.92
0.96
1 3 6 7 10 2 5 8 14 19
E
Median Wet
Minutes
360
120
60
10
1
0
0
0.8
0.4
0.4
52.6
11.1
1.8
4
6
1 3 6 7 10 2 5 8 14 19
F
Median Dry
Minutes
1440
720
360
120
60
10
1
34.2
70
18.9
1.4
0.8
0
0.4
0.3
0.3
0.4
1 3 6 7 10 2 5 8 14 19
G
N transtions
N transitions
1000
500
250
100
50
25
10
5
1
0
0
4
38
22
0
8
44
60
12
1 3 6 7 10 2 5 8 14 19
H
Max. Wet
Minutes
720
360
180
60
10
1
0
0
1.8
9.9
4.4
52.6
38.7
269.7
127.8
115.3
1 3 6 7 10 2 5 8 14 19
I
Max. Dry
Minutes
1440
720
360
180
60
10
1
34.2
70
45.3
95.8
25.6
0
2.5
11
14.8
6
1 3 6 7 10 2 5 8 14 19
J
N transtions per hour
N transtions
250
100
50
25
10
5
1
0
0
2.9
6.7
17.7
0
5.7
4.5
5.2
3.4
1 3 6 7 10 2 5 8 14 19
K
Sd Wet
Minutes
360
180
60
10
1
0
0
0.1
2.4
1.2
0
14.6
58
31
41
1 3 6 7 10 2 5 8 14 19
L
Sd Dry
Minutes
1440
720
360
180
60
10
1
0
0
21.4
26.6
8.2
0
0.6
2.6
3.4
2.2
1 3 6 7 10 2 5 8 14 19

Figure S4 (previous page): Median values (black point and numerical) and interquartile range of 11 activity metrics and total duration of the segment (not included as input variable due to multi-collinearity) averaged over all segments for 10 behavioural clusters. Black point and numeric value refer to medians, point range to interquartile range. Coloured points in the background represent segments obtained from breakpoint algorithm applied to wet-dry data. Points are jittered for clarity. Note the variable range and logarithmic scale on y-axis. Note that rate of changes is expressed here as the number of changes per hour (N of changes h^{-1}) to ease interpretability. A – J illustrates the different variable metrics. BCs semantics on the y axis: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest. Activity metrics: Prop.W = proportion wet, Dur.W = duration wet, Dur.D = duration dry, Nchanges = number of changes, Rchanges = rate of changes, Median.W = median wet duration, Median.D = median dry duration, SD.W = standard deviation wet durations, SD.D = standard deviation dry durations, Max.W = maximum wet duration, Max.D = maximum dry duration. Activity metrics: Prop.W = proportion wet, Dur.W = duration wet, Dur.D = duration dry, Nchanges = number of changes, Rchanges = rate of changes, Median.W = median wet duration, Median.D = median dry duration, SD.W = standard deviation wet durations, SD.D = standard deviation dry durations, Max.W = maximum wet duration, Max.D = maximum dry duration.

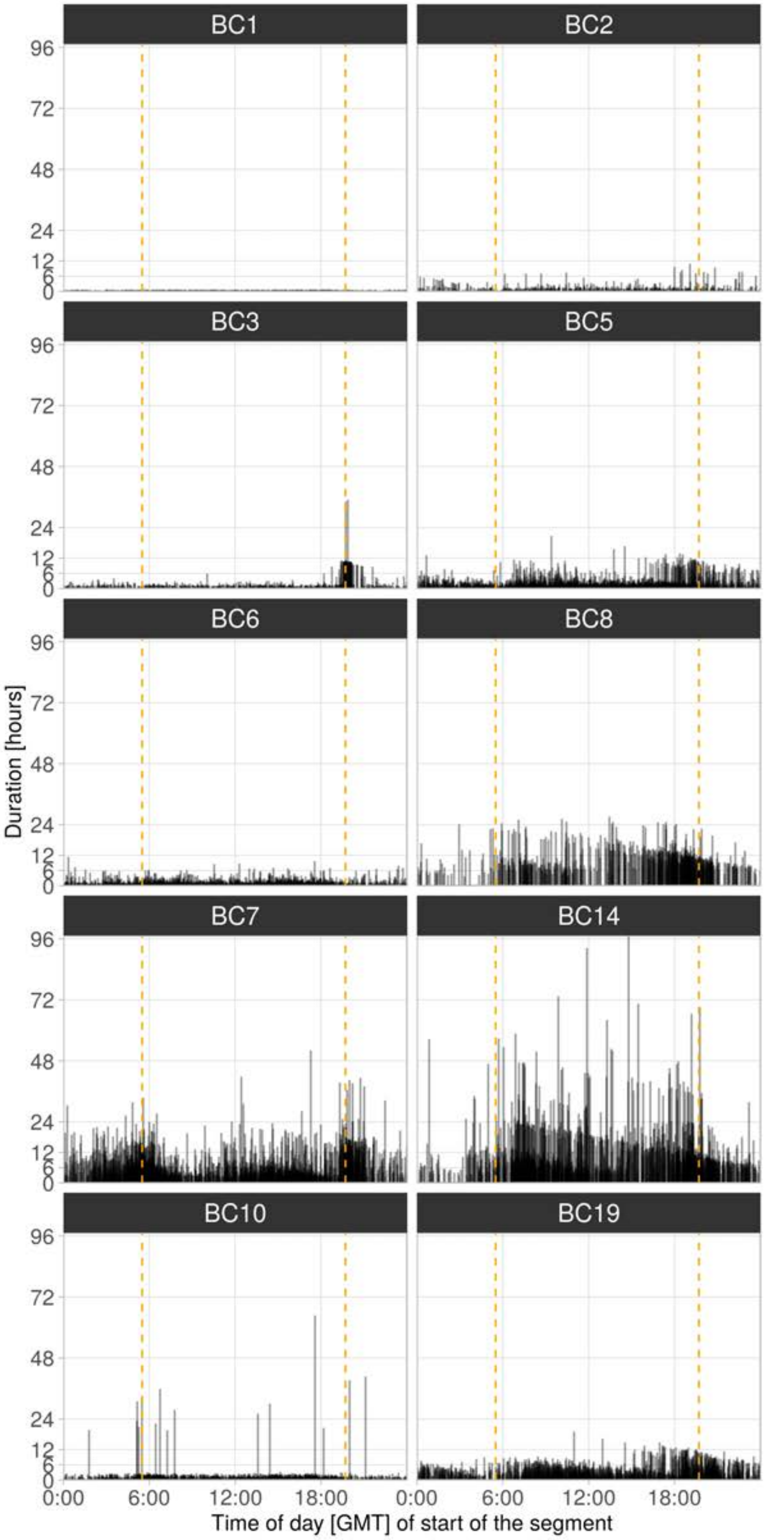

BC1
BC2
BC3
BC5
BC6
BC8
BC7
BC14
BC10
BC19
Duration [hours]
0
6
12
24
48
72
96
0:00
6:00
12:00
18:00
Time of day [GMT] of start of the segment

Figure S5 (previous page): Temporal distribution of behaviours of Cory's shearwater derived from GLS and wet-dry immersion data. Each facet corresponds to one behavioural mode (i.e. behavioural cluster, BC). Each black line represents one behavioural segment, the length corresponds to the duration of the segment. The orange vertical dashed lines correspond to the average nautical twilight over the year. BCs in the left and right column correspond to mostly dry and wet segments, respectively. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

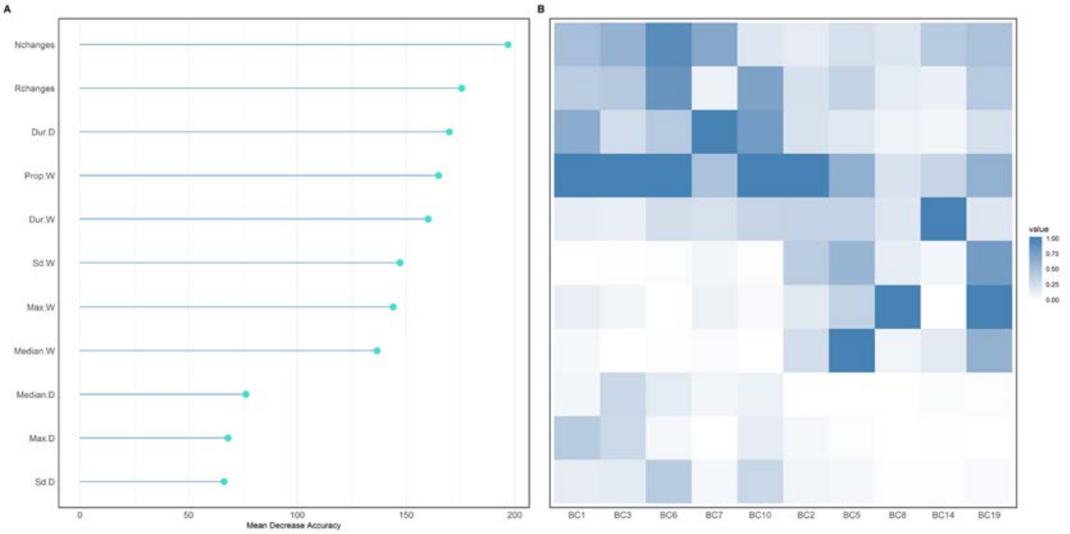


Figure S6: Variable importance plots of activity metrics used for identification of behavioural clusters (BCs) of Cory's shearwater. Values reflect the mean decrease in accuracy (MDA), resulting from Random Forest models (see Methods for more details). Higher values indicate variables that contribute more to the identification of BCs. (A) Overall variable importance of 11 activity metrics used as input variables in the protocol to classify wet-dry activity segments into BCs (see Methods). (B) Case-wise variable importance for each BC, values were rescaled to range between 0-1 for each BC. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest. Activity metrics: Prop.W = proportion wet, Dur.W = duration wet, Dur.D = duration dry, Nchanges = number of changes, Rchanges = rate of changes, Median.W = median wet duration, Median.D = median dry duration, SD.W = standard deviation wet durations, SD.D = standard deviation dry durations, Max.W = maximum wet duration, Max.D = maximum dry duration.

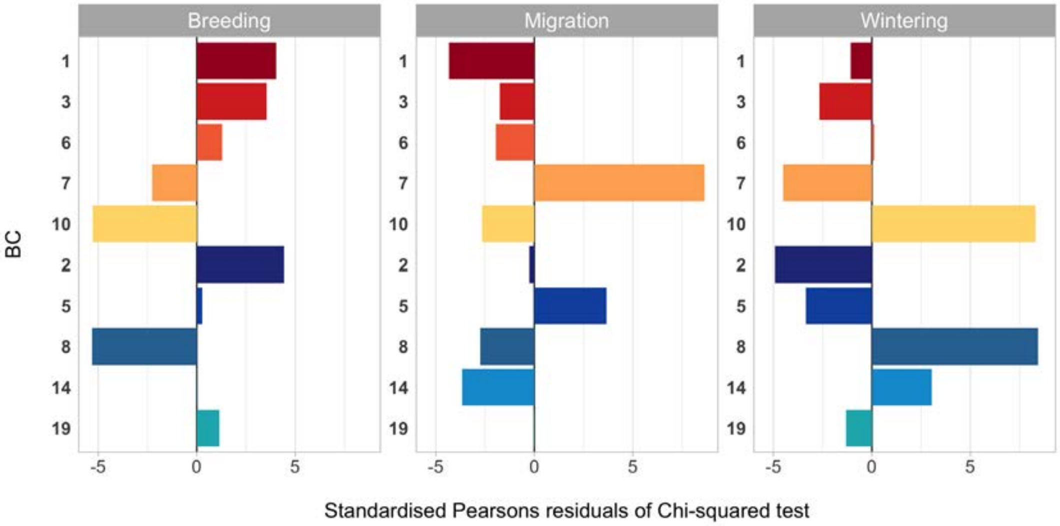


Figure S7: Standardized Pearson's residuals of chi-squared test of independence (chi.sq = 297.524, df = 18, $p < 0.001$) testing for association between behavioural clusters and phenological stage. Values below -2 and above 2 indicate significant association. BC1, BC2 and BC3 are highly associated with breeding stage (observed more than expected), BC5 and BC7 with migration and BC8, BC10 and BC14 with wintering. On the other side, BC10 and BC14 were observed less than expected during breeding, similarly BC1, BC8, BC10 and BC14 during migration and BC2, BC3, BC5 and BC7 during wintering. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

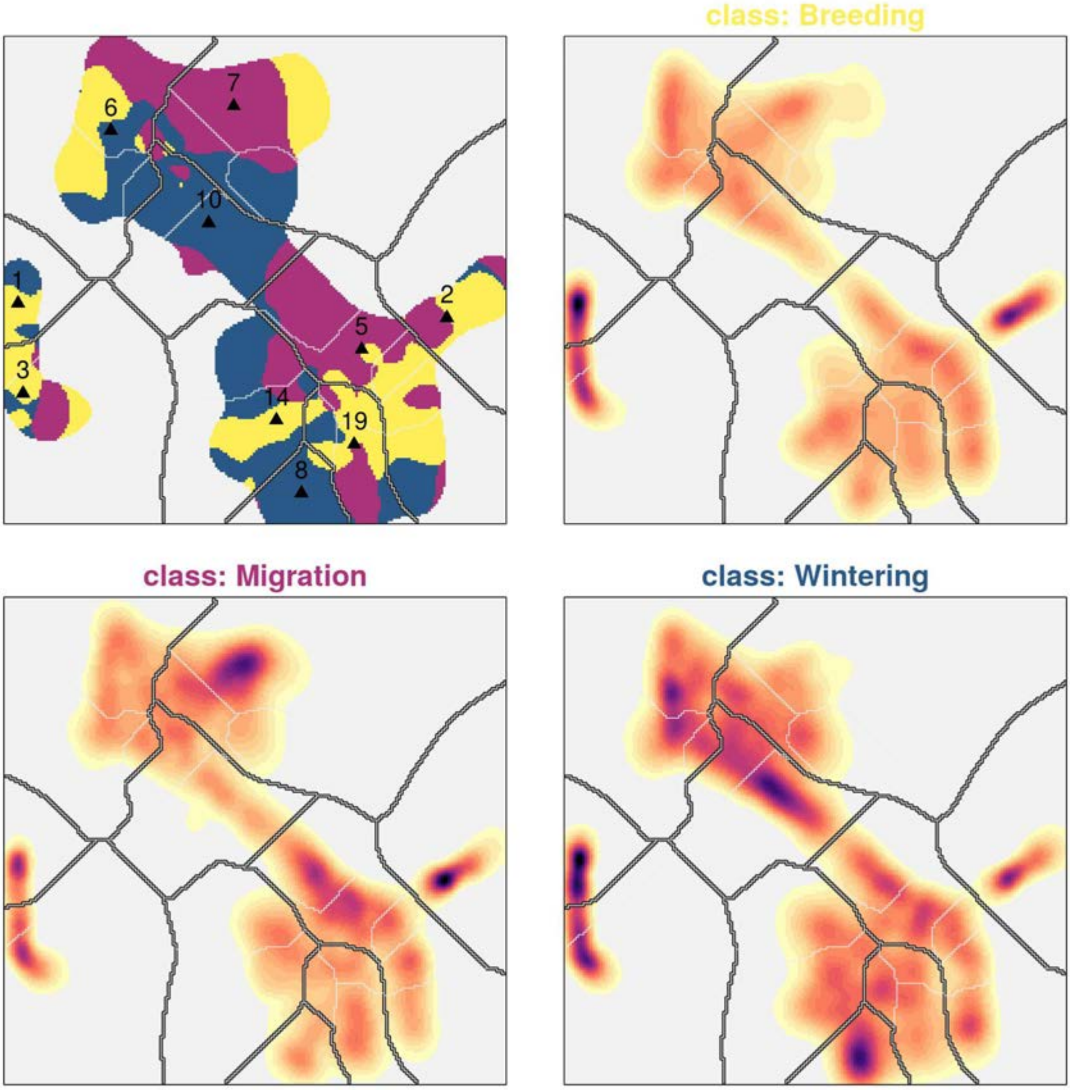
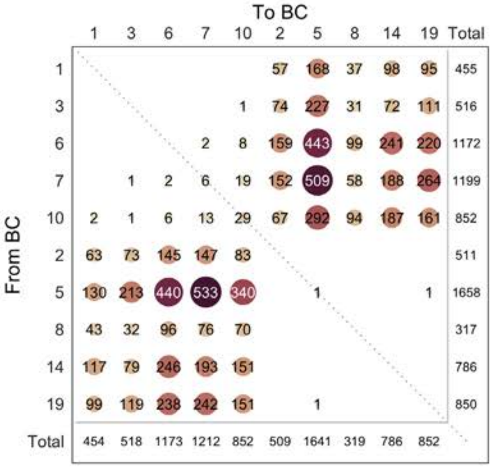
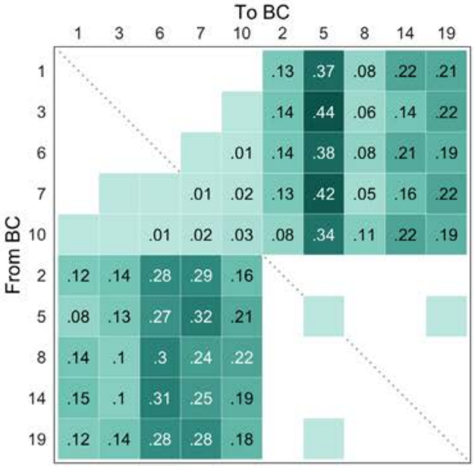


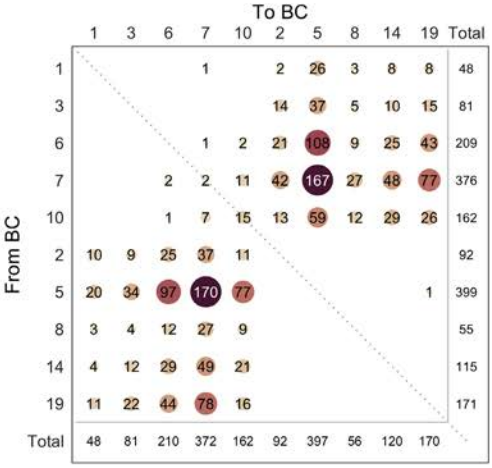
Figure S8: Changes in the behavioural space of Cory's shearwater over the annual cycle (breeding, migration, wintering). (A) Colour of each cell of the grid represents the dominant stage of the annual cycle, estimated as the highest probability to belong to one of three stages: breeding (yellow), migration (purple), wintering (darkblue). Black triangles and numbers correspond to the peaks of 10 dominant behavioural clusters. (B - D) Density estimation (colour scale from low yellow to high purple) over the behavioural space of three stages: (B) breeding, (C) migration (pooled together postnuptial and prenuptial migration) and (D) wintering. Darkgrey lines delimitate the borders of 10 behavioural clusters. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.



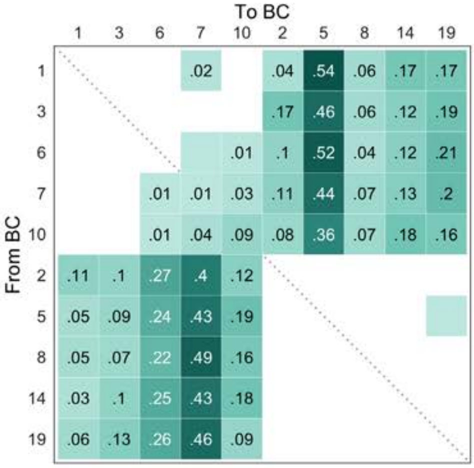
	1	3	6	7	10	2	5	8	14	19	Total
1						57	168	37	98	95	455
3					1	74	227	31	72	111	516
6				2	8	159	443	99	241	220	1172
7		1	2	6	19	152	509	58	188	264	1199
10	2	1	6	13	29	67	292	94	187	161	852
2	63	73	145	147	83						511
5	130	213	440	533	340		1			1	1658
8	43	32	96	76	70						317
14	117	79	246	193	151						786
19	99	119	238	242	151		1				850
Total	454	518	1173	1212	852	509	1641	319	786	852	



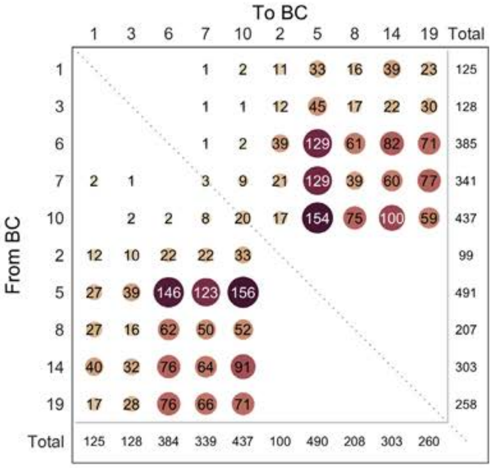
	1	3	6	7	10	2	5	8	14	19
1						.13	.37	.08	.22	.21
3						.14	.44	.06	.14	.22
6					.01	.14	.38	.08	.21	.19
7				.01	.02	.13	.42	.05	.16	.22
10			.01	.02	.03	.08	.34	.11	.22	.19
2	.12	.14	.28	.29	.16					
5	.08	.13	.27	.32	.21					
8	.14	.1	.3	.24	.22					
14	.15	.1	.31	.25	.19					
19	.12	.14	.28	.28	.18					



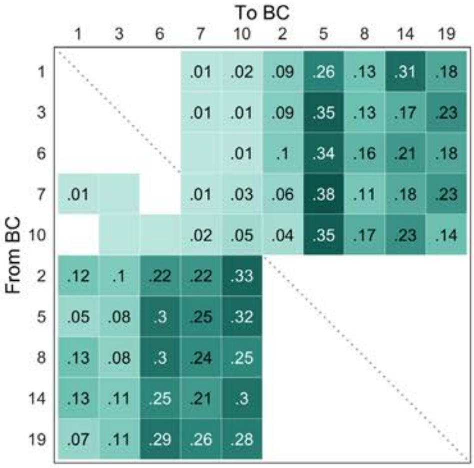
	1	3	6	7	10	2	5	8	14	19	Total
1				1		2	26	3	8	8	48
3						14	37	5	10	15	81
6				1	2	21	108	9	25	43	209
7			2	2	11	42	167	27	48	77	376
10			1	7	15	13	59	12	29	26	162
2	10	9	25	37	11						92
5	20	34	97	170	77					1	399
8	3	4	12	27	9						55
14	4	12	29	49	21						115
19	11	22	44	78	16						171
Total	48	81	210	372	162	92	397	56	120	170	



	1	3	6	7	10	2	5	8	14	19
1				.02		.04	.54	.06	.17	.17
3						.17	.46	.06	.12	.19
6					.01	.1	.52	.04	.12	.21
7			.01	.01	.03	.11	.44	.07	.13	.2
10			.01	.04	.09	.08	.36	.07	.18	.16
2	.11	.1	.27	.4	.12					
5	.05	.09	.24	.43	.19					
8	.05	.07	.22	.49	.16					
14	.03	.1	.25	.43	.18					
19	.06	.13	.26	.46	.09					



	1	3	6	7	10	2	5	8	14	19	Total
1				1	2	11	33	16	39	23	125
3				1	1	12	45	17	22	30	128
6				1	2	39	129	61	82	71	385
7	2	1		3	9	21	129	39	60	77	341
10		2	2	8	20	17	154	75	100	59	437
2	12	10	22	22	33						99
5	27	39	146	123	156						491
8	27	16	62	50	52						207
14	40	32	76	64	91						303
19	17	28	76	66	71						258
Total	125	128	384	339	437	100	490	208	303	260	



	1	3	6	7	10	2	5	8	14	19
1				.01	.02	.09	.26	.13	.31	.18
3				.01	.01	.09	.35	.13	.17	.23
6					.01	.1	.34	.16	.21	.18
7	.01			.01	.03	.06	.38	.11	.18	.23
10				.02	.05	.04	.35	.17	.23	.14
2	.12	.1	.22	.22	.33					
5	.05	.08	.3	.25	.32					
8	.13	.08	.3	.24	.25					
14	.13	.11	.25	.21	.3					
19	.07	.11	.29	.26	.28					

Figure S9 (previous page): Transitions between behavioural clusters of Cory's shearwater. Left panels (first column) reflects counts of transitions from and to behavioral clusters (BCs) for each stage of breeding cycle represented in rows: A) breeding, B) migration and C) wintering. Right panels (second column) reflects transition probabilities from BC at time t to BC at t+1. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

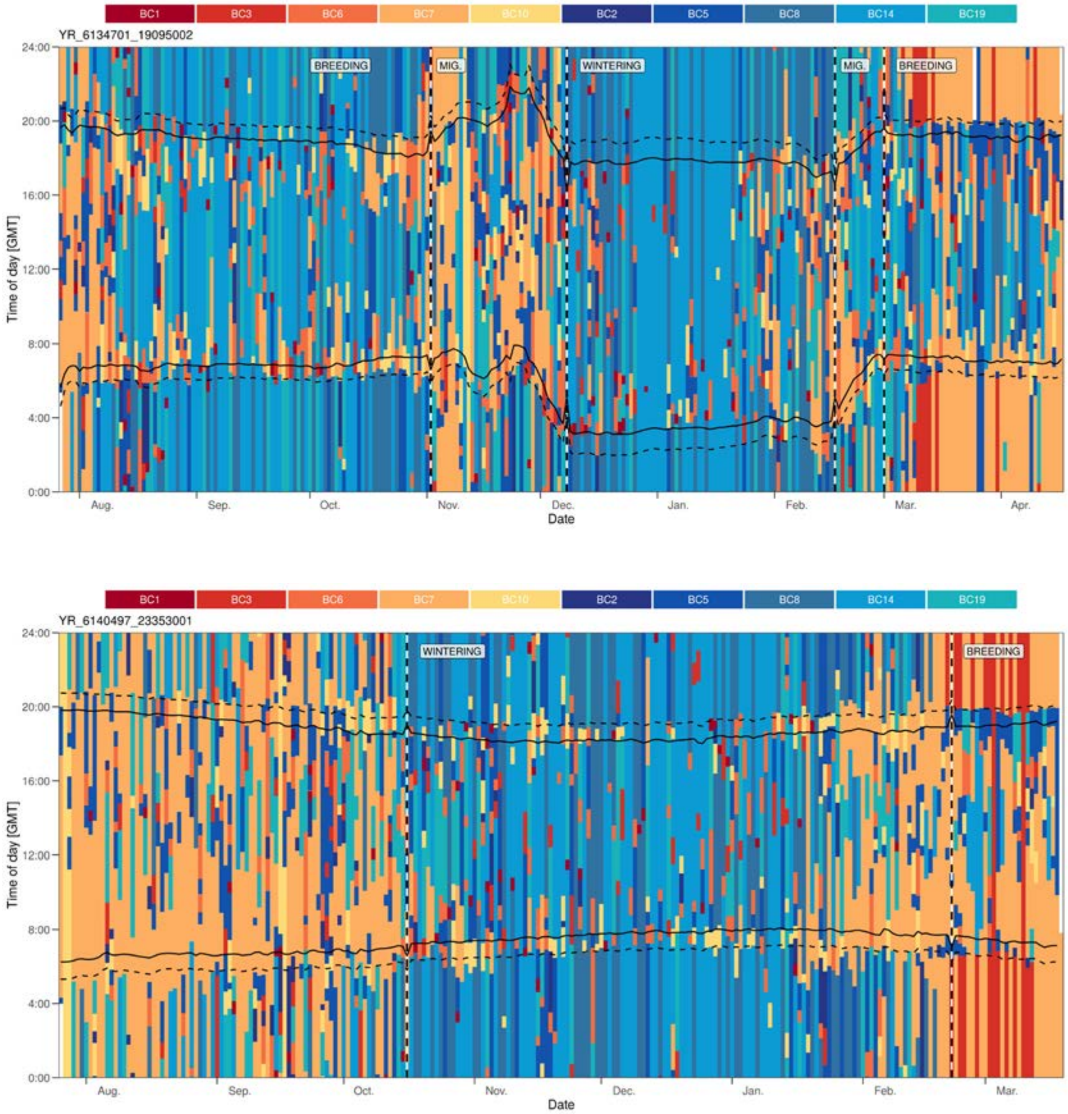


Fig. S10 (also in next three pages): Individual actograms of the year-round behavior of 8 individuals of Cory's shearwater. Each coloured segment, of variable length, represents a behavioural mode (i.e. behavioural cluster, BC) identified from unsupervised clustering of wet-dry data from geolocator-immersion loggers. Each column represents one single day (0-24h). On the x-axis data starts on the day of deployment of the logger and ends on the day of recovery the next year. Black horizontal solid and dashed lines refer to time of local sunrise/sunset and nautical twilight at bird location, respectively. Vertical black-white lines delimit stages of annual life cycle: onset of post-breeding migration, arrival to the main wintering area, onset of pre-breeding migration and arrival to the breeding area. Individual and track identity, and corresponding breeding success are indicated in the top border. BCs semantics: BC1 = SF, BC3 = StF, BC6 = TFLd, BC7 = CF, BC10 = ShD, BC2 = SRest, BC5 = ActSWD, BC8 = StlSWD, BC14 = Lsit, BC19 = Rest.

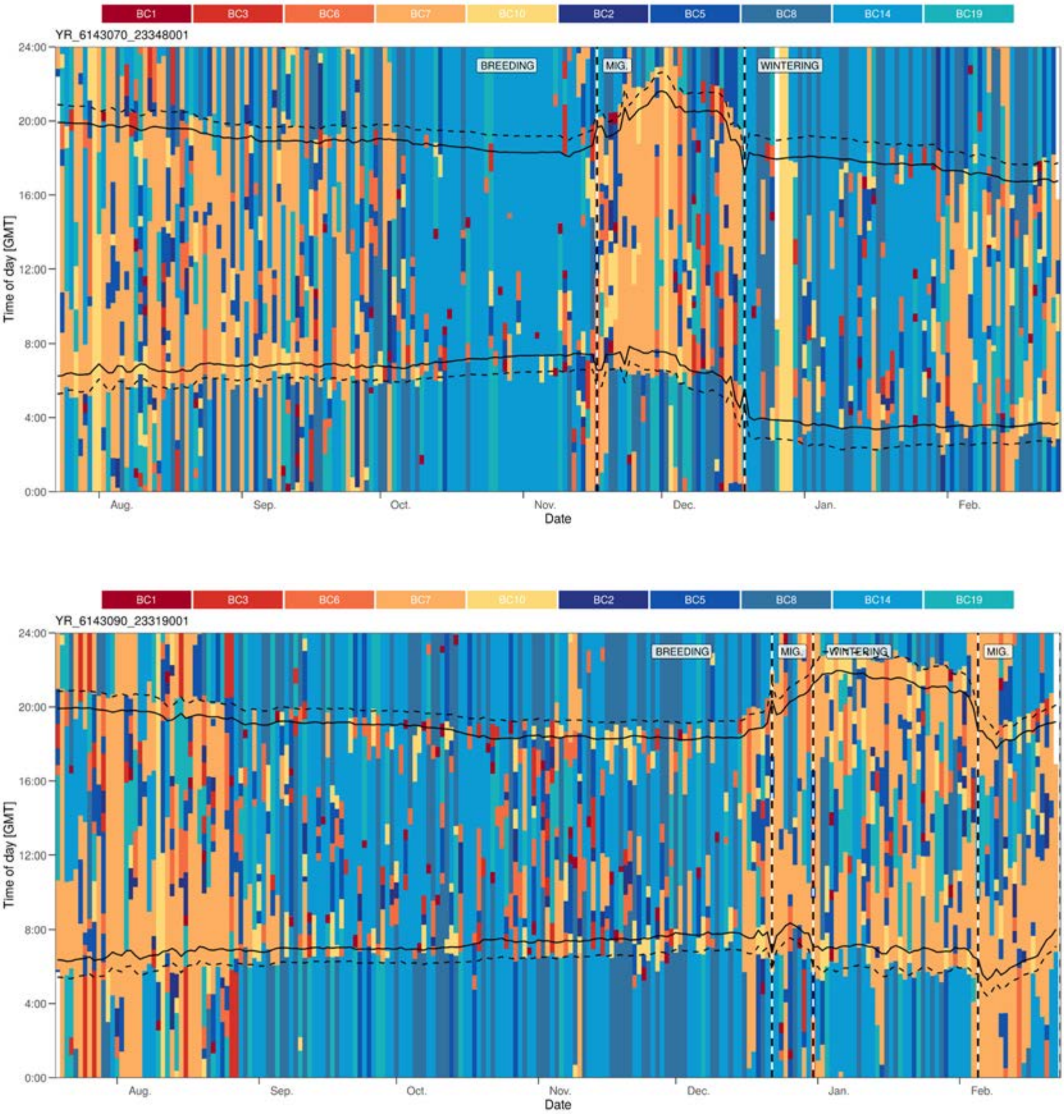

BC1
BC3
BC6
BC7
BC10
BC2
BC5
BC8
BC14
BC19
YR_6143070_23348001
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Time of day [GMT]
BREEDING
MIG.
WINTERING
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Date
BC1
BC3
BC6
BC7
BC10
BC2
BC5
BC8
BC14
BC19
YR_6143090_23319001
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Time of day [GMT]
BREEDING
MIG.
WINTERING
MIG.
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Date

Fig. S10

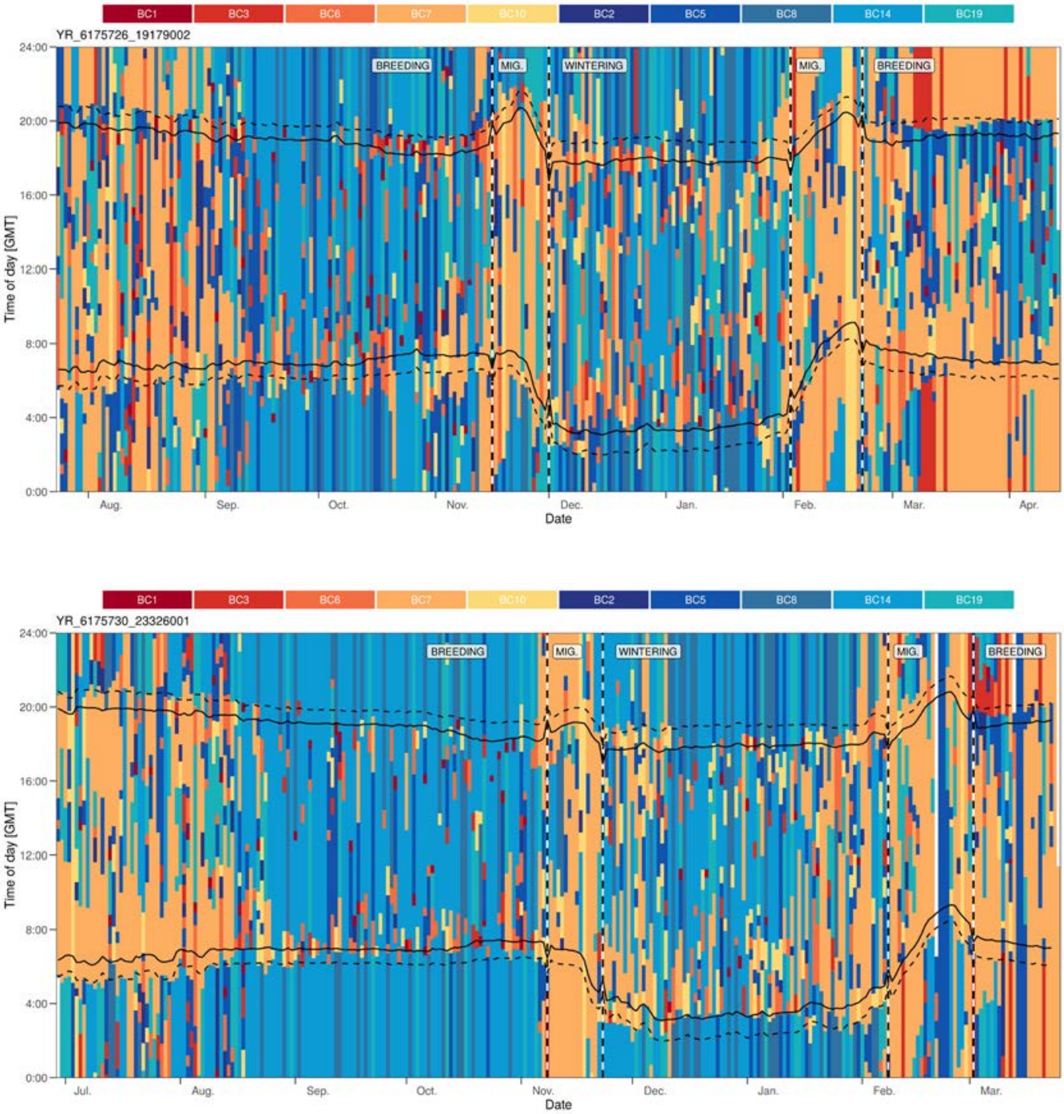

BC1
BC3
BC6
BC7
BC10
BC2
BC5
BC8
BC14
BC19
YR_6175726_19179002
BREEDING
MIG.
WINTERING
MIG.
BREEDING
Time of day [GMT]
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
Date
YR_6175730_23326001
BREEDING
MIG.
WINTERING
MIG.
BREEDING
Time of day [GMT]
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Jul.
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Date

Fig. S10

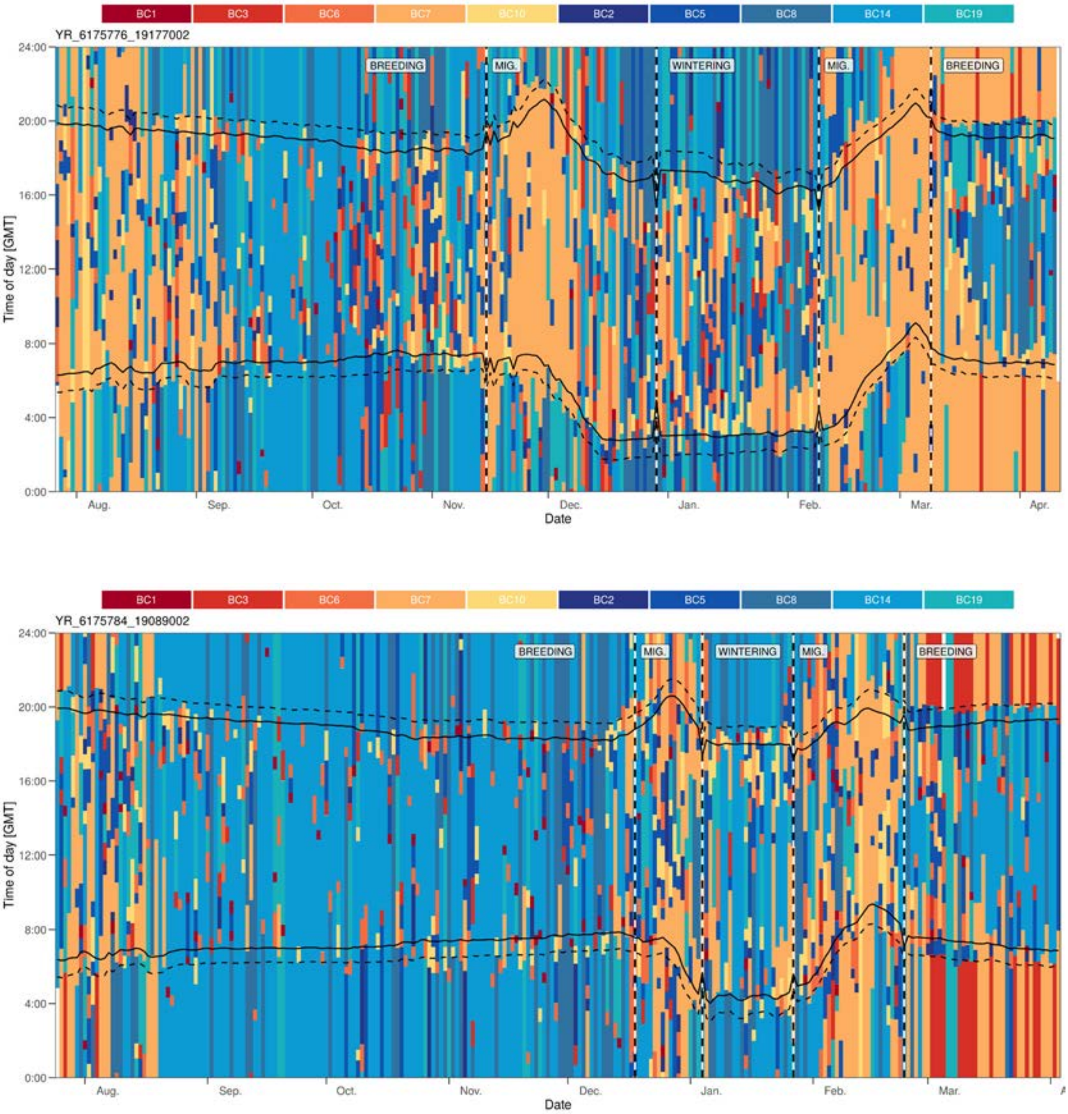

BC1
BC3
BC6
BC7
BC10
BC2
BC5
BC8
BC14
BC19
YR_6175776_19177002
BREEDING
MIG.
WINTERING
MIG.
BREEDING
Time of day [GMT]
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
Date
YR_6175784_19089002
BREEDING
MIG.
WINTERING
MIG.
BREEDING
Time of day [GMT]
24:00
20:00
16:00
12:00
8:00
4:00
0:00
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Date

Fig. S10

Table S1: Deployments of devices to 19 unique birds (Bird ID) of Cory's shearwater *Calonectris borealis* during the study at the breeding colony at Veneguera, Gran Canaria (Canary Is.). Abbreviations: GI – only geolocation-immersion logger deployed year-round, GI+GPS – geolocation-immersion logger and GPS device deployed during short-term foraging trip in incubation period. Nseg – number of segments after applying breakpoint algorithm (see Methods for details) on each track.
Table is ordered by Bird ID within the Device used.

Track ID	Bird ID	Device	Start	End	Duration	N seg.
VE6106933_10062011_25062011_c	6106933	GI + GPS	10/06/2011	25/06/2011	14,9	94
VE6134701_15072011_26072011_c	6134701	GI + GPS	15/07/2011	26/07/2011	11,0	124
VE6140497_14072011_24072011_c	6140497	GI + GPS	14/07/2011	24/07/2011	10,0	97
VE6140719_03072011_14072011_c	6140719	GI + GPS	03/07/2011	14/07/2011	11,2	70
VE6140719_23072011_30072011_c	6140719	GI + GPS	23/07/2011	30/07/2011	6,9	24
VE6140756_06062011_20062011_c	6140756	GI + GPS	06/06/2011	20/06/2011	14,7	114
VE6140855_03072011_19072011_c	6140855	GI + GPS	03/07/2011	19/07/2011	16,0	138
VE6143070_28062011_14072011_c	6143070	GI + GPS	28/06/2011	14/07/2011	16,0	115
VE6143090_05072011_17072011_c	6143090	GI + GPS	05/07/2011	17/07/2011	12,7	81
VE6143090_11062011_23062011_c	6143090	GI + GPS	11/06/2011	23/06/2011	12,0	84
VE6143093_08062011_22062011_c	6143093	GI + GPS	08/06/2011	22/06/2011	14,7	125
VE6175726_10062011_22062011_c	6175726	GI + GPS	10/06/2011	22/06/2011	12,7	117
VE6175730_04062011_18062011_c	6175730	GI + GPS	04/06/2011	18/06/2011	14,7	113
VE6175776_15072011_27072011_c	6175776	GI + GPS	15/07/2011	27/07/2011	11,1	83
VE6175776_19062011_05072011_c	6175776	GI + GPS	19/06/2011	05/07/2011	16,9	97
VE6175784_13072011_24072011_c	6175784	GI + GPS	13/07/2011	23/07/2011	10,7	88
VE6175784_20062011_01072011_c	6175784	GI + GPS	20/06/2011	01/07/2011	11,9	65
VE6188609_14072011_25072011_c	6188609	GI + GPS	14/07/2011	25/07/2011	11,1	108
VE6188705_07072011_18072011_c	6188705	GI + GPS	07/07/2011	18/07/2011	11,0	99
VE6195159_11072011_22072011_c	6195159	GI + GPS	11/07/2011	22/07/2011	11,7	109
VE6198153_03062011_16062011_c	6198153	GI + GPS	03/06/2011	16/06/2011	13,7	95
VE6198156_15062011_30062011_c	6198156	GI + GPS	15/06/2011	30/06/2011	15,8	115
VE6198172_08072011_17072011_c	6198172	GI + GPS	08/07/2011	17/07/2011	9,7	77
YR_6134701_19095002	6134701	GI	27/07/2011	17/04/2012	266	1504
YR_6140497_23353001	6140497	GI	26/07/2011	18/03/2012	237	1252
YR_6143070_23348001	6143070	GI	23/07/2011	25/02/2012	217	1044
YR_6143090_23319001	6143090	GI	19/07/2011	22/02/2012	218	1172
YR_6175726_19179002	6175726	GI	24/07/2011	14/04/2012	265	1543
YR_6175730_23326001	6175730	GI	29/06/2011	25/03/2012	270	1344
YR_6175776_19177002	6175776	GI	27/07/2011	11/04/2012	259	1456
YR_6175784_19089002	6175784	GI	25/07/2011	03/04/2012	253	1314

Table S2: Network metrics results for the different stages of the annual cycle (breeding, migration, wintering). A) Global metrics of networks. Lower value indicates more stable networks. B-D) Local metrics at node level (i.e. by BC). Values per stage and BC of in- and out- degree centrality, closeness centrality and betweenness centrality. For each stage, the number indicates the BC identity and the number within parenthesis refers to the value of the metric. Degree centrality measures the number of edges (i.e. connections to other BCs) of each BC. Closeness centrality quantifies how close a BC is to all other BCs. Betweenness centrality measures the number of shortest paths that pass through each BC. In the case of equal number of edges for various BCs, they are listed by descending BC identity.

S2.A. GLOBAL METRICS

	Breeding	Migration	Wintering
Size	10	10	10
Diameter	2	2	2
Edge density	0.72	0.67	0.71
Av. path length	1.31	1.36	1.31
Entropy rate	2.21	2.09	2.23

S2.B. LOCAL (NODE) METRICS

Degree centrality								
Breeding			Migration			Wintering		
in	out	all	in	out	all	in	out	all
10 (9)	10 (10)	10 (19)	7 (9)	7 (8)	7 (17)	7 (10)	7 (9)	7 (19)
7 (8)	7 (9)	7 (17)	10 (8)	10 (8)	10 (16)	10 (10)	10 (9)	10 (19)
3 (7)	5 (7)	5 (14)	6 (7)	6 (7)	6 (14)	3 (7)	1 (7)	3 (14)
5 (7)	6 (7)	6 (14)	19 (6)	1 (6)	1 (11)	1 (6)	3 (7)	1 (13)
6 (7)	3 (6)	3 (13)	1 (5)	5 (6)	5 (11)	6 (6)	6 (7)	6 (13)
1 (6)	19 (6)	19 (12)	2 (5)	2 (5)	19 (11)	2 (5)	2 (5)	2 (10)
19 (6)	1 (5)	1 (11)	3 (5)	3 (5)	2 (10)	5 (5)	5 (5)	5 (10)
2 (5)	2 (5)	2 (10)	5 (5)	8 (5)	3 (10)	8 (5)	8 (5)	8 (10)
8 (5)	8 (5)	8 (10)	8 (5)	14 (5)	8 (10)	14 (5)	14 (5)	14 (10)
14 (5)	14 (5)	14 (10)	14 (5)	19 (5)	14 (10)	19 (5)	19 (5)	19 (10)

S2.C. LOCAL (NODE) METRICS

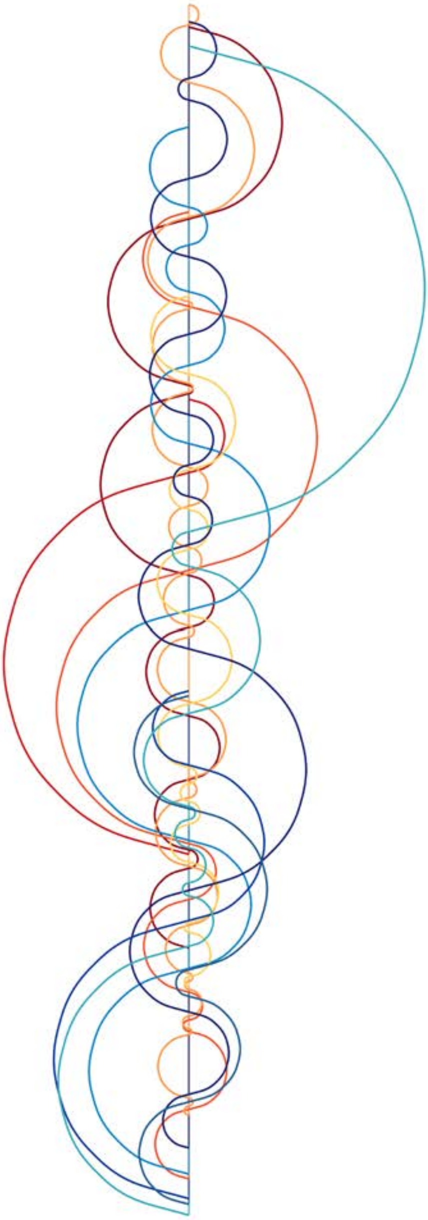
Closeness centrality								
Breeding			Migration			Wintering		
in	out	all	in	out	all	in	out	all
10 (0.90)	10 (1.00)	10 (1.00)	7 (0.90)	6 (0.82)	7 (0.90)	7 (1.00)	7 (0.90)	7 (1.00)
3 (0.82)	7 (0.90)	7 (0.9)	6 (0.82)	7 (0.82)	6 (0.82)	10 (1.00)	10 (0.90)	10 (1.00)
6 (0.82)	6 (0.82)	3 (0.82)	10 (0.82)	10 (0.82)	10 (0.82)	3 (0.82)	1 (0.82)	1 (0.82)
7 (0.82)	3 (0.75)	6 (0.82)	19 (0.75)	1 (0.75)	1 (0.75)	1 (0.75)	3 (0.82)	3 (0.82)
1 (0.75)	5 (0.75)	1 (0.75)	1 (0.69)	5 (0.75)	5 (0.75)	6 (0.75)	6 (0.82)	6 (0.82)
5 (0.75)	19 (0.75)	5 (0.75)	2 (0.69)	2 (0.69)	19 (0.75)	2 (0.69)	2 (0.69)	2 (0.69)
19 (0.75)	1 (0.69)	19 (0.75)	3 (0.69)	3 (0.69)	2 (0.69)	5 (0.69)	5 (0.69)	5 (0.69)
2 (0.69)	2 (0.69)	2 (0.69)	5 (0.69)	8 (0.69)	3 (0.69)	8 (0.69)	8 (0.69)	8 (0.69)
8 (0.69)	8 (0.69)	8 (0.69)	8 (0.69)	14 (0.69)	8 (0.69)	14 (0.69)	14 (0.69)	14 (0.69)
14 (0.69)	14 (0.69)	14 (0.69)	14 (0.69)	19 (0.69)	14 (0.69)	19 (0.69)	19 (0.69)	0.69)

S2.D. LOCAL (NODE) METRICS

Betweenness centrality		
Breeding	Migration	Wintering
10 (4.58)	7 (4.13)	10 (4.79)
7 (3.74)	1 (3.80)	7 (4.79)
1 (3.60)	3 (3.80)	1 (4.00)
3 (3.60)	6 (3.80)	3 (4.00)
6 (3.60)	10 (3.80)	6 (4.00)
2 (1.78)	2 (2.53)	2 (1.29)
5 (1.78)	5 (2.53)	5 (1.29)
8 (1.78)	8 (2.53)	8 (1.29)
14 (1.78)	14 (2.53)	14 (1.29)
19 (1.78)	19 (2.53)	19 (1.29)

Table S3: Results from the one-way repeated-measures ANOVA to test the effect of stage on the amount of time invested in each behavioral cluster (BC) by each of 8 individuals of Cory's shearwater tracked by wet-dry immersion loggers. BCs where significant effect was found are marked in bold.

BC	BC description	Df stage	Df resid	Within variance	Between variance	F	p-value
1	SF	2	12	0.046	0.084	1.830	0.202
3	**StF**	2	13	1.143	8.461	7.400	**0.007**
6	TFLd	2	13	1.878	3.920	2.087	0.164
7	**RFLd**	2	13	82.752	1530.475	18.495	< 0.001
10	ShD	2	13	4.879	11.720	2.402	0.130
2	SRest	2	13	0.827	0.331	0.400	0.678
5	ActSWD	2	13	8.893	0.282	0.032	0.969
8	**StlSWD**	2	13	28.179	266.663	9.463	**0.003**
14	**Lsit**	2	13	75.543	855.911	11.330	**0.001**
19	Rest	2	13	10.138	0.623	0.061	0.941



GENERAL DISCUSSION

This thesis comprises 4 chapters addressing different topics in the context of seabird ecology. Every chapter provides new insights into the factors shaping the at-sea behaviour of pelagic seabirds from the Atlantic Ocean. Through this thesis I have shown and highlighted the usefulness of wet-dry data, a source of information that can greatly enrich our knowledge of seabird ecology in a diversity of dimensions. In Chapters 1, 2 and 3, I and my co-authors provide new insights about at-sea ecology of little-known seabird species so far, reporting year-round movements and migratory schedules. In Chapters 2 and 3 we further revealed differences in activity budgets between different groups (males vs females, successful vs failed breeders, respectively), discussing the causes and consequences of these differences. In the Chapter 4, we revealed the complexity of seabird behaviour, and at the same time we presented a set of new analytical techniques and data visualization tools that allowed us to get the most from wet-dry data, which may open new avenues to understand the complexity of seabird behavioural patterns from manifold perspectives.

Using geolocators in seabird research

Understanding movements and spatial ecology over the annual cycle is nowadays the most studied topic in seabird research using geolocators (see Box 1 in the Introduction of this thesis). But before entering in the era of biologging, movements and distribution of many seabirds at sea were mostly studied from shipboard or coastal observations (Louzao et al. 2006, Ballance 2007). However, this approach does not inform about intrinsic factors of the individuals observed, such as origin or breeding status, precluding to properly interpret movement, behaviour and seasonal timing at individual level. Paraphrasing Nathan et al. (2008), two of the main fundamental questions regarding causes and consequences of animal movement are to know where and when the animals go. Moreover, these questions are also fundamental to address conservation actions (Lascelles et al. 2016). Therefore, the use of tracking devices is essential to understand seabirds' movements and timing of life-history events.

The increasing miniaturization of geolocators has allowed to progressively address the tracking of medium-to-small sized species, overcoming the initial bias towards research carried out on large-sized seabirds such as albatrosses (e.g. Weimerskirch & Wilson, 2000). In the last decade a numerous research undertaken uncovered spectacular migrations and non-breeding areas of several species (e.g. Shaffer et al. 2006, González-Solís et al. 2007, Egevang et al. 2010). Yet basic information regarding migratory movements and seasonal timing is still lacking for a few seabird species (Grémillet & Boulinier, 2009), including medium-to-small sized species from polar to temperate to tropical regions, such as the species studied in this thesis.

Seabirds' year-round movements and seasonal timing of life-history events can be inferred from positional and wet-dry data

Along this thesis I have shown that wet-dry data from geolocator-immersion loggers provide a powerful source of information to describe not only the movements but also the seasonal timing of life-history events. Our articles contribute to the published literature supporting the usefulness of wet-dry data to this end (e.g. Hedd et al. 2014, Rayner et al. 2016, Militão et al. 2017). This utility is even more relevant for elusive species and for those where location of breeding sites impedes periodic on-site nest monitoring. In this thesis, I and my co-authors have provided new insights about the year-round movements and the seasonal timing of life-history events in three little-studied seabird species of medium-to-small body size: Boyd's shearwater, Atlantic petrel and Common tern (**Chapters 1 to 3**).

For many medium-to-small sized seabirds, identification of closely related species at sea is challenging or even unreliable (Ballance 2007), precluding to know their actual distribution, even at broad scale, just from at-sea observations from vessels. One example in this regard is the Little–Audubon's shearwater complex, which species are hard to distinguish at sea (Flood & van der Vliet 2019). Some of them, such as the Boyd's shearwater, are distributed in the tropical latitudes in the North Atlantic Ocean. In **Chapter 1** I revealed for the first time the year-round movements of this little-known tropical seabird using geolocators. This study allowed us to place on the map the wintering areas and migratory routes of the **Boyd's shearwater**. Unexpectedly, the findings were quite contrary to the movements previously known from closely related species. Barolo shearwaters from the Azores and Salvagens Islands (Neves et al. 2012, Paiva et al. 2016) disperse mostly in the vicinity of their breeding colonies and forage also over the rich cool waters of the African shelf. Similarly, Audubon's shearwaters breeding in Caribbean archipelagos forage year round over the continental shelf (Precheur 2015). In contrast, our results revealed that Boyd's shearwaters spent their non-breeding season in oligotrophic waters in the centre of the Atlantic Ocean. In addition to the positional data, I could also define the timing of major life-history events thanks to wet-dry data. The timing of important life-history events, such as migration or arrival to the breeding colonies, among others, is influenced by many different factors, both intrinsic (e.g. sex, breeding status) and extrinsic (e.g. habitat seasonality, inter-annual environmental variability) (Cubaynes et al. 2010, Votier et al. 2009, Keogan et al. 2018). In this regard, we observed high inter-individual variability in the timing of various aspects of breeding biology of Boyd's shearwaters. This variation might arise from the marked seasonal and inter-annual variability in the abundance of food resources in tropical oligotrophic waters (Catry et al. 2013a, Hennicke & Weimerskirch 2014). This may lead to differences in the breeding success among individuals and years, which can influence the onset of post-breeding migration (Catry et al. 2013b, Ramos et al. 2018). Analysing wet-dry data in depth would provide important insights in this regard, as we did in the study of the Atlantic petrel (see below).

Another example of closely related species difficult to distinguish at sea are the gadfly petrels (*Pterodroma sp.*). They are medium-sized seabirds with a broad distribution across the world oceans, and their movements at sea have remained unknown until recently (Ramos et al. 2017). In **Chapter 3** we analysed in detail geolocator data from the **Atlantic petrel**, a gadfly petrel endemic as breeder to Gough Island and Tristan da Cunha archipelago. We provided a detailed description of year-round movements and spatial distribution of tracked individuals thanks to the combined use of positional and wet-dry data. As in our study with Boyd's shearwaters, I also found high inter-individual variability in the timing of events related to breeding biology, which again made me suspect that such variability may arise from breeding success. In fact, Atlantic petrels suffer an extremely high rate of breeding failure due to predation of chicks by the introduction of house mice (*Mus musculus*) in Gough Island (Caravaggi et al. 2019). As we did not have information regarding the breeding success from nest monitoring, I used exploratory data visualization to evaluate breeding success based on phenology, and classified the individuals as presumed successful and failed breeders using multivariate clustering. It could be expected that movement, behaviour and timing of major life-history events differ according to breeding output (Catry et al. 2013b). Indeed, for each group (successful and failed) we found the annual timing of these events to correlate in time, i.e. failed breeders advanced their post-breeding migration, stayed longer in the wintering areas, and returned earlier to the breeding colony in the next breeding stage. However, we did not find differences in spatial distribution, as all individuals wintered in the same area on the South American shelf slope. These results may suggest carry-over effects at some extent in relation to breeding success, as reported for other seabird species (Catry et al. 2013b, Schultner et al. 2014, Shoji et al. 2015, Fayet et al. 2016, Ramos et al. 2018). The impact of invasive species on seabirds is well known (Dias et al. 2019). However, our results also suggest that predation and subsequent breeding failure could also affect the timing of life-history events over the annual cycle mediated by carry-over effects, an unexpected impact of invasive species on seabirds yet not reported in literature and that should receive more attention in the future.

Unlike the species discussed previously, some other species have more coastal habits, which make them easier to observe and study, both using direct observation and ringing. This is the case of Common terns, for which ring recoveries pointed out the importance of West African coast during winter for individuals breeding in Europe (Wernham et al. 2002, Bairlein et al. 2014). Nevertheless, ring recoveries and coastal observations alone cannot inform about year-round movements and behaviour in detail, and therefore these aspects have remained unknown so far. In **Chapter 2** we unveiled for the first time the timing of migration along the East Atlantic flyway and the importance of the West African Coast for **Common terns** breeding in continental Europe, throughout the use of geolocators. Moreover, using wet-dry data we showed that wintering habitat in Common terns differs between sexes, as females tended to winter in more offshore areas, contrary to males wintering nearby the coastline. Since males usually care the offspring during migration and might be at wintering sites (Nisbet et al. 2011), differences in wintering habitat would be reflecting constraints related to sex and parental care. We also found that pairs did not overlap in their wintering areas. Sexual segregation in wintering areas has been reported for several large-to-medium sized seabirds using tracking devices (e.g. González-Solís et al. 2007), but our study is one of the few reporting such segregation in small sized seabird species, if not the unique so far, to the best of my knowledge.

Circadian and circa-annual at-sea activity rhythms of seabirds

In this thesis, we have explored how seabirds adjust their activity budgets and change their behaviour in response to biological and environmental constraints. The different constraints over the annual life cycle should be reflected in behavioural budgets and activity rhythms (Phillips et al. 2017).

Wet-dry data have been used by many researchers to evaluate this expectation (see Box 1 in Introduction of this thesis). In this thesis we have confirmed that individuals adapt their activity budgets over the different stages of the annual cycle. We verified this expectation in Chapter 2, Chapter 3 and Chapter 4. In the case of Common terns (Chapter 2), we found that inter-individual variability in post-breeding (autumn) migration but especially during pre-breeding (spring) migration was much lower than during winter (see Fig. 3 in Chapter 2). Similarly, in the case of Cory's shearwater (Chapter 4), we found inter-individual variability in those behaviours where most time was invested to be overall much lower during migration than during winter (see Fig. 5 in Chapter 4). In the case of Atlantic petrels (Chapter 3), we did not account directly to inter-individual variability, but time spent on water was overall much higher during wintering than during migration (see Fig. 3 in Chapter 3). Thus, the findings in the three species support the importance of phenology in constraining individual behaviour, shaping circa-annual at-sea activity rhythms. During breeding, central place foraging and particularities of each species also shaped behavioural budgets, complicating possible comparisons. On a daily basis, Common terns showed circadian activity rhythms that varied across the stages of the annual cycle (see Fig. 4 in Chapter 2). The same occurs for Boyd's shearwaters. Despite in Chapter 1 and the related published article we did not include an explicit analysis of wet-dry data, I carried out such analysis independently for illustrating purposes, and found a similar pattern (see Fig. 1 below). Therefore, we found clear evidences that activity budgets are shaped by circadian and circa-annual rhythms.

Wet-dry data for behavioural annotation reveal the complexity of behavioural organization in seabirds

It is obvious that a greater capacity to interpret behavioural patterns will allow us to link behavioural strategies with the rest of individuals' traits, enhancing our understanding about the causes and consequences of behavioural decisions within the life-history of animals (Sih et al. 2010). Along this thesis I have highlighted the usefulness of wet-dry data to decipher behavioural patterns. However, I have remarked in the Introduction that most studies have used raw data to quantify duration of a state (wet or dry) (e.g. Phalan et. 2007, Mackley et al. 2010, Dias et al. 2012, Rayner et al. 2012), without accounting for the inherent temporal correlations contained in the structure of wet-dry data, which is in fact a valuable information to infer behaviours (e.g. Phalan et. 2007, Mackley et al. 2010, Dias et al. 2012, Rayner et al. 2012). At most, some studies using this source of data were limited to identify the basic behaviours 'foraging', 'flying' and 'sitting on water' (Guilford et al 2009, Dias et al. 2012, Gutowsky et al. 2014, Ponchon et al. 2019). Guilford et al. (2009) used unsupervised clustering using solely wet-dry data but aggregating data on predefined daily blocks. Even in this thesis, in Chapter 2 and Chapter 3 we also used an approach aggregating information in predefined blocks (stage, day, etc.) to calculate the amount of time birds spent on water or in flight. Thus, despite its potential utility to distinguish behaviours, wet-dry data have never been used so far to annotate more complex behaviours. In **Chapter 4** we filled this gap, extending the use of wet-dry data for behavioural annotation. We took advantage of machine learning (Valletta et al. 2017) to analyze within a multidimensional unsupervised framework an array of metrics derived solely from wet-dry data. Multidimensionality reduction techniques allowed us to map samples on a behavioural space and

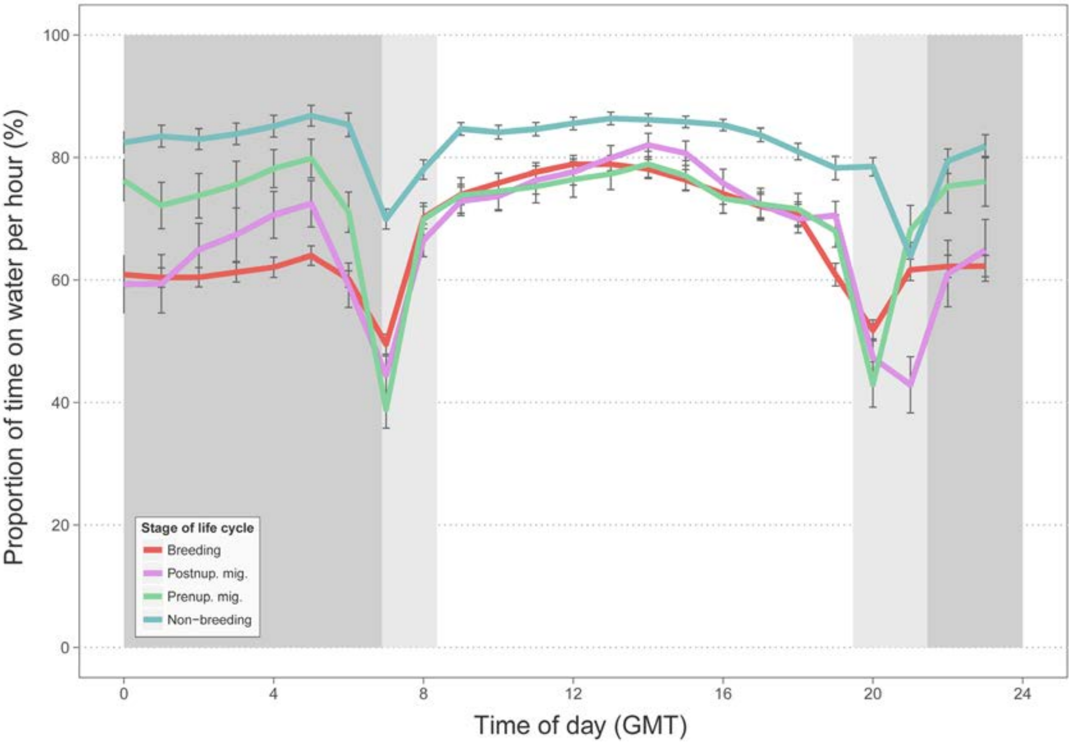


Fig. 1. This figure illustrates activity budgets of Boyd's shearwaters on a daily basis and for the different stages of the annual cycle, supporting that birds change the behaviour according to circadian and annual rhythms. Analysis performed with wet-dry data from 37 individuals from Raso and Ilheu de Cima (Cape Verde), tracked with geolocator-immersion loggers.

identify 10 different behaviours based on wet-dry data, thus surpassing the basics 'foraging', 'flying' and 'sitting' behaviours. However, the greater the number of behaviours, the more difficult is their interpretation. We initially found 23 behaviours, but we grouped them later in 10 by proximity, facilitating their interpretability. We used a combination of data visualization and statistical tools to interpret and give semantics to each behaviour. Hence, it is important to underline that interpretation may not be trivial and that a good knowledge on biology of the model species may be required for a successful depicting of behaviours.

Quantifying complexity of seabirds' behavioural strategies

Studying how individuals allocate their time budgets to different behaviours is an important keystone in ecology, as it could enhance the interpretation of behavioural strategies of animals under variable conditions within a life-history context (Sih et al. 2010, Wong & Candolin 2012, 2015). In the Introduction of this thesis I exposed how wet-dry data have been used to quantify activity budgets in seabirds. I also highlighted that most research intended to analyze activity patterns typically settled for aggregated wet-dry data at different scales (daily, monthly, by day/night). In that way, behavioural budgets are too broad to allow a proper and detailed investigation of constraints, causes and consequences of behavioural strategies.

In contrast with previous research, in **Chapter 4** we did not quantify broadly the foraging effort but went beyond, first identifying a variety of behaviours related to foraging, flying and resting and later quantifying their relative importance within the behavioural budgets over time. This quantification provided a variety of insights about the variability of behavioural strategies over the annual cycle and its constraints. For example, we found that most dominant behaviours in terms of time invested are also those more constrained by phenology, limiting inter-individual variability and thus shaping behavioural patterns at population scale. These insights open the door to consider differences in detailed behavioural budgets when comparing populations within meta-population approaches (Frederiksen et al. 2012, Ramos et al. 2013, Dean et al. 2015) or even to compare closely related species (Ramos et al. 2017), enriching the repertoire of possible ecological dimensions analyzed to evaluate aspects such as competition or diversification.

Moreover, we inspected the results from a multidimensional view, tackling individual variability trough time, i.e. seasonal variability, circadian and circa-annual rhythms, by using actograms. Actograms potentially allow linking behavioural budgets and strategies trough time with a whole range of intrinsic (age, sex, breeding status, breeding timing, breeding success, migration strategies, moulting strategies, etc.) and extrinsic factors (photoperiod, moonlight phase, environmental seasonality, etc.). Similarly, carrying out detailed behavioural annotation of positional data (e.g. GPS tracking, see Fig. 6 in Chapter 4) enhance our ability to interpret the role of extrinsic factors in behavioural budgets and strategies. In this regard, our approach for behavioural annotation at fine scale or at large spatio-temporal scale could be combined with currently available tools for track annotation, i.e. merging trajectories with environmental data provided from a variety of satellite-derived data sources (Kemp et al. 2012, Dodge et al. 2013, White et al. 2019) in order to understand the actual landscape faced by the birds. While this has been addressed at some extent using other devices and sources of data with some species (Vansteelant et al. 2017, Dodge et al. 2014), to date no research has been addressed in such detail using year-round data of pelagic and diving seabird species, since detrimental effects of long-lasting device deployment methods impede their use in such species. It is well known that environmental drivers such as wind (González-Solís et al. 2009) or human activities such as fisheries (Bartumeus et al. 2010) shape behaviour of seabirds. Therefore, the use of our approach for behavioural annotation combined with environmental data will assist to decipher the role of extrinsic factors such as marine habitat, wind direction and speed, food availability or fishing activity, among others, in shaping year-round behaviour of seabirds in an unprecedented detail (Obringer et al. 2017).

As commented above, to interpret every behaviour and give semantics we inspected results from manifold perspectives. Inspecting data through actograms allowed us to notice one behaviour likely corresponding to moult. The state of plumage and feathers depend on a physiological process decisive for seabirds' fitness (Cherel et al. 2016, Weimerskirch et al. 2019. As evidences of moulting have been rarely addressed explicitly in seabird tracking studies (Cherel et al. 2016), our results open the door to inspect in depth the impact of moulting strategies on behaviour, including the identification of the moulting period and moulting areas in different species.

As highly gregarious species, social interaction plays an important role for seabirds (Gaston 2004). For example, bearing of individuals departing from waters surrounding the colony seems to be used a cue by conspecifics to head towards foraging grounds (Weimerskirch et al. 2010). Behaviours displayed by individuals in the proximity of breeding colonies, such as rafting (Wilson et al. 2008, Carter et al. 2016) or bathing (Granadeiro et al. 2018) can be important for social interaction. Thus, our protocol for behavioural annotation and visualization may shed light on the way individuals' behaviour relates with social interaction in the vicinity of the breeding colonies.

Among seabird species, we can find a complete spectrum from mostly diurnal to those mostly nocturnal species. This variability is related to different strategies of foraging. Several species of albatross and petrels, such as the Boyd's shearwaters or the Atlantic petrel, are more active at twilight or at night (Shealer 2002). This has been related to availability of their potential prey, which become more available at night during dial vertical migrations (Elliott & Gaston 2015). On the other side of the day-night spectrum, we may find seabird species mostly restricted to daylight foraging activities, such as Cory's shearwaters or Common terns, which greatly rely on vision to localize prey (Fauchald 2009). Within seabird species, nocturnal/diurnal behaviour can also change across time and space, such as the Atlantic petrel, according to prey availability (Regular et al. 2011, Dias et al. 2012). These changes can be easily detected by plotting the time spent on water during the daylight and darkness over the different stages of the annual cycle (see for example Fig 1 in this Discussion or Fig. 3 in Chapter 3). Nevertheless, behavioural annotation and actograms may allow to evaluate the nocturnal/diurnal behaviours from a richer perspective, showing for instance how a same behaviour could be displayed during daylight or darkness depending on seasons or how specific behaviours are more displayed in oceanic environments during darkness, indicating specific foraging tactics to take advantage of resources more available at night (Regular et al. 2011, Krüger et al. 2017), while others are more exhibited during daylight in neritic waters, indicating foraging tactics relying on vision (Collet et al. 2015).

Data visualization and network analysis in animal movement and behavioural ecology

Data visualization is an essential part of the scientific process, although many times only remains restricted to report results in hypothesis-driven studies. Nevertheless, data visualization should become an important part of the scientific process, also in movement and behavioural studies. Appropriate data visualization may lead to the discovery of new patterns in data, thus promoting the generation of new hypothesis previously not "visible" (Williams et al. 2019). Recently, increasing interest in visual movement analysis have led researchers to gather at specific workshops (Shamoun-Baranes et al. 2011), to promote an interdisciplinary research network (Demšar et al. 2015) or to cover the topic in the special section of a journal (Demšar et al. 2019). Moreover, several innovative tools for exploration and visualization of animal movement from tracking devices have been developed (Kavathekar et al. 2013, Slingsby & Van Loon, 2016, Dodge et al. 2018, Konzack et al. 2019, Schwalb-Willmann 2019). Similarly, in visualization of behaviour, new techniques have been developed to ease the visualization and enhance the understanding of behaviours inferred from complex data such as that from accelerometers or magnetometers (Grundy et al. 2009, Williams et al. 2017).

Within studies presented in this thesis, data visualization has represented an essential tool, applied at various aspects along the research process, from positional data to phenology to wet-dry data analysis. As it has been mentioned previously, the estimation of positions from GLS comes inherently with a certain error, variable especially around the equinoxes and in tropical regions. Even though the newly emerged analytical tools may significantly increase the accuracy of positional estimates from geolocation and therefore minimize the errors (Lisovski et al. 2019), it is always essential to pair these analyses with additional data visualizations. In **Chapter 1**, we initially inferred from positional data that the distribution of Boyd’s shearwaters during the incubation and chick-rearing period shifted from north to south, respectively. However, the visualization of longitudinal and latitudinal positions as time series indicated clear effect of equinoxes and therefore prevented us to come up with misleading conclusions (see Fig. S1-S3 in Supplementary Material of Chapter 1).

In **Chapter 3** data visualization of phenology at individual level together with longitudinal movements of Atlantic petrels drove our hypothesis of the possible existence of two different groups, which we later classified and related with successful and failed breeders. Furthermore, data visualization helped us to consider the likely existence of carry-over effects related to breeding success.

In **Chapter 4** I presented effective visualizations of wet-dry data and inferred behaviours. Actogram plots have been used for many years in ethology and chronobiology to present behavioural or activity rhythms of animals from behavioural studies in laboratory (Aschoff 1979, Numata & Helm 2014). However, new detailed information obtained from biologging devices currently allow us to record, visualize and analyse information in much more detail even over long periods of time (Zúñiga et al. 2016, Bäckman et al. 2017). I used actogram plots to represent time series of behaviours inferred from wet-dry data on daily and seasonal scales at the same time. Actograms allow for visualization of behavioural budgets and behavioural strategies (i.e. how the different behaviours are arranged over time) simultaneously. I acknowledge that visualizing raw wet-dry data already provides us with several hints indicating changes in behaviour (see **Box 2**). However, by applying the protocol proposed in Chapter 4 and visualizing inferred behaviours using actograms, we can explore in much more detail circadian and circannual rhythms in behaviour of seabirds at individual level, which could greatly help to infer the biological meaning of the different behaviours and decipher the different constraints that shape them. Similar visualizations illustrating detailed daily and seasonal activity or movement based on data from biologging devices can be find in several studies, i.e. flight and activity of swifts (Liechti et al. 2013), activity of lynxes (Heurich et al. 2014), flight behaviour of shrikes (Bäckman et al. 2017) or as spatial chronogram of fishes (Aspillaga et al. 2016). Freeman et al. (2013) visualized time invested in 3 behaviours (foraging, resting, flight) of seabirds year-round, yet showing only daily aggregates of those basic behaviours. To my knowledge, the work I present in Chapter 4 is the first study where a diverse array of behaviours has been presented and visualized in such detail.

Visualizing behaviour in a spatially explicit framework is particularly useful to study animals that move over vast areas and present different space-use (Papastamtiou et al. 2018, Dodge et al. 2018). Moreover, their behaviour may change over time even when remain in the same area. Therefore, not only it is important to know where the animals go and how they use the space (which is commonly addressed using different approaches of kernel density estimations), but also in which behaviours they mostly engage across the areas used. According to this, in **Chapter 4** we constructed spatially explicit behavioural landscapes as a data visualization tool, based on behavioural annotation of trajectories from behaviours inferred from wet-dry data (see Fig. 9 in Chapter 4). These “activity seascapes” or “behavioural seascapes” mapped the spatial distribution and prevalence of behaviours over the annual life cycle of tracked seabirds. Some other approaches have been carried out to visualize behaviour in a spatial framework. For example, some authors used multi-sensor data from Manx shearwater (*Puffinus puffinus*) and kernel density estimation to point out regions were birds mostly engaged in one of three basic behaviours (foraging, resting and flying, Guilford et al. 2009, Freeman et al. 2013). However, when a great spatial overlap between those basic behavioural modes occurs, such approach does not achieve an effective visualization to highlight important areas for each behaviour. Our approach copes with a great number of behaviours and can highlight at global scale prevalent behaviours at each region and stage of the annual cycle, assisting for a quick identification of areas important for different foraging modes, moulting, commuting within migratory flyways or refuelling at stop-over sites (see Fig. 7 and 9 in Chapter 4). Other authors have focused to visualize the rate of nocturnal versus diurnal activity, through calculating the so-called “night flight index” using wet-dry data (Dias et al. 2012, Ramos et al. 2015). We could go beyond with our method and visualizations, since through disaggregating by day and night we could for example differentiate areas of nocturnal foraging, which kind of nocturnal foraging behaviour birds use, or evaluate whether those areas overlap with resting areas, at both coarse and fine scale (see Fig. 6 and 9 in Chapter 4). Lastly, since our approach can cope with high diversity of behaviours, it allows for mapping even behavioural diversity at global scale (see Fig. 9 in Chapter 4), which might provide a tool to evaluate the capacity of populations to cope with changing environments (Wong & Candolin 2015).

Other tool widely used in behavioural studies is network visualization and analysis. It is well established in biology and ecology, in contexts encompassing studies of social interactions (Hasenjager & Dugatkin 2015), molecular biology (Barabási & Oltvai, 2004), trophic dynamics and interactions (Bascompte et al. 2003, Oshima & Leaf 2018) and space-use (Jacoby et al. 2012, Stehfest et al. 2013). Its potential in the field of movement ecology has been acknowledged by some authors (Jacoby & Freeman, 2016). Moreover, in behavioral studies, the transition rates between described behaviours are also visualized as network graphs (Dankert et al. 2009, Berman et al. 2016) or as transition matrices (Dragon et al. 2012, Chimienti et al. 2016). However, the analysis of the properties of behavioural networks is not so settled, even despite it may reveal in more detail the structure of behavioural strategies and changes in their organization and complexity (Bradbury & Vehrencamp 2014, Todd et al. 2017). Thus, in **Chapter 4**, taking advantage of the variety of behaviours raised from our protocol, I explored the analysis of network properties and network visualization of relations (i.e. transitions) between inferred behaviours. This approach allowed me to reveal that changes in the prevalence of certain transitions and behaviours are shaped by breeding stages, but the method could be easily applied to compare behavioural strategies between individuals from different groups such as sexes, ages, populations or species (Stauss et al. 2012, de Grissac et al. 2017, Mendez et al. 2017, Ramos 2017).

BOX 2:

From heatmaps to actograms: a visualization journey through complexity in wet-dry data

The structure of wet-dry data recorded by geolocation-immersion sensors has change over time according to the models developed. Models manufactured by the *British Antarctic Survey* were widely used, most of them recording wet-dry data in 0-200 schedule. Later models, provided for example by *Biotrack Ltd*. and also widely deployed on seabirds, record changes in wet-dry state in a continuous way. Figures included in this Box illustrate the extent of inference about individual behaviour that we could achieve from wet-dry data. Fig. B1 and Fig. B2 are heatmaps displaying wet-dry states over a year-round cycle from raw data recorded in 0-200 format. Note that Fig. B1 corresponds to an individual of Boyd's shearwater and Fig. B2 to an individual of Cory's shearwater. Fig. B3 is a replica of the actogram previously shown (Fig. 8 in Chapter 4), where behavioural annotation on a year-round trip of Cory's shearwater is represented. Fig. B4 shows wet-dry data recorded in continuous format corresponding to a short-term foraging trip of Cory's shearwater. Finally, for comparison purposes, Fig. B5 refers to the same individual foraging trip than Fig. B4 but illustrates an actogram after applying our method exposed in Chapter 4. Data visualization highlights the insight enrichment accomplished with our behavioural annotation method.

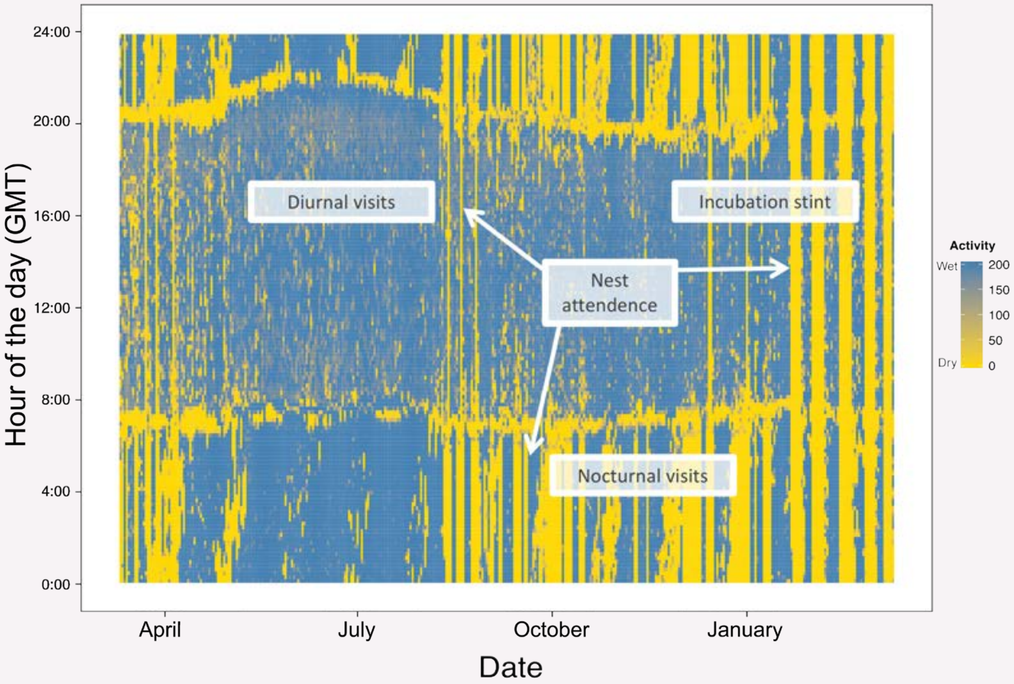


Fig. B1. Heatmap illustrating year-round activity patterns from an individual of Boyd's shearwater. Data come from geolocation-immersion loggers recording wet-dry data in 0-200 format. Each pixel corresponds to a 10-minutes block. The colour code from yellow to blue correspond to the scale from totally dry to totally wet. The data start on the date of logger deployment at the end of breeding stage and end on the date of logger recovery in the next breeding season. We can clearly identify prolonged periods in dry state (yellow) as colony attendance events: diurnal and nocturnal visits and incubation stints, which identification is essential to define timing of annual cycle life-history events.

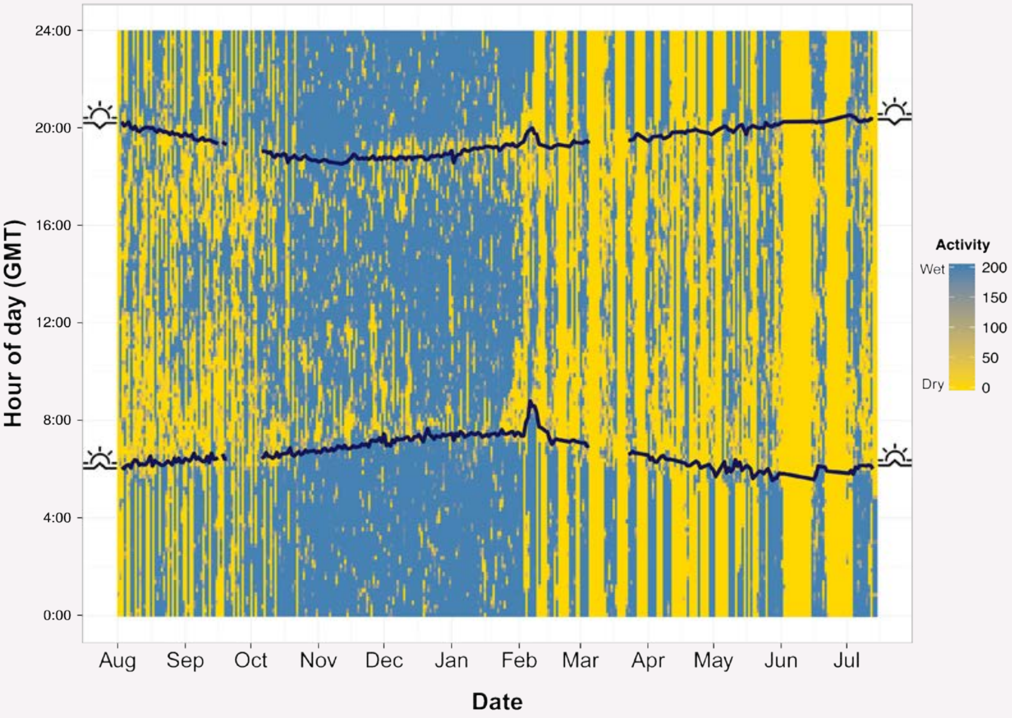


Fig. B2. Heatmap illustrating year-round activity patterns from an individual of Cory's shearwater. Data come from geolocation-immersion loggers recording wet-dry data in 0-200 format. Each pixel corresponds to a 10-minutes block, so the colour scale codes from totally dry (yellow) to totally wet (blue). The data start on the date of logger deployment at the end of breeding stage and end on the date of logger recovery in the next breeding season. We can clearly observe a circadian pattern (0-24h on y-axis), as birds adjust their activity according to local sunrise and sunset.

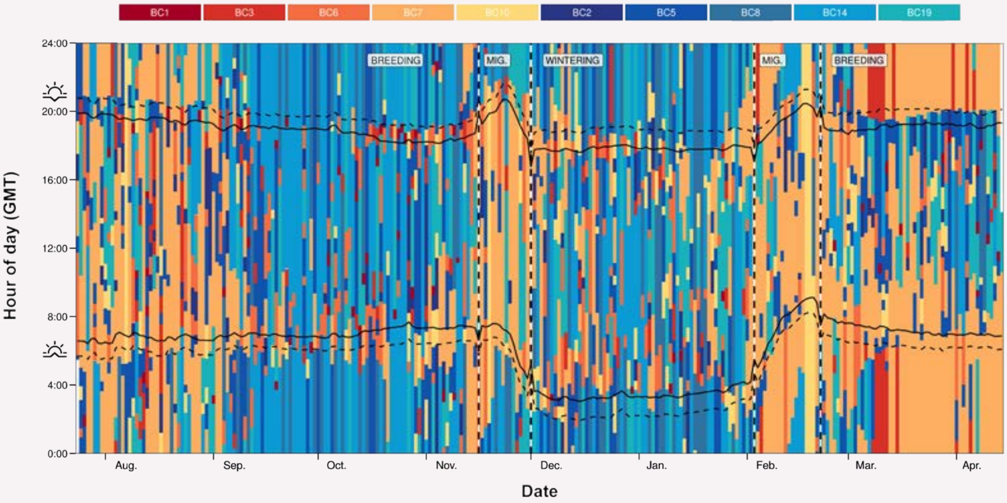


Fig. B3. Actogram illustrating year-round behavioural patterns from an individual of Cory's shearwater. Raw data come from geolocation-immersion loggers recording wet-dry data in continuous format. We applied on such data our method for behavioural annotation explained in Chapter 4, so each colour represents a different inferred behaviour. Each column represents one single day (0-24h). On the x-axis data start on the day of deployment of the logger and end on the day of recovery the next year. Black horizontal solid and dashed lines refer to time of local sunrise/sunset and nautical twilight at bird location, respectively. Vertical black-white lines delimit stages of annual life cycle: onset of post-breeding migration, arrival to the main wintering area, onset of pre-breeding migration and arrival to the breeding area, respectively. Note, for example, a clear shift in the circadian rhythm in December, indicating that the bird arrived at the wintering area -in this case in South-African waters-, and adjusted the behaviour to local sunrise and sunset times.

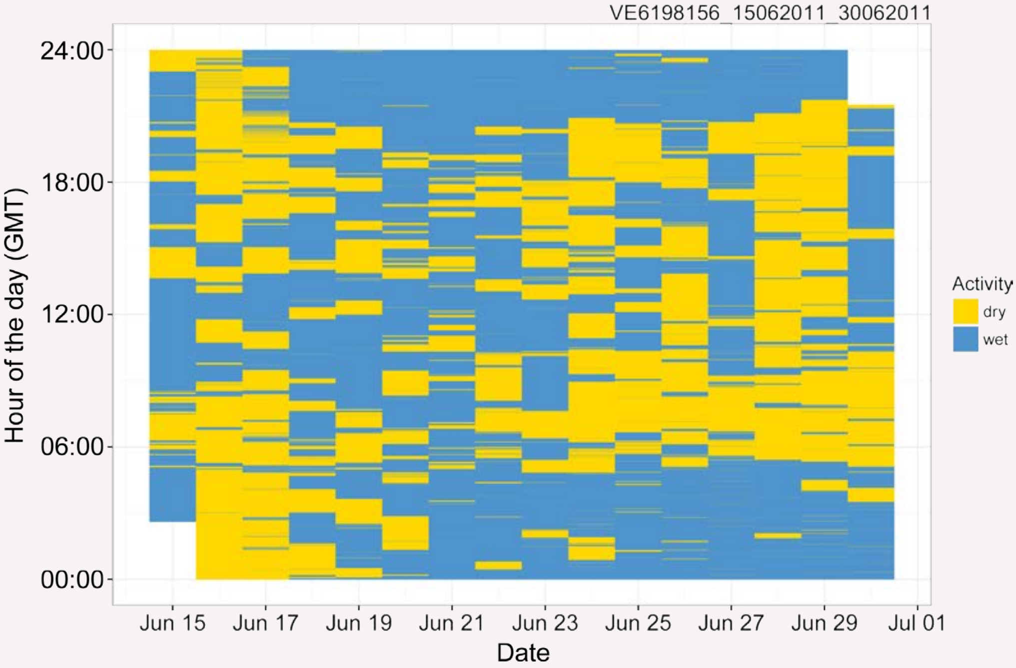


Fig. B4. Wet-dry activity patterns during a short-term foraging trip of a Cory's shearwater. Raw data come from geolocation-immersion loggers recording wet-dry data in continuous format. Each column represents one single day (0-24h). On the x-axis data start with the bird leaving the colony for a foraging trip and end when the bird returns to the colony 15 days later. In contrast with 0-200 wet-dry heatmaps, this actogram illustrates the actual changes between states, but getting insights in terms of behaviour based on frequency, duration and time sequence of states is an arduous task.

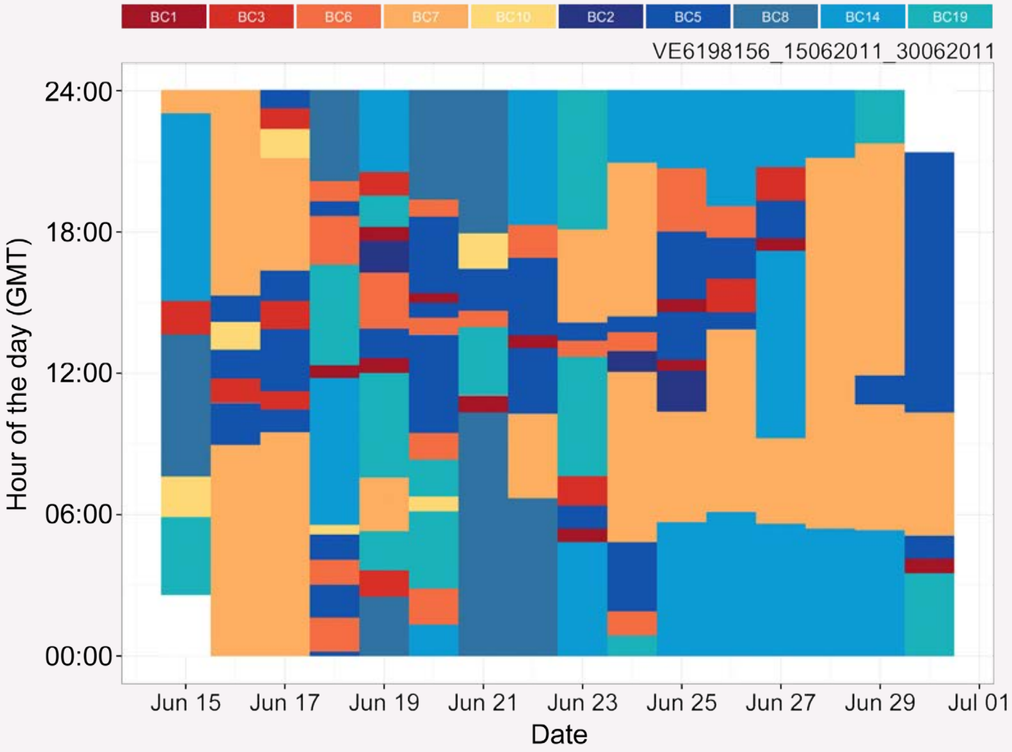
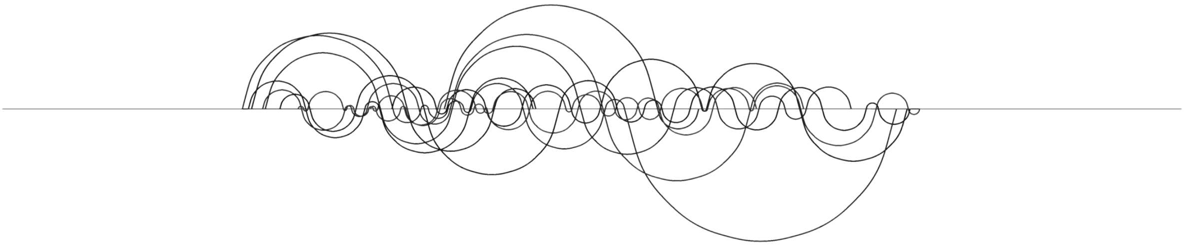


Fig. B5. Actogram illustrating behavioural patterns during a short-term foraging trip of a Cory's shearwater, the same trip than the one illustrated in Fig. 4. Raw data come from geolocation-immersion loggers recording wet-dry data in continuous format. We applied on such data our method for behavioural annotation explained in Chapter 4, so each colour represents a different inferred behaviour. Each column represents one single day (0-24h). On the x-axis data start with the bird leaving the colony for a foraging trip and end when the bird returns to the colony 15 days later. As we showed in Chapter 4, interpretation of behaviours arisen from our protocol allowed us to give semantics to each of them. In this actogram we can visualize in which behaviour the bird engaged along the trip and how it allocated the time between behaviours.

Concluding remarks and future directions

Along the four chapters of this thesis I have provided new analytical and visualization approaches to show how wet-dry data can bring new insights in several dimensions of seabird ecology. A very basic source of data, the wet-dry data recorded by geolocator-immersion loggers, can assist to understand movements and behaviour at multiple scales. Despite its utility, wet-dry data are underused by the seabird research community. In this thesis, I have presented a new protocol using state-of-the-art analytical techniques to show the incredible extent to which wet-dry data can help us to understand behavioural patterns of elusive species. Moreover, as it is based on multidimensional techniques, the protocol is also suitable for other sources of data. That is, it could also handle multi-sensor data together with external sources of data such as, for example, environmental annotation. For example, we could address which behaviours the different individuals display, how they differently arrange behavioural budgets and how their behavioural strategies change throughout life stages and in different environmental contexts. At population level, we could evaluate whether a more diverse array of behaviours exhibited in population relates to a greater resilience to face changes in the environment (Wong & Candolin 2015, Beever et al. 2017). At species level, we could study in detail whether distinct species arrange their behaviours to avoid competition without spatial or temporal segregation. Our framework paves the way to use behavioural annotations for addressing a repertoire of old and new questions of interest in ecology from new perspectives, and from individuals to populations to species level. Considering geolocator-immersion sensors continue to be the most extended loggers to track year-round movements of seabirds, and based on results compiled in this thesis, I encourage researchers to incorporate the use of wet-dry data within hypothesis-driven frameworks, which would surely contribute to increase our knowledge of seabird ecology at sea.



CONCLUSIONS

1. Wet-dry data from geolocator-immersion loggers constitute a powerful and irreplaceable source of information to study movement, at-sea behaviour and timing of life-history events of seabirds, but such data have been largely underused by the seabird research community.

2. Analysis of wet-dry data clearly highlights the circadian and circa-annual rhythms of behaviour. Wet-dry data allowed us to verify that migratory species adjust their internal biological clock to local conditions. We found evidences across four different seabird species with contrasting migratory patterns and spread over the Atlantic Ocean.

3. Wet-dry data enhance our ability to describe timing of major life-history events. We revealed the previously unknown phenology of two pelagic seabird species that perform longitudinal migratory movements, Boyd's shearwater and Atlantic petrel.

4. Behavioural patterns are shaped by a diverse array of intrinsic factors (age, sex, breeding status, breeding timing, breeding success, migration strategies, moulting strategies, etc.). We found sex to condition behaviour in Common tern, and breeding success to influence year-round behaviour in Atlantic petrel, including timing of migration. We also found moonlight intensity to shape behaviour during winter in the Atlantic petrel.

5. Wet-dry dynamics have great behavioural content of at-sea movement and behaviour, spanning scales from elementary motion patterns (e.g. at scale of minutes, hours) to complex ecological interactions (e.g. seasonality, annual life cycle). We used cutting-edge techniques to build up a new analytical protocol that evidences how a broad repertoire of behaviours can be deciphered uniquely from wet-dry data.

6. Through this protocol, we uncovered both flexible and structural components of the behavioural organization of a highly-mobile migratory seabird, the Cory's shearwater, a pelagic species with a complex annual cycle that involves central place foraging, ocean-basin long migratory movement and wandering in wintering areas.

7. Knowing the actual landscape faced by individuals will lead to understand the role of extrinsic factors shaping behavioural strategies and decision-making in elusive species. In this regard, our approach allows for behavioural annotation over long periods and large scales, which combined with currently available tools for environmental annotation from satellite-derived data sources (e.g. winds, fisheries) will provide new insights at an unprecedented detail.

8. Data visualization is a powerful tool to reveal insights from complex multidimensional information, such as data from animal movement and behaviour collected through biologging. We devised effective data visualizations such as actograms, behavioural landscapes and networks to assist the research proccess and provide new insights, otherwise hard to find, about behavioural patterns of species spending most of their live out of the human's sight.

BIBLIOGRAPHY

Altmann, J. (1974) Observational study of behavior: sampling methods. *Behaviour*, 49(3): 227-267.

Aschoff, J. (1979) Circadian rhythms: influences of internal and external factors on the period measured in constant conditions. *Zeitschrift für Tierpsychologie*, 49(3): 225-249.

Aspillaga, E., Bartumeus, F., Linares, C., Starr, R. M., López-Sanz, À., Díaz, D., Zabala, M. & Hereu, B. (2016) Ordinary and extraordinary movement behaviour of small resident fish within a Mediterranean marine protected area. *PloS one*, 11(7): e0159813.

Bäckman, J., Andersson, A., Pedersen, L., Sjöberg, S., Tøttrup, A.P. & Alerstam, T. (2017) Actogram analysis of free-flying migratory birds: new perspectives based on acceleration logging. *Journal of Comparative Physiology A*, 203(6-7): 543-564.

Bairlein, F., Dierschke, J., Dierschke, V., Salewski, V., Geiter, O., Hüppop, K., Köppen, U. & Fielder, W. (2014) *Atlas des Vogelzugs.* AULA,Wiebelsheim.

Ballance, L.T. (2007) Understanding seabirds at sea: why and how? *Marine Ornithology*, 35: 127-135.

Barabasi, A. L. & Oltvai, Z. N. (2004) Network biology: understanding the cell's functional organization. *Nature Reviews Genetics*, 5(2): 101.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D. & Levin, S.A. (2010) Fishery discards impact on seabird movement patterns at regional scales. *Current Biology*, 20(3): 215-222.

Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16): 9383-9387.

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M. K., Smith, F.A. & Lawler, J.J. (2017) Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, 15(6): 299-308.

Berman, G.J., Bialek, W. & Shaevitz, J.W. (2016) Predictability and hierarchy in Drosophila behavior. *Proceedings of the National Academy of Sciences*, 113(42): 11943-11948.

BirdLife International (2015) *Puffinus lherminieri*. The IUCN Red List of Threatened Species 2015: eT45959182A84678618.

BirdLife International (2018a) *Calonectris borealis. The IUCN Red List of Threatened Species* 2018: e.T22732244A132661794.

BirdLife International (2018b) *Pterodroma incerta. The IUCN Red List of Threatened Species* 2018: e.T22698084A132623707.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J. et al. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475(7354): 86.

Bouten, W., Baaij, E.W., Shamoun-Baranes, J. & Camphuysen, K.C. (2013) A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology,* 154(2): 571-580.

Boyd, I.L., Kato, A. & Ropert-Coudert, Y. (2004) Bio-logging science: sensing beyond the boundarie. *Memoirs of National Institute of Polar Research (Special Issue),* 58: 1-14.

Bradbury, J.W. & Vehrencamp, S.L. (2014) Complexity and behavioral ecology. *Behavioral Ecology,* 25(3): 435-442.

Brlík, V., Koleček, J., Burgess, M. et al. (2019) Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias. *Journal of Animal Ecology,* 2019; 00: 1-14.

Brooke, M. (1990) *The Manx shearwater.* Academic Press, London.

Brooke, M. (2004) *Albatrosses and petrels across the world.* Oxford University Press, Oxford

Bugoni, L. & Vooren, C.M. (2004) Feeding ecology of the Common Tern *Sterna hirundo* in a wintering area in southern Brazil. *Ibis,* 146: 438-453.

Burger, A. E. & Shaffer, S. A. (2008) Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *The Auk,* 125(2): 253-264.

Candolin, U. & Wong, B.B. (Eds.) (2012) *Behavioural responses to a changing world: mechanisms and consequences.* Oxford University Press.

Caravaggi, A., Cuthbert, R.J., Ryan, P.G., Cooper, J. & Bond, A.L. (2019) The impacts of introduced House Mice on the breeding success of nesting seabirds on Gough Island. *Ibis,* 161(3): 648-661.

Carboneras, C. (1992) Family Procellariidae (petrels and shearwaters). In: del Hoyo, J. et al. (Eds.) *Handbook of the birds of the world, Vol 1.* Lynx Edicions, Barcelona, p 216–271.

Carboneras, C., Jutglar, F. & Kirwan, G.M. (2016) Audubon'sshearwater (*Puffinus lherminieri*). In: del Hoyo J. et al. (Eds.) *Handbook of the birds of the world alive.* Lynx Edicions, Barcelona.

Carter, M. I., Cox, S. L., Scales, K. L., Bicknell, A. W., Nicholson, M. D., Atkins, K. M., Morgan, G., Morgan, L., Grecian, W.J., Patrick, S.M. & Votier, S.C. (2016) GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): implications for foraging ecology and conservation. *Bird Study,* 63(1): 83-95.

Catry, P., Dias, M.P., Phillips, R.A. & Granadeiro, J.P. (2011) Different means to the same end: long-distance migrant seabirds from two colonies differ in behaviour, despite common wintering grounds. *PLoS One,* 6(10): e26079.

Catry, T., Ramos, J.A., Catry, I., Monticelli, D. & Granadeiro, J. P. (2013a) Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. *Marine Biology,* 160(5): 1189-1201.

Catry, P., Dias, M.P., Phillips, R.A. & Granadeiro, J.P. (2013b) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology,* 94(6): 1230-1235.

Catry, P., Granadeiro, J.P., Ramos, J., Phillips, R.A. & Oliveira, P. (2011) Either taking it easy or feeling too tired: old Cory's Shearwaters display reduced activity levels while at sea. *Journal of Ornithology,* 152(3): 549-555.

Catry, P., Phillips, R. A., Phalan, B., Silk, J.R. & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology Progress Series,* 280: 261-273.

Cherel, Y., Quillfeldt, P., Delord, K. & Weimerskirch, H. (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution,* 4: 3.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J. & Scott, B.E. (2016) The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecology and Evolution,* 6(3): 727–741.

Chmura, H.E., Glass, T.W. & Williams, C.T. (2018) Biologging physiological and ecological responses to climatic variation: New tools for the climate change era. *Frontiers in Ecology and Evolution,* 6: 92.

Cianchetti-Benedetti, M., Catoni, C., Kato, A., Massa, B. & Quillfeldt, P. (2017) A new algorithm for the identification of dives reveals the foraging ecology of a shallow-diving seabird using accelerometer data. *Marine Biology,* 164(4): 77.

Clay, T.A., Pearmain, E. J., McGill, R.A., Manica, A. & Phillips, R.A. (2018) Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. *Functional Ecology,* 32(7): 1832-1846.

Collet, J., Patrick, S.C. & Weimerskirch, H. (2015) Albatrosses redirect flight towards vessels at the limit of their visual range. *Marine Ecology Progress Series,* 526: 199-205.

Cooke, S.J, Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004) Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution,* 19: 334-343.

Cramp, S. & Simmons, K.E.L. (1977) *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, Vol I.* Oxford University Press, London.

Croxall, J.P., Butchart, S.H., Lascelles, B.E.N., Stattersfield, A.J., Sullivan, B.E.N., Symes, A. & Taylor, P.H.I.L. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* 22(1): 1-34.

Cubaynes, S., Doherty, P.F., Schreiber, E. A. & Gimenez, O. (2010) To breed or not to breed: a seabird's response to extreme climatic events. *Biology Letters,* 7(2): 303-306.

Cuthbert, R.J. (2004) Breeding biology of the Atlantic Petrel, *Pterodroma incerta,* and a population estimate of this and other burrowing petrels on Gough Island, South Atlantic Ocean. *Emu,* 104: 221-228.

Damschen, E.I., Brudvig, L.A., Haddad, N.M., Levey, D.J., Orrock, J.L. & Tewksbury, J.J. (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. *Proceedings of the National Academy of Sciences,* 105(49): 19078-19083.

Dankert, H., Wang, L., Hoopfer, E.D., Anderson, D.J. & Perona, P. (2009) Automated monitoring and analysis of social behavior in Drosophila. *Nature Methods,* 6: 297-303.

Dean, B., Freeman, R., Kirk, H., Leonard, K, Phillips, R.A., Perrins, C.M. & Guilford, T. (2013) Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society Interface,* 10(78): 20120570.

Dean, B., Kirk, H., Fayet, A., Shoji, A., Freeman, R., Leonard, K., Perrins, C.M. & Guilford, T. (2015) Simultaneous multi-colony tracking of a pelagic seabird reveals cross-colony utilization of a shared foraging area. *Marine Ecology Progress Series,* 538: 239-248.

de Grissac, S., Bartumeus, F., Cox, S.L., & Weimerskirch, H. (2017) Early-life foraging: Behavioral responses of newly fledged albatrosses to environmental conditions. *Ecology and Evolution,* 7(17): 6766-6778.

del Hoyo, J., Collar, N. & Kirwan, G.M. (2019) Cory's Shearwater (*Calonectris borealis*) In: del Hoyo et al. (Eds.) *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona.

Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., Weiskop, D. & Weibel, R. (2015) Analysis and visualisation of movement: an interdisciplinary review. *Movement ecology,* 3(1): 5.

Demšar, U., Slingsby, A. & Weibel, R. (2019) Introduction to the special section on Visual Movement Analytics. *Information Visualization,* 18(1): 133-137.

Dias, M.P., Granadeiro, J.P. & Catry, P. (2012) Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. *Marine Ecology Progress Series,* 467: 245-252.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C. Phillips, R.A., Yates, O., Lascelles, B., Garcia Borboroglu, P. & Croxall, J.P. (2019) Threats to seabirds: A global assessment. *Biological Conservation,* 237: 525-537.

Dias, M.P., Romero, J., Granadeiro, J.P., Catry, T., Pollet, I.L. & Catry, P. (2016) Distribution and at-sea activity of a nocturnal seabird, the Bulwer's petrel *Bulweria bulwerii,* during the incubation period. *Deep Sea Research Part I: Oceanographic Research Papers,* 113: 49-56.

Dodge, S., Bohrer, G., Bildstein, K., Davidson, S.C., Weinzierl, R., Bechard, M.J., Barber, D., Kays, R., Brandes, D., Han, J. & Wikelski, M. (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1643): 20130195.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S. Han, J. Brandes, D. & Wikelski, M. (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology*, 1(1): 3.

Dodge, S., Xavier, G. & Wong, W.Y. (2018) *DynamoVis - Dynamic Visualization of Animal Movement Data*. Retrieved from the Data Repository for the University of Minnesota, https://doi.org/10.13020/D6PH49.

Dragon, A.C., Bar-Hen, A., Monestiez, P. & Guinet, C. (2012) Horizontal and vertical movements as predictors of foraging success in a marine predator. *Marine Ecology Progress Series*, 447: 243-257.

Durant, J.M., Hjermann, D.Ø., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M. & Stenseth, N.C. (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research*, 39(2): 115-129.

Egevang, C., Stenhouse, I. J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R. (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, 107(5): 2078-2081.

Elliott, K.H. & Gaston, A.J. (2015) Diel vertical migration of prey and light availability constrain foraging in an Arctic seabird. *Marine Biology*, 162(9): 1739-1748.

Enticott, J.W. (1991) Distribution of the Atlantic Petrel *Pterodroma incerta* at sea. *Marine Ornithology*, 19: 49-60.

Fauchald, P. (2009) Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series*, 391: 139-151.

Fayet, A.L., Freeman, R., Shoji, A., Kirk, H.L., Padget, O., Perrins, C.M. & Guilford, T. (2016) Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology*, 85(6): 1516-1527.

Flood, R.L. & van der Vliet, R. (2019) Variation and identification of Barolo Shearwater and Boyd's Shearwater. *Dutch Birding*, 41: 215-237.

Fox, J. W. (2010) *Geolocator manual v8*. British Antarctic Survey, Cambridge.

Frederiksen, M., Moe, B., Daunt, F., Phillips, R.A., Barrett, R. T., Bogdanova, M.I. et al. (2012) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions*, 18(6): 530-542.

Freeman, R., Dean, B., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M. & Guilford, T. (2013) Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx Shearwater. *Journal of the Royal Society Interface*, 10(84): 20130279.

Furness, R.W. & Camphuysen, K. (1997) Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, 54(4): 726-737.

Gaston, A.J. (2004) *Seabirds: a natural history.* Yale University Press.

Gochfeld, M., Burger, J., Christie, D.A. & Garcia, E.F.J. (2019) *Common Tern* (Sterna hirundo) In: del Hoyo et al. (Eds.) *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona.

González-Solís, J., Croxall, J.P. & Afanasyev, V. (2007) Offshore spatial segregation in giant petrels *Macronectes* spp.: differences between species, sexes and seasons. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 17(S1): S22-S36.

González-Solís, J., Croxall, J.P., Oro, D. & Ruiz, X. (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment,* 5(6): 297-301.

González-Solís, J., Felicísimo, A., Fox, J.W., Afanasyev, V., Kolbeinsson, Y. & Muñoz, J. (2009) Influence of sea surface winds on shearwater migration detours. *Marine Ecology Progress Series,* 391: 221-230.

Granadeiro, J. P., Campioni, L. & Catry, P. (2018) Albatrosses bathe before departing on a foraging trip: implications for risk assessments and marine spatial planning. *Bird Conservation International,* 28(2): 208-215.

Granadeiro, J.P., Monteiro, L.R., Silva, M.C. & Furness, R.W. (2002) Diet of common terns in the Azores, Northeast Atlantic. *Waterbirds,* 25(2): 149-156.

Grémillet, D. & Boulinier, T. (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series,* 391: 121-137.

Grundy, E., Jones, M.W., Laramee, R.S., Wilson, R.P. & Shepard, E.L. (2009) Visualisation of sensor data from animal movement. *Computer Graphics Forum,* 28(3): 815-822.

Guilford, T., Meade, J., Willis, J., Phillips, R.A., Boyle, D., Roberts, S., Collett, M., Freeman, R. & Perrins, C.M (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society B: Biological Sciences,* 276(1660): 1215-1223.

Gutowsky, S.E., Gutowsky, L.F., Jonsen, I.D., Leonard, M.L., Naughton, M.B., Romano, M.D. & Shaffer, S.A. (2014) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. *Movement Ecology,* 2(1): 23.

Halpern, B.S., Selkoe, K.A., Micheli, F. & Kappel, C.V. (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology,* 21(5): 1301-1315.

Harcourt, R., Sequeira, A.M.M., Zhang, X., Roquet, F., Komatsu, K., Heupel, M. et al. (2019) Animal-Borne Telemetry: An Integral Component of the Ocean Observing Toolkit. *Frontiers in*

Marine Science, 6, 326.

Hasenjager, M.J. & Dugatkin, L.A. (2015) Social network analysis in behavioral ecology. In: Naguib, M. et al. (Eds.) *Advances in the Study of Behavior* - Vol. 47. pp. 39-114. Academic Press.

Hays, G.C., Ferreira, L.C., Sequeira, A.M., Meekan, M.G., Duarte, C.M., Bailey, H. et al. (2016) Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution*, 31(6): 463-475.

Hazevoet, C.J. (1995) *The birds of the Cape Verde Islands. An annotated check list*. British Ornitologists Union, London.

Hedd, A., Montevecchi, W.A., Phillips, R.A. & Fifield, D.A. (2014) Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period. *PLoS One*, 9(1): e85572.

Hennicke, J. C. & Weimerskirch, H. (2014) Coping with variable and oligotrophic tropical waters: foraging behaviour and flexibility of the Abbott's booby *Papasula abbotti*. *Marine Ecology Progress Series*, 499: 259-273.

Hertel, F. & Ballance, L.T. (1999) Wing ecomorphology of seabirds from Johnston Atoll. *The Condor*, 101(3): 549-556.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, D. C., J. (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS One*, 9(12): e114143.

Hill, R.D. & Braun, M.J. (2001) Geolocation by light level, electronic tagging and tracking in marine fisheries. *Proceedings of the symposium on tagging and tracking marine fish with electronic devices. East-West Center*. University of Hawaii. Berlin: Springer. pp. 315–330.

Igual, J.M., Forero, M.G., Tavecchia, G., González-Solís, J., Martínez-Abraín, A., Hobson, K.A., Ruiz, X. & Oro, D. (2005) Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Marine Biology*, 146(3): 619-624.

Jacoby, D.M., Brooks, E.J., Croft, D.P. & Sims, D.W. (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*, 3(3): 574-583.

Jacoby, D. M. & Freeman, R. (2016) Emerging network-based tools in movement ecology. *Trends in Ecology & Evolution*, 31(4): 301-314.

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N. et al. (2013) Integrating movement ecology with biodiversity research-exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1(1): 6.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science,* 348(6240): aaa2478.

Kavathekar, D., Mueller, T. & Fagan, W.F. (2013) Introducing AMV (Animal Movement Visualizer), a visualization tool for animal movement data from satellite collars and radiotelemetry. *Ecological informatics,* 15: 91-95.

Kemp, M.U., Emiel van Loon, E., Shamoun-Baranes, J. & Bouten, W. (2012) RNCEP: global weather and climate data at your fingertips. *Methods in Ecology and Evolution,* 3(1): 65-70.

Keogan, K., Daunt, F., Wanless, S., Phillips, R.A., Walling, C.A. et al. (2018) Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change,* 8(4): 313.

Klages, N.T.W. & Cooper, J. (1997) Diet of the Atlantic petrel *Pterodroma incerta* during breeding at South Atlantic Gough Island. *Marine Ornithology,* 25: 13-16.

Konzack, M., Gijsbers, P., Timmers, F., van Loon, E., Westenberg, M. A. & Buchin, K. (2019) Visual exploration of migration patterns in gull data. *Information Visualization,* 18(1): 138-152.

Krüger, L., Paiva, V.H., Petry, M.V. & Ramos, J. A. (2017) Strange lights in the night: using abnormal peaks of light in geolocator data to infer interaction of seabirds with nocturnal fishing vessels. *Polar Biology,* 40(1): 221-226.

Kürten, N., Vedder, O., González-Solís, J., Schmaljohann, H. & Bouwhuis, S. (2019) No detectable effect of light-level geolocators on the behaviour and fitness of a long-distance migratory seabird. *Journal of Ornithology.*

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S. et al. (2016) Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions,* 22(4): 422-431.

Lewison, R., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P. et al. (2012) Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research,* 17(2): 93-121.

Liechti, F., Witvliet, W., Weber, R. & Bächler, E. (2013) First evidence of a 200-day non-stop flight in a bird. *Nature Communications,* 4: 2554.

Lisovski, S., Bauer, S., Briedis, M., Davidson, S.C., Dhanjal-Adams, K.L., Hallworth, M.T. et al. (2019) Light-Level Geolocator Analyses: A user's guide. *Journal of Animal Ecology.*

López-López, P. (2016) Individual-based tracking systems in ornithology: welcome to the era of big data. *Ardeola,* 63(1): 103-137.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abelló, P., Sola, L.G. & Oro, D. (2006) Oceanographic habitat of an endangered Mediterranean procellariform: implications for Marine Protected Areas. *Ecological Applications,* 16: 1683-1695.

Mackley, E.K., Phillips, R.A., Silk, J.R., Wakefield, E.D., Afanasyev, V., Fox, J.W. & Furness, R.W. (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Marine*

Ecology Progress Series, 406: 291-303.

Mallory, M.L. & Gilbert, C.D. (2008) Leg-loop harness design for attaching external transmitters to seabirds. *Marine Ornithology,* 36: 183-188.

Mattern, T., Masello, J.F., Ellenberg, U. & Quillfeldt, P. (2015) Actave.net – a web-based tool for the analysis of seabird activity patterns from saltwater immersion geolocators. *Methods in Ecology and Evolution,* 6(7): 859-864.

McIntyre, T. (2014) Trends in tagging of marine mammals: a review of marine mammal biologging studies. *African Journal of Marine Science,* 36(4): 409-422.

McKnight, A., Irons, D.B., Allyn, A.J., Sullivan, K.M. & Suryan, R.M. (2011) Winter dispersal and activity patterns of post-breeding black-legged kittiwakes *Rissa tridactyla* from Prince William Sound, Alaska. *Marine Ecology Progress Series,* 442: 241-253.

Mendez, L., Prudor, A. & Weimerskirch, H. (2017) Ontogeny of foraging behaviour in juvenile red-footed boobies (*Sula sula*). *Scientific Reports,* 7(1): 13886.

Militão, T., Dinis, H.A., Zango, L., Calabuig, P., Stefan, L.M. & González-Solís, J. (2017) Population size, breeding biology and on-land threats of Cape Verde petrel (*Pterodroma feae*) in Fogo Island, Cape Verde. *PloS one,* 12(4): e0174803.

Missagia, R.V., Ramos, J.A., Louzao, M., Delord, K., Weimerskirch, H. & Paiva, V.H. (2015) Year-round distribution suggests spatial segregation of Cory's shearwaters, based on individual experience. *Marine Biology,* 162(11): 2279-2289.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences,* 105(49): 19052-19059.

Nathan, R. & Giuggioli, L. (2013) A milestone for movement ecology research. *Movement Ecology,* 1:1.

Neves, V.C., Bried, J., González-Solís, J., Roscales, J.L. & Clarke, M.R. (2012) Feeding ecology and movements of the Barolo shearwater *Puffinus baroli baroli* in the Azores, NE Atlantic. *Marine Ecology Progress Series,* 452: 269-285.

Nisbet, I.C.T., Szczys, P., Mostello, C.S. & Fox, J.W. (2011) Female Common Terns *Sterna hirundo* start autumn migration earlier than males. *Seabird,* 24: 103-106.

Numata, H. & Helm, B. (2014) *Annual, lunar, and tidal clocks.* Springer Verlag.

Obringer, R., Bohrer, G., Weinzierl, R., Dodge, S., Deppe, J., Ward, M., Brandes, D., Kays, R. & Wikelski, M. (2017) Track Annotation: Determining the Environmental Context of Movement Through the Air. In: Chilson P. et al. (Eds.) *Aeroecology.* Springer, Cham

O'Connor, C. M., Norris, D. R., Crossin, G. T. & Cooke, S. J. (2014) Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere,* 5(3): 1-11.

Orgeira, J.L. (2001) Nuevos registros del Petrel Atlántico (*Pterodroma incerta*) en el océano Atlántico Sur y Antártida. *Ornitología Neotropical,* 12: 165-171.

Oshima, M.C. & Leaf, R.T. (2018) Understanding the structure and resilience of trophic dynamics in the northern Gulf of Mexico using network analysis. *Bulletin of Marine Science,* 94(1): 21-46.

Paiva, V.H., Fagundes, A.I., Romao, V., Gouveia, C. & Ramos, J.A. (2016) Population-scale foraging segregation in an apex predator of the North Atlantic. *PloS one,* 11(3): e0151340.

Papastamatiou, Y.P., Watanabe, Y.Y., Demšar, U., Leos-Barajas, V., Langrock, R., Bradley, D., Weng, K., Lowe, C., Friedlander, A. & Caselle, J. (2018) Activity seascapes highlight central place refuging strategies in marine predators that never stop swimming. *Movement Ecology,* 6(1): 9.

Phalan, B., Phillips, R.A., Silk, J. R., Afanasyev, V., Fukuda, A., Fox, J., Catry, P., Higuchi, H. & Croxall, J. P. (2007) Foraging behaviour of four albatross species by night and day. *Marine Ecology Progress Series,* 340: 271-286.

Phillips, R.A., Lewis, S., González-Solís, J. & Daunt, F. (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series,* 578: 117-150.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. (2004) Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series,* 266: 265-272.

Pinet, P., Jaquemet, S., Phillips, R.A. & Le Corre, M. (2012) Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Animal Behaviour,* 83(4): 979-989.

Pollet, I.L., Hedd, A., Taylor, P.D., Montevecchi, W.A. & Shutler, D. (2014) Migratory movements and wintering areas of Leach's Storm-Petrels tracked using geolocators. *Journal of Field Ornithology,* 85(3): 321-328.

Ponchon, A., Cornulier, T., Hedd, A., Granadeiro, J.P. & Catry, P. (2019) Effect of breeding performance on the distribution and activity budgets of a predominantly resident population of black-browed albatrosses. *Ecology and Evolution,* 9(15): 8702-8713.

Precheur, C. (2015) *Ecologie et conservation du puffin d'Audubon (*Puffinus lherminieri lherminieri*) de la réserve naturelle des* îlets *de Sainte-Anne (Martinique).* These de Doctorat de l'Universite des Antilles.

Quillfeldt, P., Masello, J.F., Navarro, J. & Phillips, R.A. (2013) Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *Journal of Biogeography,* 40(3): 430-441.

Ramos, R., Carlile, N., Madeiros, J., Ramírez, I., Paiva, V. H., Dinis, H.A., Zino, F., Biscoito, M., Leal, G.R., Bugoni, L., Jodice, P.G.R., Ryan, P.G. & González-Solís, J. (2017) It is the time for oceanic seabirds: Tracking year-round distribution of gadfly petrels across the Atlantic Ocean.

Diversity and Distributions, 23(7): 794-805.

Ramos, R., Granadeiro, J.P., Rodríguez, B., Navarro, J., Paiva, V.H., Bécares, J., Reyes-González, J.M., Fagundes, I., Ruiz, A., Arcos, J.M., González-Solís, J. & Catry, P. (2013) Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of Marine Protected Areas based on tracking studies. *Diversity and Distributions,* 19(10): 1284-1298.

Ramos, R., Llabrés, V., Monclús, L., López-Béjar, M. & González-Solís, J. (2018) Costs of breeding are rapidly buffered and do not affect migratory behavior in a long-lived bird species. *Ecology,* 99(9): 2010-2024.

Ramos, R., Ramírez, I., Paiva, V.H., Militão, T., Biscoito, M., Menezes, D., Phillips, R.A., Zino, F. & González-Solís, J. (2016) Global spatial ecology of three closely-related gadfly petrels. *Scientific Reports,* 6: 23447.

Ramos, R., Sanz, V., Militão, T., Bried, J., Neves, V. C., Biscoito, M., Phillips, R.A., Zino, F. & González-Solís, J. (2015) Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). *Journal of Biogeography,* 42: 1651-1664.

Rayner, M.J., Carlile, N., Priddel, D., Bretagnolle, V., Miller, M.G.R., Phillips, R.A., Ranjard, L., Bury, S.J. & Torres, L.G. (2016) Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. *Marine Ecology Progress Series,* 549:217-229.

Rayner, M.J., Taylor, G.A., Gummer, H.D., Phillips, R.A., Sagar, P.M., Shaffer, S.A. & Thompson, D.R. (2012) The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu - Austral Ornithology,* 112(2): 107-116.

Regular, P.M., Hedd, A. & Montevecchi, W.A. (2011) Fishing in the dark: a pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. *PLoS One,* 6(10): e26763.

Reyes-González, J.M. & González-Solís, J. (2016) Pardela cenicienta atlántica – *Calonectris borealis.* In: Salvador, A. & Morales, M.B. (Eds.) *Enciclopedia Virtual de los Vertebrados Españoles.* Museo Nacional de Ciencias Naturales, Madrid.

Richardson, M.E. (1984) Aspects of the ornithology of the Tristan da Cunha group and Gough Island 1972-1974. *Cormorant,* 12: 123-201.

Rodríguez, A., Arcos, J. M., Bretagnolle, V., Dias, M. P., Holmes, N. D., Louzao, M. et al. (2019) Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science,* 6: 94.

Roncon, G., Bestley, S., McMahon, C.R., Wienecke, B. & Hindell, M.A. (2018) View from below: inferring behavior and physiology of Southern Ocean marine predators from dive telemetry. *Frontiers in Marine Science,* 5: 1-23.

Ropert-Coudert, Y., Kato, A., Grémillet, D. & Crenner, F. (2012) Bio-logging: recording the ecophysiology and behavior of animals moving freely in their environment. In: Le Galliard, J.F. et al. (Eds.) *Sensors for ecology: towards integrated knowledge of ecosystems.* CNRS INEE, Paris.

Ropert-Coudert, Y. & Wilson, R.P. (2005) Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment,* 3: 437-444.

Rutz, C. & Hays, G.C. (2009) New frontiers in biologging science. *Biology Letters,* 5(3): 289-292.

Schultner, J., Moe, B., Chastel, O., Tartu, S., Bech, C. & Kitaysky, A.S. (2014) Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series,* 496: 125-133.

Schwalb-Willmann, J. (2019) *moveVis: Movement Data Visualization*. R package version 0.10.2. https://CRAN.R-project.org/package=moveVis

Shaffer, S.A., Costa, D.P. & Weimerskirch, H. (2001) Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology,* 70: 864-874.

Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M., Moller, H., Taylor, G.A., Foley, D.G., Block, B.A. & Costa, D. P. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences,* 103(34): 12799-12802.

Shamoun-Baranes, J., van Loon, E.E., Purves, R.S., Speckmann, B., Weiskopf, D. & Camphuysen, C.J. (2011) Analysis and visualization of animal movement. *Biology Letters,* 8: 6-9.

Shealer, D. A. (2001) Foraging behavior and food of seabirds. In: Schreiber, E.A. & Burger, J. (Eds.) *Biology of marine birds.* CRC press.

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., Juarez-Martinez, I., Boyle, D., Nakata, T., Perrins, C.M. & Guilford, T. (2015) Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters,* 11(10): 20150671.

Sih, A., Stamps, J., Yang, L.H., McElreath, R. & Ramenofsky, M. (2010) Behavior as a key component of integrative biology in a human-altered world. *Integrative and Comparative Biology,* 50(6): 934-944.

Slingsby, A. & Van Loon, E. (2016) Exploratory visual analysis for animal movement ecology. *Computer Graphics Forum,* 35: 471–480.

Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, M.E., Knight, J. Newton, S.C. Patrick, Phillips, R.A., Waggitt, J.J. & Votier, S.C. (2012) Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. *Marine Ecology Progress Series,* 457: 151-162.

Stehfest, K.M. Patterson, T.A., Barnett, A. & Semmens, J.M. (2015) Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. *Oikos,* 124: 307-318.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T. et al. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology,* 101(1): 58-67.

Tavares, D.C., Moura, J.F., Acevedo-Trejos, E. & Merico, A. (2019) Traits shared by marine megafauna and their relationships with ecosystem functions and services. *Frontiers in Marine Science,* 6: 262.

Todd, J.G., Kain, J.S. & Bivort, B.L. (2017) Systematic exploration of unsupervised methods for mapping behavior. *Physical Biology,* 14(1): 015002.

Tukey, J.W. (1977) *Exploratory Data Analysis.* New York: Addison-Wesley.

Valletta, J.J., Torney, C., Kings, M., Thornton, A. & Madden, J. (2017) Applications of machine learning in animal behaviour studies. *Animal Behaviour,* 124: 203-220.

Van Buskirk, J. (2012) Behavioural plasticity and environmental change. In: Candolin, U. & Wong, B.B.M. (Eds.) *Behavioural Responses to a Changing World. Mechanisms and Consequences.* Oxford University Press.

Vandenabeele, S.P., Shepard, E.L., Grogan, A. & Wilson, R.P. (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology,* 159: 1-14.

Vandenabeele, S.P., Wilson, R.P. & Grogan, A. (2011) Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare-The UFAW Journal*: 20(4): 559.

Vansteelant, W.M., Shamoun-Baranes, J., van Manen, W., van Diermen, J. & Bouten, W. (2017) Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. *Journal of Animal Ecology,* 86(2): 179-191.

Votier, S.C., Hatchwell, B.J., Mears, M. & Birkhead, T.R. (2009) Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. *Marine Ecology Progress Series,* 393: 225-233.

Warham, J. (1990) *The petrels: their ecology and breeding systems.* Academic Press, London.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography,* 54(3-4): 211-223.

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. & Goya, E. (2010) Use of social information in seabirds: compass rafts indicate the heading of food patches. *PloS one,* 5(3): e9928.

Weimerskirch, H., Pinet, P., Dubos, J., Andres, S., Tourmetz, J., Caumes, C., Caceres S, Riethmuller, M. & Corre, M.L. (2019) Wettability of juvenile plumage as a major cause of mortality threatens endangered Barau's petrel. *Journal of Avian Biology,* 50(1).

Weimerskirch, H. & Wilson, R.P. (2000) Oceanic respite for wandering albatrosses. *Nature,* 406(6799): 955.

Wendeln, H. & Becker, P.H. (1999) Significance of ring removal in Africa for a Common tern Sterna hirundo colony. *Ringing & Migration*, 19: 210-212.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A. Siriwardena, G.M. & Baillie, S.R. (2002) *The migration atlas: movements of the birds of Britain and Ireland*. T & AD Poyser, London.

White, T.D., Ferretti, F., Kroodsma, D.A., Hazen, E.L., Carlisle, A.B., Scales, K.L., Bograd, S.J. & Block, B.A. (2019). Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the northeast Pacific. *Science Advances*, 5(3): eaau3761.

Williams, H.J., Holton, M.D., Shepard, E.L., Largey, N., Norman, B., Ryan, P.G. et al. (2017) Identification of animal movement patterns using tri-axial magnetometry. *Movement Ecology*, 5(1): 6.

Williams, H.J., Taylor, L.A., Benhamou, S., Bijleveld, A.I., Clay, T.A. et al. (2019) Optimising the use of bio-loggers for movement ecology research. *Journal of Animal Ecology*.

Wilmers, C.C., Nickel, B., Bryce, C.M., Smith, J.A., Wheat, R.E. & Yovovich, V. (2015) The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*, 96: 1741-1753.

Wilson, L.J., McSorley, C.A., Gray, C.M., Dean, B.J., Dunn, T.E., Webb, A. & Reid, J.B. (2008) Rafting behaviour of Manx Shearwaters *Puffinus puffinus*. *Seabird*, 21: 85-92

Wilson, R.P. (1992) Estimation of location: global coverage using light intensity. In: Priede, S. (Ed.) *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, New York.

Wilson, R.P. & Vandenabeele, S.P. (2012) Technological innovation in archival tags used in seabird research. *Marine Ecology Progress Series*, 451: 245-262.

Wilson, R.P., Weimerskirch, H. & Lys, P. *(*1995*)* A device for measuring seabird activity at sea. *Journal of Avian Biology*, 26: 172-175.

Wong, B. & Candolin, U. (2015) Behavioral responses to changing environments. *Behavioral Ecology*, 26(3): 665-673.

Yamamoto, T., Takahashi, A., Yoda, K., Katsumata, N., Watanabe, S., Sato, K. & Trathan, P.N. (2008) The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked shearwater, *Calonectris leucomelas. Animal Behaviour*, 76(5): 1647-1652.

Yoda, K. (2019) Advances in bio-logging techniques and their application to study navigation in wild seabirds. *Advanced Robotics*, 33(3-4): 108-117.

Zúñiga, D., Falconer, J., Fudickar, A.M., Jensen, W., Schmidt, A., Wikelski, M. & Partecke, J. (2016) Abrupt switch to migratory night flight in a wild migratory songbird. *Scientific Reports*, 6: 34207.

ANNEX 1: Published articles

of Chapter 1. Zajková Z, Militão T, González-Solís J (2017) Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Mar Ecol Prog Ser* 579:169-183

of Chapter 2. Becker, P.H., Schmaljohann, H., Riechert, J., Wagenknecht, G., Zajková, Z. & González-Solís, J. (2016) Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period. *J. Ornithol*. 157: 927– 940

Vol. 579: 169–183, 2017
https://doi.org/10.3354/meps12269

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 14

Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic

Zuzana Zajková*, **Teresa Militão**, **Jacob González-Solís**

Institut de Recerca de la Biodiversitat (IRBio) and Dept. Biologia Evolutiva, Ecologia i Ciències Ambientals,
Universitat de Barcelona, Av. Diagonal 643, Barcelona 08028, Spain

ABSTRACT: Despite the proliferation of seabird tracking studies, there is a relative paucity of studies on small tropical seabirds. We present for the first time the distribution and movements of the little-known Boyd's shearwater *Puffinus boydi*, a Procellariiform endemic to the Cape Verde Islands. We tracked 28 birds from 2 breeding sites (Ilhéu Raso and Ilhéu de Cima) with geolocator loggers from 2007 to 2012. We also analysed stable isotopes of carbon and nitrogen in the 1st primary (P1), the 6th rectrice (R6) and the 1st (S1) and 8th (S8) secondary feathers to reveal moulting pattern and oceanic isotopic gradients. Birds migrated on average 1450 km westward, to the central Atlantic Ocean (5 to 15° N, 30 to 40° W), where they stayed on average 114 d, from May to August. Boyd's shearwaters exploited oceanic waters year-round and showed $\delta^{13}C$ values similar to other oceanic seabird species and $\delta^{15}N$ values indicating the lowest known trophic level among all central Atlantic seabirds. Isotope values in flight feathers suggest most animals moult their P1 and R6 around the breeding ground, whereas all birds moult S1 and S8 at the non-breeding quarters. Correlations of $\delta^{13}C$ and $\delta^{15}N$ values from S8 with the longitude of the non-breeding area indicate the existence of large-scale isotopic gradients matching those known at baseline levels. Combining geolocator tracking and stable isotope analyses in feathers not only allowed us to describe in detail the annual life cycle and distribution of the species, but also the oceanic isotopic gradients in the tropical Atlantic.

KEY WORDS: Global Location Sensing geolocators · Little-Audubon's shearwater complex · Moulting patterns · Trophic ecology · Stable isotopes · Migration · Boyd's shearwater · *Puffinus boydi*

INTRODUCTION

Over recent decades, studies on the biology and ecology of tropical seabirds have been mainly focused on diet, foraging and performance at the breeding colonies (Ashmole & Ashmole 1967, Ballance & Pitman 1999, Spear et al. 2007). More recently, studies have been extended to include the relationship between breeding performance and environmental features (Surman et al. 2012, Catry et al. 2013). In contrast, at-sea distribution of many tropical seabirds remains poorly known and the sparse information available is mostly based on shipboard and coastal observations (Jaquemet et al. 2004, Ballance 2007). Despite the standardized approaches used in ship surveys (Tasker et al. 1984, Camphuysen & Garthe 2004), unreliable at-sea identification of some species (Ainley et al. 2012) and usually unknown origin and breeding status of observed individuals make these counts difficult to interpret.

In the last 2 decades, the rise in the use of extrinsic and intrinsic markers has underpinned an exponential increase in studies on the pelagic ecology of seabirds. Regarding extrinsic markers, the light level logger (geolocator) has become an essential device for studying year-round movements in much more detail than ever before, improving our understanding on the ecological needs and constraints of seabirds at sea (e.g. González-Solís et al. 2007, Guilford et al. 2012). However, the increasing use of geolocators to

---

*Corresponding author: zuzulaz@gmail.com study seabird distribution and behaviour has been clearly biased towards species from temperate and subantarctic waters. Thus, there is still a clear lack of knowledge about the year-round at-sea ecology and distribution of tropical seabirds, with only a few species well studied (Catry et al. 2009, Pinet et al. 2011, Dias et al. 2015, Precheur 2015, Paiva et al. 2016, Ramos et al. 2016).

Similarly, intrinsic markers, such as stable isotope analysis (SIA) of $\delta^{13}C$ and $\delta^{15}N$ of various tissues have been widely used to study seabird trophic ecology. Typically, $\delta^{13}C$ values have been used to determine the diet of seabirds whereas $\delta^{15}N$ values reflect trophic level in a general manner (Hobson et al. 1994, Cherel et al. 2008). However, isotopic values of $\delta^{13}C$ and $\delta^{15}N$ at baseline are also known to vary geographically in the marine environment (McMahon et al. 2013a,b). Spatial maps of isotopic landscapes, so called 'isoscapes', reflecting this variability, are just now beginning to emerge, mostly based on large-scale studies on plankton (Somes et al. 2010, McMahon et al. 2013a,b). Whether this spatial isotopic variability propagates up to the food chain and can provide insights into the foraging movements or wintering areas of predators is still a matter of study (Quillfeldt et al. 2005, Cherel & Hobson 2007, Navarro et al. 2013). In this regard, combining SIA with tracking studies can help validate the relationship between isotope values and foraging movements (Jaeger et al. 2010). Despite increasing interest in linking isotope values of feathers to seabird movements, especially during the less known non-breeding season, only few studies showed a correspondence between $\delta^{13}C$ and $\delta^{15}N$ in feather isotope values and non-breeding distribution of seabirds tracked with geolocators (Phillips et al. 2009, González-Solís et al. 2011, Hedd et al. 2012).

The lack of basic knowledge regarding year-round distribution, phenology and trophic ecology becomes a matter of conservation concern in polytypic species difficult to identify at sea and with unclear taxonomic status. The Little–Audubon's shearwater complex (*Puffinus assimilis–lherminieri*, Procellariiformes), small-sized seabirds spread within tropical and temperate waters, is a particularly poorly known seabird complex as shown by the various taxonomic revisions that occurred over recent decades (reviewed in Austin et al. 2004). After many years of controversy, Audubon's shearwater is now suggested to include 3 subspecies, the Audubon's shearwater *P. l. lherminieri*, the Barolo shearwater *P. l. baroli* and the Boyd's shearwater *P. l. boydi*, with a conservation status of 'Least Concern' (BirdLife International 2015, Carboneras et al. 2016a), although in the present study we preferred to follow a precautionary principle and maintain the specific status of the taxon *P. boydi* (Hazevoet 1995, Robb & Mullarney 2008). Indeed, the conservation status and taxonomy of several closely related seabird taxa still remain controversial partly due to our lack of knowledge on their spatial ecology, since this is important for understanding migratory connectivity, reproductive isolation mechanisms, and therefore potential for lineage divergence (Ramos et al. 2016). Therefore, studies on the phenology and year-round distribution of species within seabird complexes with controversial taxonomic relationships are particularly timely.

Recent geolocation and stable isotope studies on Barolo shearwater breeding on the Macaronesian archipelagos of the Azores and the Salvagens (Neves et al. 2012, Paiva et al. 2016) showed this subspecies to disperse in the surroundings of the breeding colonies outside the breeding period. However, there is very little knowledge about detailed biology of the closely related Boyd's shearwater *P. boydi* Mathews, 1912, endemic to the Cape Verde Islands, especially those aspects related to phenology, year-round distribution and trophic ecology. Roscales et al. (2011) revealed the distribution and trophic position of Boyd's shearwaters only at the end of the breeding season, when animals foraged close to the colony. Away from breeding grounds, Boyd's shearwater has only been seen in small numbers off the Senegal coast in October (Hazevoet 1997, Dubois et al. 2009), in 1976 1 bird was trapped on St. Helena (Bourne & Loveridge 1978) and a suspected observation of 1 individual was reported from the Canary Islands in December 2012 (Velasco 2013). However, the majority of the observations of individuals of this species have been reported all year round in Cape Verde and surrounding waters (Bourne 1955, Hazevoet 1995, Dubois et al. 2009), which suggests a non-migratory behaviour, even though non-breeding grounds remain unknown.

To fill in this gap, we provide the first detailed study on the year-round movements and distribution of the Boyd's shearwater, based on geolocation and SIA of feathers over multiple years. We aim to (1) reveal main foraging areas during breeding and non-breeding seasons, the detailed phenology of their life cycle and, in particular, clarify whether Boyd's shearwater performs dispersal movements or oriented migration to a specific non-breeding area; and (2) to bring new insights into the existence of isoscapes and their potential use to study the movement of tropical top predators by linking the isotopic values of feathers with individual non-breeding areas.

MATERIALS AND METHODS

Study site and species

We conducted fieldwork during the breeding seasons of 2007 to 2012 in the Cape Verde Islands, on Ilhéu Raso (16° 36′ N, 24° 35′ W) and Ilhéu de Cima (14° 58′ N, 24° 38′ W), 2 islets 180 km apart. We visited the colonies during the incubation period, from February to early April, depending on the year. Additionally, we visited Raso in November 2009.

The Boyd's shearwater is a taxon within the Little–Audubon's shearwater complex (*Puffinus assimilis–lherminieri*, Procellariiformes) (reviewed in Austin et al. 2004). Traditionally, '*assimilis*' and '*lherminieri*' were recognized as 2 species groups, but with numerous taxa within each group (Cramp & Simmons 1977, Warham 1990, Carboneras 1992, Brooke 2004). In the last decade, a molecular study by Austin et al. (2004) proposed 3 geographically discrete clades of the complex identified in the North Atlantic, Southern (Australasia) and tropical Pacific and Indian oceans. A recent revision (Carboneras et al. 2016a,b) has suggested the separation of little shearwater *Puffinus assimilis*, distributed in the southern hemisphere, from the Audubon's shearwater *Puffinus lherminieri*, distributed in the North Atlantic Ocean and Caribbean Sea. Particularly, 2 North-Atlantic taxa, Barolo shearwater *Puffinus baroli* (breeding in the Azores, Madeira, and the Canary Islands) and Boyd's shearwater *Puffinus boydi* (breeding in the Cape Verde Islands) have been switched between '*assimilis*' and '*lherminieri*' groups by various authors over the years. Hazevoet (1995) considered *P. boydi* as an independent species. The Boyd's shearwater is endemic to the Cape Verde Islands, where it is thought to breed on most islands and islets (not known from Maio and extinct on Sal) (Hazevoet 1995), with a population estimation of ca. 5000 pairs (BirdLife International 2015). Birds (body mass ≈ 160 g) nest in burrows in soft soil or in rocky cavities. Both parents share incubation of a single white egg that may take 44–60 d to hatch (Carboneras et al. 2016a) and breeding lasts from January to June. Birds are thought to disperse after breeding; however, some were reported visiting the breeding colony at the end of August (Bourne 1955) and throughout the year (Hazevoet 1995). Diet is not well known; the few stomachs examined by Bourne (1955) contained fish and cephalopods up to 8 cm. A closely related species (*P. baroli*) from the Azores feeds mostly on cephalopods and fish (Neves et al. 2012, J. A. Ramos et al. 2015).

Bird tracking and spatial data analysis

During the study period (2007–2012) we deployed a total of 90 geolocators on 68 individuals of Boyd's shearwaters. We captured breeding birds by hand in the burrow and deployed geolocators, which we retrieved after ≥1 yr. Over the course of the study, we used 3 different types of loggers from the British Antarctic Survey (BAS): Mk9 (n = 32), Mk13 (n = 15) and Mk18-H (n = 43). Each logger was attached with a cable tie to a plastic ring, which was deployed on the tarsus of the bird; weight of equipment was approximately 2 g (1.25 % of body mass). We deployed only 1 geolocator per breeding pair.

Geolocators recorded ambient light intensity, time and immersion in seawater. Light levels were measured every 60 s and, depending on the type of device, the maximum value within each 5 min (Mk18-H logger) or 10 min (Mk9 and Mk13 loggers) interval was recorded. We processed raw light data and visually supervised each transition using TransEdit from BASTrack software (British Antarctic Survey). The sunrise and sunset times were estimated applying the light threshold value of 20. To estimate sun elevation angle, we calibrated the loggers before deployment and after recovery on an open site without shading. The value of sun elevation angle was calculated and applied for each logger, ranging from −5.82 to −3.49 (mean −4.54). Light level data were converted into latitude derived from day length and longitude derived from the time of local midday with respect to Greenwich Mean Time, using BASTrack software. This process results in estimation of 2 positions of the animal per day (Delong et al. 1992, Hill 1994, Afanasyev 2004), with a mean error ± SD of 186 ± 114 km (Phillips et al. 2004). Furthermore, as the latitude estimates are highly sensitive to errors and changes in day length, positions in equatorial regions may present lower accuracy (Hill & Braun 2001). In addition, cloudy weather at sunrise and/or sunset may lead to error estimated to 340 km in latitude and 105 km in longitude (Nisbet et al. 2011).

It is worth mentioning that interpretation of geolocation positions especially in equatorial latitudes should be accepted with caution, especially the latitude estimations around equinoxes (Hill & Braun 2001, Ekstrom 2004, Lisovski et al. 2012). Detailed examination of error in latitude estimation is necessary to avoid the possible misleading interpretation of geolocation positions. Particularly in this study, previous visual examination of positions showed a clear pattern (Figs. S1 & S2 in Supplement 1 at www.int-res.com/articles/suppl/m579p169_supp/) repeated in all individuals during the breeding period and resulting from a shift in the latitudinal error between interequinoctial intervals: positions before spring equinox — reflecting mostly incubation and the early chick-rearing period — were distributed northerly from the colony, whereas the positions after the spring equinox — reflecting the chick-rearing period — were distributed southerly from the colony. To avoid possible misleading interpretation that during incubation animals forage in the north and during chick rearing in the south of the colony, we pooled together prelaying, incubation and chick-rearing as a breeding period.

Obtained positions were filtered for each logger separately applying a 3-level filtering method, removing positions (1) 15–30 d before and after equinoxes, (2) with obvious interference at dawn or dusk, and (3) when flight speeds sustained over a 48 h period were higher than 30 km h^{-1} applying iterative backward/forward speed filtering (McConnell et al. 1992). The speed threshold was defined after visual examination of distributions of flight speeds. We also excluded positions from the day of deployment and recovery of the logger. Overall, 66% of original locations were retained for further analysis.

Kernel density utilization distribution (UD) estimates were generated from filtered locations (projection: Lambert Equal-Area Azimuthal, centred to the centroid of all locations) during different periods of the life cycle separately for each bird and year of tracking using package *adehabitatHR* (Calenge 2006) in R (R Core Team 2016). Kernel contours of 50% ('core-area') were calculated using a smoothing parameter (h) equivalent to the mean error of the geolocators (Phillips et al. 2004). We examined various spatial parameters for each track: (1) the area exploited during the breeding and non-breeding periods (50% UD; in km^2); (2) location of the centroids of breeding and non-breeding areas (50% UD), which were calculated using 'centroid' function from package *geosphere* (Hijmans et al. 2012); (3) the total distance (great-circle) from the breeding colony to the centroid of the non-breeding area and (5) the accumulated distance covered within the non-breeding area (without migration), which were estimated using the functions 'distance' and 'distanceTrack' from the *argosfilter* package (Freitas 2012), respectively.

Geolocators also recorded salt-water immersion data sampled every 3 s and registered summary value every 10 min (varying from 0, when the logger was dry the entire 10 min period, to 200, when the logger was permanently wet). This information was used to help define some phenological parameters (see next subsection).

Phenology

Dates defining the phenology of species were identified visually from geographical positions, light and immersion data. During equinox periods, when latitude estimation is not accurate (Hill & Braun 2001), we used only changes in longitude and in immersion data to detect changes in movements and estimate dates of arrival to and departure from the breeding colony.

We estimated various phenological parameters: last night spent at the colony (continuous dry record over prolonged period of time during darkness), departure from the breeding and non-breeding area (the first day that the bird's location was outside the cluster of previous day's positions and was followed by directed movement away from this area), duration of the non-breeding period and migratory movements, arrival to the breeding and non-breeding area (the first day the bird entered the cluster of positions after a directed movement towards that area), the first day and night an individual spent in the burrow (detected by a continuous dry record over a prolonged period of time during daylight and darkness), first day of incubation (min. 2 consecutive days spent in the burrow), duration of the incubation period (from the first day of incubation until the return from the last foraging trip, including time spent outside on foraging trips between incubation shifts), and, finally, incubation shift and foraging trip duration.

Parameters referring to incubation duration were estimated only for individuals with 2 or more continuous years of tracking data (with the same geolocator or the geolocator that was replaced during incubation and recovered the following year). For those individuals we could estimate the onset, duration and end of incubation from light and immersion data. As some loggers failed to collect data for the entire deployment period or some animals did not breed, sample sizes for different phenological parameters vary somewhat between analyses. Based on these parameters, we identified and considered 4 periods of the life cycle: (1) breeding, period between logger deployment and departure on migration and period between the arrival to the colony from migration and recovery of the logger, (2) postnuptial migration, (3) non-breeding, period between arrival to non-breeding area and start of prenuptial migration and (4) prenuptial migration. One individual did not migrate and spent the non-breeding season in the vicinity of the Cape Verde Islands, so we considered the last night the animal spent at the colony (burrow) as the end of the breeding period. Similarly, the start of the subsequent breeding season was assigned as the first night the animal visited the burrow.

We used repeated measures ANOVA with individual as an error term (to account for pseudo-replication as few individuals were tracked >1 yr) to test for differences between the duration of the post- and prenuptial migration and the size of the core range areas between the breeding and non-breeding periods.

Stable isotope analysis

Boyd's shearwater is expected to moult the first primary feather at the end of the breeding period, just before migration, reflecting the isotopic composition of the breeding area (Cramp & Simmons 1977, Roscales et al. 2011). Known primary moult patterns of similar shearwater species are described as descendent, i.e. from the innermost to the outermost primary feather, with a duration of 3–5 mo, while the outermost rectrice feather is among the last to be moulted (Monteiro et al. 1996, Bridge 2006, Ramos et al. 2009). Moult of secondary feathers of shearwaters has been previously linked with the non-breeding area (Neves et al. 2012, Paiva et al. 2016). In this study, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios were examined in different wing-feather types: 1st primary (the innermost), 1st and 8th secondary and 6th rectrices (the outermost) feathers (hereafter named as P1, S1, S8 and R6, respectively). All feathers were sampled when we recovered the geolocator and they were stored in plastic bags before the analysis. For birds with the same logger recovered after ≥2 yr, feather sampling also occurred at the point of logger recovery, but these feathers are only related with the last year of tracking. In total, the dataset for statistical analysis consisted of 32 sets of 4 feathers from 28 individuals (4 individuals with feathers from 2 different years).

To avoid any possible contamination, feather samples were washed in 0.25 M sodium hydroxide solution, rinsed with distilled water and oven dried at 40°C for 24 h. Subsequently, we manually cut each feather to small fragments using stainless steel scissors and weighed a sample of 0.30–0.32 mg on a precision scale. Stable isotope values are expressed in delta notation (δ) as parts per thousand (‰) according to the following: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. R_{standard} values for ^{15}N and ^{13}C were based on atmospheric N_2 and the Vienna Pee Dee Belemnite standard, respectively. Replicate measurements of laboratory standards (2 standards for every 12 unknowns) indicated measurement errors of approximately 0.2 and 0.1‰ for nitrogen and carbon, respectively. The analysis of stable isotopes was carried out at Scientific-Technical Services of the University of Barcelona.

Statistical analyses of isotopic data

We could not directly test for differences between the 2 colonies as they were sampled in different years (Ilhéu Raso: 2007 and 2008; Ilhéu de Cima: 2009, 2010 and 2011). After visual comparison, there was no indication in systematic differences in isotopic values between colonies; therefore, all the statistical analyses were performed with isotopic data of both colonies pooled together. To test for differences among feathers in isotopic data, we first checked $\delta^{13}C$ and $\delta^{15}N$ values for normal distribution using Q-Q plots and Shapiro-Wilks' test. We used linear mixed models (LMM, R package *lmerTest*; Kuznetsova et al. 2015) to compare isotopic values among feathers (fixed factor) and we accounted for pseudo-replication including individual and sampling year as random factors. The p-values were calculated from Type 3 *F*-statistics with Satterthwaite's approximation for degrees of freedom, while pairwise comparisons were calculated based on differences of least squares means (function 'difflsmeans' package *lmerTest*) and adjusted using Bonferroni correction.

Based on the isotopic differences found among feathers (see 'Results'), we inferred that the S1 and S8 were moulted during the non-breeding period. Because both showed similar isotopic values, and to allow a comparison with the isotopic data of previous studies on a closely related species (Neves et al. 2012, Paiva et al. 2016), we used S8 for subsequent analyses. To link isotopic values of S8 feathers with the non-breeding area of each individual we determined the individual centroids of 50% kernel of non-breeding area. We used LMM to examine whether the variation in S8 feather isotopic values could be explained by the location of their non-breeding area (latitude and/or longitude of centroid as fixed, individual and year as random factors; R package *lmerTest*; Kuznetsova et al. 2015). The best-supported model was selected using the Akaike Information Criteria corrected for small sample sizes (AIC_c) (R package *MuMIn*; Bartoń 2016). To understand the possible influence of the sampling year we verified its importance based on the likelihood ratio test (function 'rand' from package *lmerTest*) and by calculating the variance explained by the sampling year.

Statistical analyses were carried out using the R software version 3.2.1 (R Core Team 2016). All values are presented as means ± SD, and we assumed a significance level $p < 0.05$.

RESULTS

Recovery of loggers

We retrieved 43 loggers (recovery rate 47.8 %) from 32 unique individuals. Most loggers were recovered in the year following deployment; however, 7 loggers were retrieved after 2 consecutive years. Eight other individuals (n = 6 and n = 2, respectively) were tracked over 2 and 3 consecutive years, by recovering and deploying a new logger each year. Eleven loggers failed or did not contain enough data for further analysis. Overall, the final dataset contained 38 year-long tracks of 28 unique individuals (9 from Ilhéu Raso, 19 from Ilhéu de Cima), including 10 individuals with 2 yr of tracking. We calculated kernel UD density for 38 tracks for non-breeding (2007, 9 tracks; 2008, 3 tracks; 2009, 6 tracks; 2010, 12 tracks; 2011, 8 tracks) and 35 tracks for breeding season, as 3 tracks from 2010/2011 did not contain enough locations for kernel estimation.

Phenology of annual cycle

Boyd's shearwaters presented some variability in their phenological parameters, especially in the timing of the first day and the first night in the burrow (Table 1) and on the duration of the non-breeding period (Table 1, Fig. 1 with individual phenologies). Furthermore, the duration of the prenuptial migration was statisticaly longer than the postnuptial migration (repeated-measures ANOVA, $F_{1,45} = 7.463$, $p = 0.009$), with birds travelling for 7.2 ± 6.0 d to reach the breeding colony on their prenuptial migration in contrast with 4.9 ± 2.6 d to reach the non-breeding area on their postnuptial migration (Table 1).

Table 1. Year-round phenology of Boyd's shearwaters from Ilhéu de Cima and Raso (Cape Verde), tracked with geolocators from 2007–2012; data are mean ± SD and range values over 5 yr of tracking study

Phenological parameter	n	Mean ± SD	Range
Last night colony	36	26 Apr ± 17.4	21 Mar–28 May
Colony departure	38	4 May ± 16.5	4 Apr–7 Jun
Non-breeding area arrival	38	9 May ± 16.6	7 Apr–12 Jun
Non-breeding area departure	37	31 Aug ± 18.6	1 Aug–16 Oct
Colony arrival	37	7 Sep ± 19.5	4 Aug–22 Oct
First night burrow	33	18 Sep ± 28.5	4 Aug–2 Dec
First day burrow	32	31 Oct ± 59.6	13 Aug–11 Jan
Incubation start	24	9 Feb ± 12.2	22 Jan–6 Mar
Number of incubation shifts	6	3.8 ± 0.8	3–5
Duration of incubation (d)	6	47.0 ± 2.8	42–50
Duration of incubation shift (d)	23	6.0 ± 1.9	2–10
Duration of incubation foraging trip (d)	23	6.3 ± 1.9	2–9
Duration of postnuptial migration (d)	38	4.9 ± 2.6	0–13
Duration of non-breeding period (d)	37	114.0 ± 18.1	50–140
Duration of prenuptial migration (d)	37	7.2 ± 6.0	0–33

Seasonal changes in at-sea distribution

During breeding, birds dispersed in different directions around the breeding colony and in proximity to Cape Verde Islands. With 1 exception (bird ID 2007_047), which foraged in the neritic area of the African coast in November-December, the tracked birds did not forage in neritic waters but north of the breeding colonies, reaching up to 30° N (Fig. 2, Fig. S3 in Supplement 1 and the animation in Supplement 2 at www.int-res.com/articles/suppl/m579p169_supp/). The estimated individual core range area during the breeding season (50 % kernel UD) ranged from 292 000 to 764 400 km² (470 600 ± 111 500 km², n = 35).

At the beginning of May, birds started their postnuptial migration consistently in a westward direction along a migration corridor between 7° and 15° N (Fig. S4). The mean distance between the breeding colony and non-breeding area (to the centroid of 50% kernel UD) was 1450 ± 398 km (range 106–2391 km, n = 38). The main non-breeding area of Boyd's shearwaters was in the Central Atlantic Ocean, west of Cape Verde Basin, over the Mid-Atlantic Ocean Ridge, from 5 to 15° N and from 30 to 40° W (50 % kernel UD; Fig. 3, Fig. S3 in Supplement 1, and Supplement 2). However, 1 individual migrated further west to 9° N, 43° W (bird ID 2009_510), while another went further north to

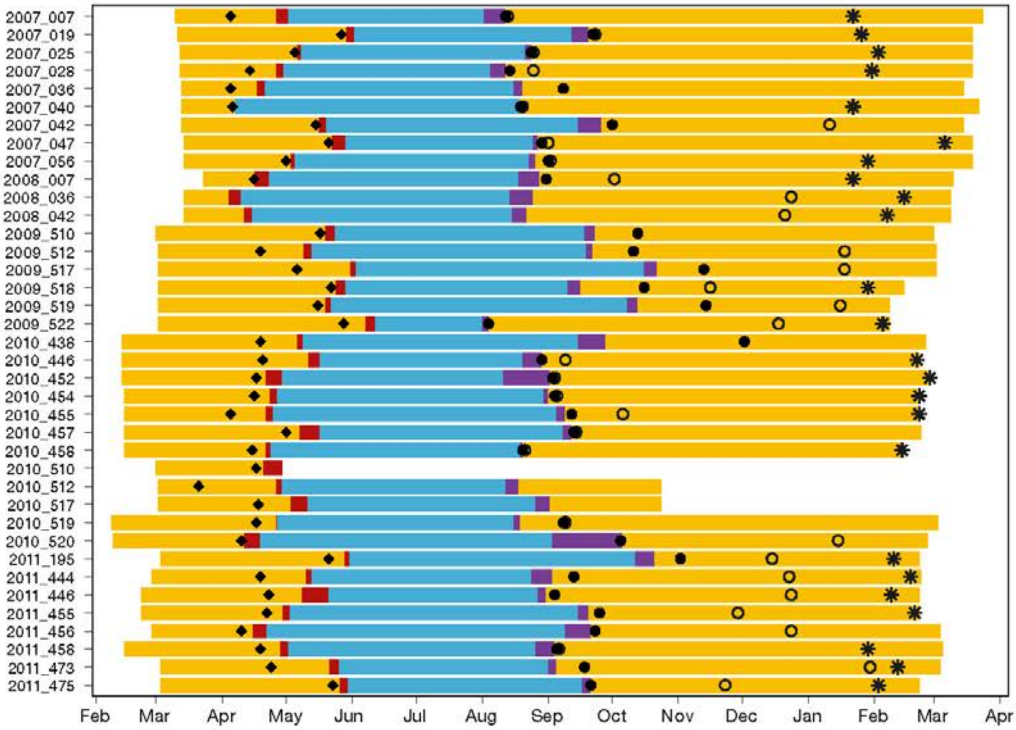


Fig. 1. Individual phenologies of Boyd's shearwaters, ordered by year of logger deployment (year of deployment_bird ID; n = 38). Each horizontal bar represents 1 yr of tracking, colours represent different stages of breeding cycle: breeding in yellow, postnuptial migration in dark red, non-breeding in blue, prenuptial migration in purple. Points refer to last night (◆), first night (●) and first day (○) the bird spent in the burrow, and onset of incubation (✱). Starts on the day of deployment, ends on the day of retrieval of the logger (or when logger stopped collecting data)

21° N, 36° W (bird ID 2007_007). The estimated individual core range area during the non-breeding season (50% kernel UD) ranged from 300 700 to 795 400 km^2 (467 700 ± 120 000 km^2, n = 38), which did not significantly differ from the size of core range areas during the breeding season (repeated measures ANOVA, $F_{1,41} = 0.027$, p = 0.870, n = 35). During the non-breeding period, birds dispersed or steadily moved over a huge area. Total distance covered within the non-breeding area was on average 33 670 ± 5628 km (range 17 440–47 690 km, n = 38), moving on average 253.1 ± 32.8 km over approximately 24 h by a mean velocity of 10.5 ± 1.4 km h^{-1}. From all tracked birds, only 1 individual (bird ID 2007_040) did not migrate and stayed in the vicinity of Cape Verde Island year-round. The timing of prenuptial migration mostly overlapped with the autumn equinox period, but data for a few individuals suggest that animals use a similar route to return to breeding grounds (Fig. S4).

Stable isotope analysis

Boyd's shearwaters presented a wider range of nitrogen (6.39 to 12.60‰) than carbon values (−17.96 to −15.24‰) (Table 2, Fig. 4). Significant differences were found between feathers (P1, S1, S8 and R6) in both nitrogen (LMM, $F_{3,94.323} = 29.965$, $p < 0.001$) and carbon values (LMM, $F_{3,91.355} = 53.684$, $p < 0.001$). The differences in nitrogen values were between P1 and both S1 and S8 (pairwise comparison, both $p < 0.001$; Table S1 in Supplement 1). No difference was found between P1 and R6 (pairwise comparison, p = 0.719), or between S1 and S8 (pairwise comparison, p = 1.000). Significant differences were found between all feathers for carbon values (pairwise comparison, for all $p < 0.001$), except for S1 and S8 (p = 0.417). Although differences found between feathers were statistically significant, the magnitude of those differences was small (Table S1 in Supplement 1), comparing with variation among individuals (Fig. 4).

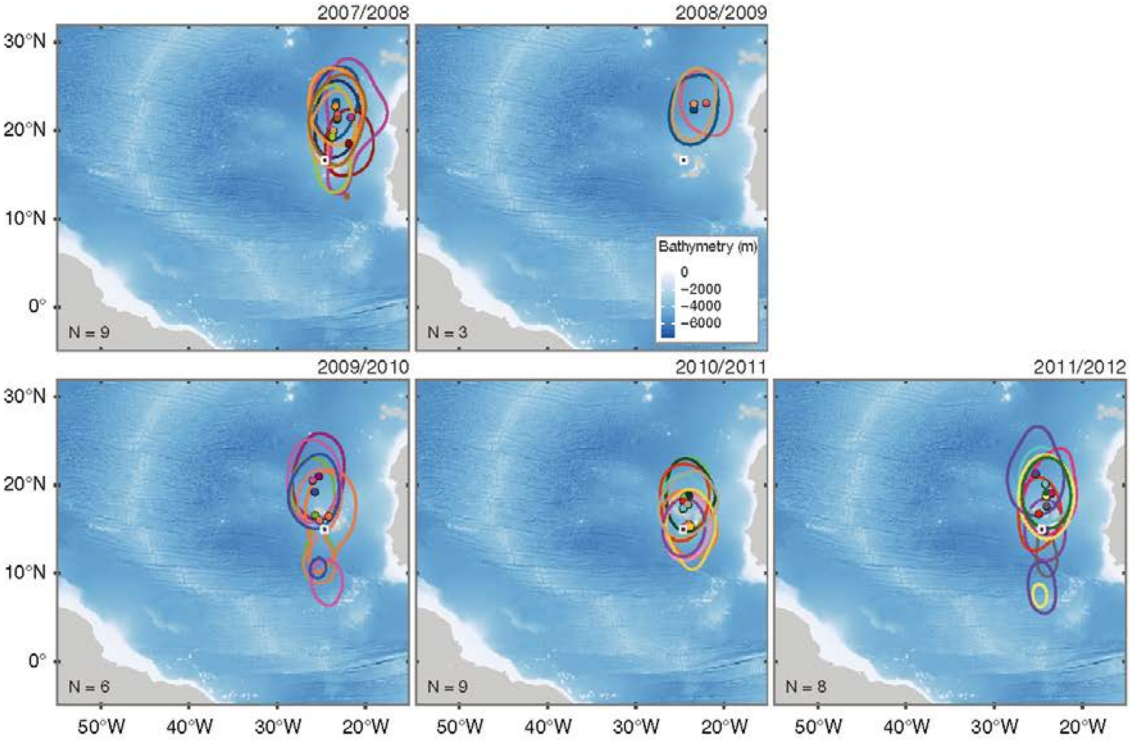


Fig. 2. Individual kernel density utilisation distributions for Boyd's shearwaters during the breeding season, tracked with geolocators during 5 yr (2007–2012). Ellipses: individual 50% density contours; points: individual centroids of 50% density contours; black square: breeding colony. Bathymetry used as background

Geographic isotopic gradient (isoscapes)

The best-supported models (Table 3, Table S2a) suggest that the variation of isotope values of S8 was highly related with longitude (LMM, δ^{15}N: $F_{1,29.915}$ = 57.945, p < 0.001; δ^{13}C: $F_{1,28.326}$ = 29.139, p < 0.001; Fig. 5A,B), but not with latitude (LMM, δ^{15}N: $F_{1,25.094}$ = 1.512, p = 0.230; δ^{13}C: $F_{1,29.200}$ = 0.511, p = 0.485) values of the non-breeding centroid of Boyd's shearwaters. Indeed, the R^{2}m values, which describe the proportion of variance explained by the fixed factor alone, were high in the model with the fixed factor longitude (0.63 and 0.39 for δ^{15}N and δ^{13}C, respectively; Fig. 5A,B), but not in the ones with latitude (0.05 and 0.01 for δ^{15}N and δ^{13}C, respectively). Accounting for both longitude and latitude did not significantly improve the longitude-gradient model (LMM, δ^{15}N: χ^2 = 0.121, df = 1, p = 0.729; δ^{13}C: χ^2 = 0.012, df = 1, p = 0.913). Our best-supported models suggest that annual isotopic variability was negligible for nitrogen values of S8, accounting for 0% of random variance (χ^2 = 0, df = 1, p = 1.000) (Table S2b). In contrast, annual variation accounted for almost half (53.3%) of the random variance of the carbon values (χ^2 = 7.630, df = 1, p = 0.006).

DISCUSSION

This is the first study on the movements and year-round distribution of the Boyd's shearwater. We showed that Boyd's shearwaters perform oriented migratory movements and exploit oceanic habitats year-round. Furthermore, we revealed the existence of a longitudinal isotopic gradient in the tropical north Atlantic by relating the isotopic values of the feathers moulted during the non-breeding period and the location of the individual non-breeding area.

Boyd's shearwaters showed some variability in various aspects of their breeding phenology. Small species breeding in the tropics may experience relatively constant environmental conditions, which may cause

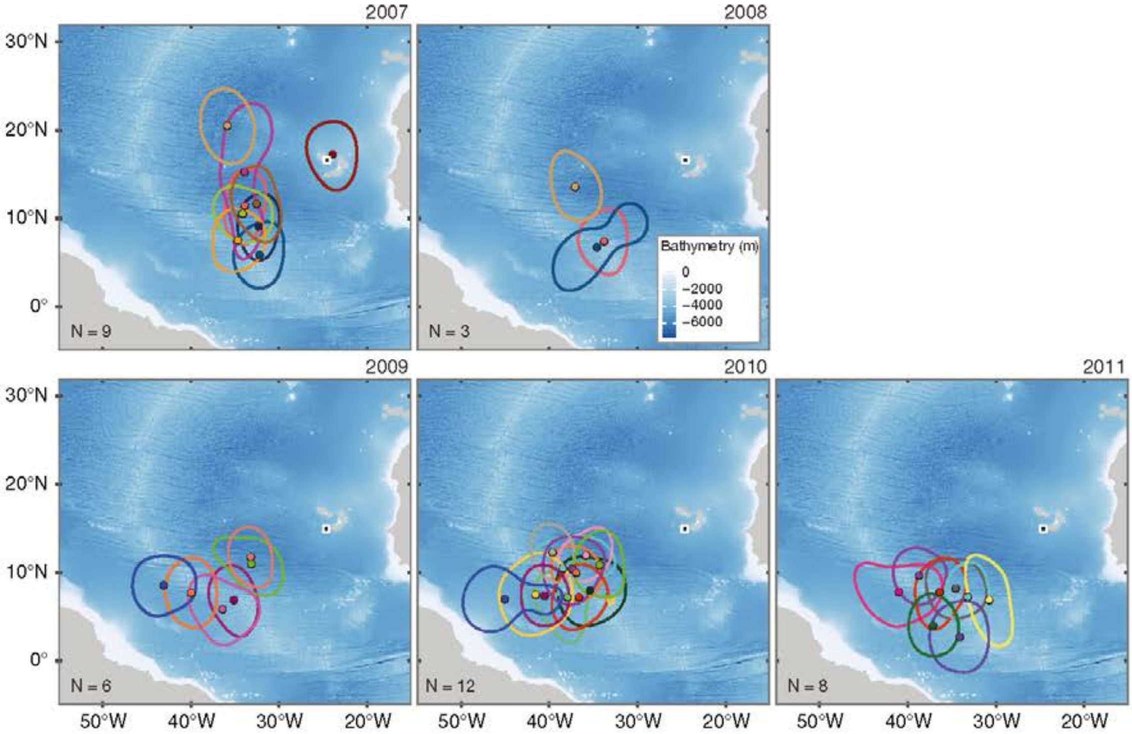


Fig. 3. Individual kernel density utilisation distributions for Boyd's shearwaters during the non-breeding season. Other details as in Fig. 2

Table 2. Isotopic values of $\delta^{15}N$ and $\delta^{13}C$ (‰) in the 1st primary (P1), the 1st (S1) and 8th (S8) secondary feathers and the 6th rectrice (R6) of Boyd's shearwaters breeding in the Cape Verde Islands. P1 and R6 feathers showed similar isotopic values but distinct than S1 and S8

Feather	n	$\delta^{15}N$		$\delta^{13}C$	
		Mean ± SD	Range	Mean ± SD	Range
P1	32	8.75 ± 1.12	7.29 to 12.60	−16.68 ± 0.43	−17.96 to −16.10
S1	32	7.61 ± 0.59	6.39 to 9.46	−16.04 ± 0.30	−16.93 to −15.59
S8	32	7.57 ± 0.61	6.44 to 9.82	−15.92 ± 0.35	−16.83 to −15.24
R6	32	8.51 ± 1.13	6.64 to 11.01	−16.37 ± 0.44	−17.20 to −15.51

minimal synchrony in breeding (Brooke 1990). The few individuals that started the postnuptial migration relatively earlier, in the beginning of April, were presumably failed breeders; however, we do not have breeding success information of each bird to confirm this hypothesis. The longer duration of prenuptial migration in relation to the postnuptial one is an opposite pattern to many long-distance migrants (Nilsson et al. 2013) and may be a consequence of prevailing trade winds which advantaged shearwaters during postnuptial migration through a tailwind but disadvantaged them during prenuptial migration through a headwind (Liechti 2006). Birds started to arrive at the colony in early August, which confirms observations of shearwaters visiting Ilhéu de Cima at the end of August (Bourne 1955). After returning to the breeding colony, birds were asynchronous in terms of the first day spent in the burrow during daylight; these dates were spread over 4 mo. Those differences might be sex-related, with males visiting burrows earlier than females in some shearwater species (Hedd et al. 2012, Müller et al. 2014), probably due to their role in nest defence. However, this asynchrony was also observed in Barolo shearwaters, in a study where only males were tracked (Neves et al. 2012). As sex of animals tracked in this study was unknown and only 1 member of the breeding pair was tracked, we could not estimate the laying date and define the first incubation shift. However, we were able to estimate the

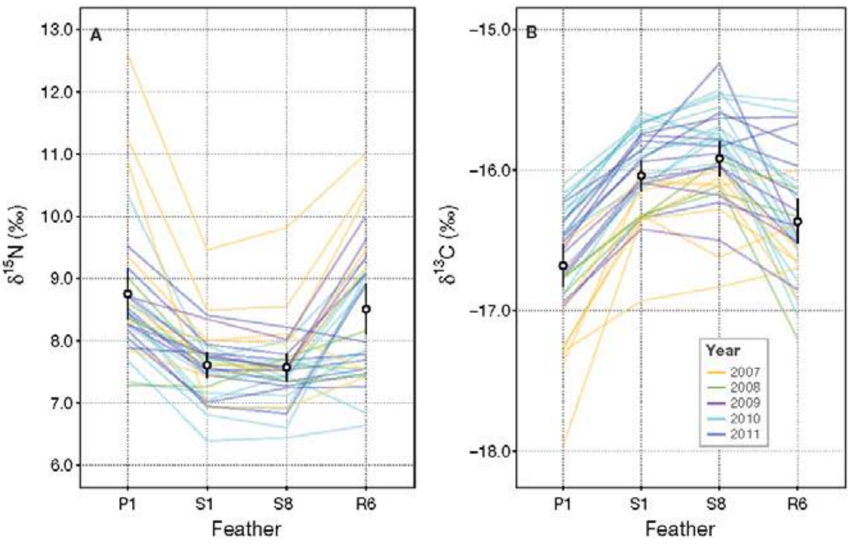


Fig. 4. Stable isotopes (A) $\delta^{15}N$ and (B) $\delta^{13}C$ of sampled feathers (P1: 1st primary; S1 and S8: 1st and 8th secondary, respectively; R6: 6th rectrice) of tracked Boyd's shearwaters breeding in the Cape Verde Islands (n = 32) in 2007–2012. Each line corresponds to 1 individual coloured by the year of tracking. Circle with range represents mean ± 95% confidence interval

Table 3. Linear mixed models testing for spatial gradient in isotopic values of nitrogen and carbon of Boyd's shearwaters breeding in the Cape Verde Islands. Results of second-order Akaike's Information Criterion (AIC_c), delta AIC_c and Akaike weights are shown. The best supported model (in **bold**) includes longitude as fixed factor. All models include individual and year as random factors

Model	df	$\delta^{15}N$			$\delta^{13}C$		
		AIC_c	ΔAIC_c	AIC_c wt	AIC_c	ΔAIC_c	AIC_c wt
Long	**5**	**37.56**	**0.00**	**0.81**	**0.75**	**0.00**	**0.82**
Long + Lat	6	40.49	2.93	0.19	3.79	3.04	0.18
Null	4	66.45	28.90	0.00	19.62	18.87	0.00
Lat	5	67.60	30.03	0.00	21.83	21.08	0.00

beginning of incubation, on average February 9, which is earlier than Barolo's shearwaters in the Azores (Neves et al. 2012, but see Monteiro et al. 1996). Indeed, the incubation period (42–50 d) was slightly shorter than the periods reported for *Puffinus lherminieri* (44–60 d, Carboneras et al. 2016b), *P. assimilis assimilis* (55 d) breeding at Lord Howe Island (Priddel et al. 2003) and *P. a. haurakiensis* (54–57 d) on Lady Alice Island (Booth et al. 2000). Incubation shift length and duration of foraging trips during incubation were similar to Barolo shearwaters tracked in the Azores (Neves et al. 2012). However, the foraging-trip durations of Boyd's shearwaters differed from those of Barolo shearwaters foraging mostly within the Canary Current system (being longer than those of birds breeding in Salvagem Grande but shorter than those in Porto Santo) (Paiva et al. 2016). Since we would expect incubation behaviour and foraging strategies to be similar among such closely related taxa, this variability most likely reflects differences in environmental conditions across localities, such as differences in the distance to suitable foraging areas and their typically low predictability in tropical waters, which possibly results in differences in egg neglect episodes (and therefore duration of the incubation) and foraging trip length (and therefore duration of incubation shifts) across populations.

During the breeding period, Boyd's shearwaters mainly foraged around the Cape Verde archipelago. Individual core ranges seemed to fluctuate north and south of the archipelago, and some geolocator positions may have even reached the Canary Islands or the Azores (Fig. S3 in Supplement 1, and Supplement 2), but this is most likely due to the effect of the equinoxes on the latitudinal errors (Figs. S1 & S2). Since longitudinal errors of the geolocator methodology are relatively small and the African coast is just east of the archipelago, our results clearly showed that birds do not visit the African shelf to forage in neritic waters. With the exception of 1 individual for a few weeks, all birds were largely oceanic during breeding and over the 5 yr of the study (Fig. 2). Similarly, the closely related Barolo shearwaters breeding in Madeira and other small seabird species in Cape Verde also show oceanic distribution during the breeding period (J. A. Ramos et al. 2015, R. Ramos et al. 2015, 2016, Paiva et al. 2016). The oceanic behaviour of Boyd's shearwaters is also suggested by the low carbon values in

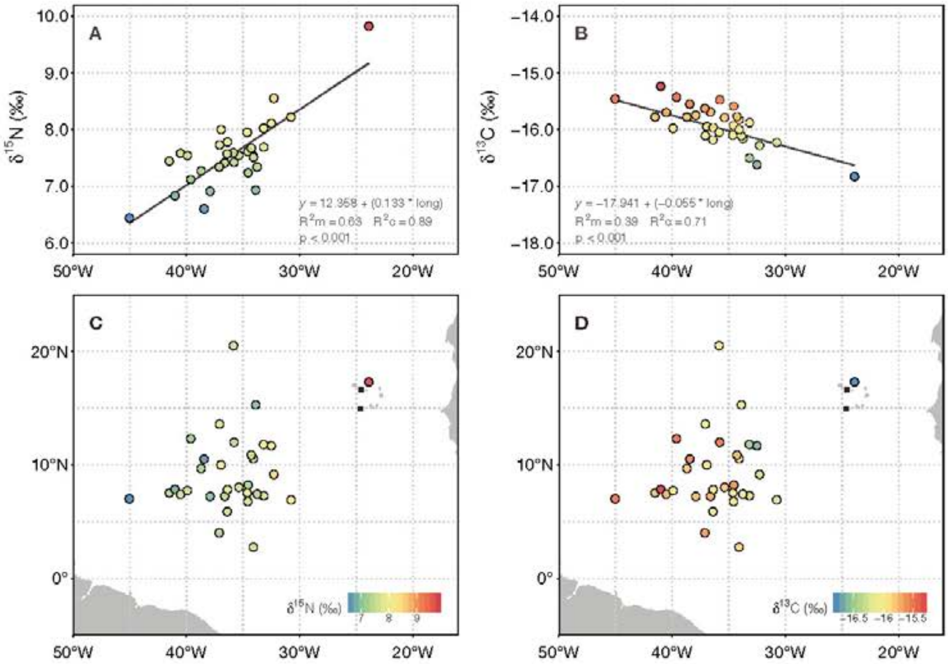


Fig. 5. Relationship between (A) $\delta^{15}N$ and (B) $\delta^{13}C$ values of 8th secondary feather (S8) of Boyd's shearwaters tracked with geolocators (n = 32; 2007–2012) and the longitude of the centroid, reflecting the area exploited during the non-breeding season (May–August). Points represent individual centroids of 50% kernel utilization distribution during the non-breeding season. Equation (negative values for western longitude) and dark grey line refer to intercept and slope for fixed factors of linear mixed model (longitude as fixed factor, with year and individual as random) for all years pooled together. (C,D) Spatial distribution of individual centroids of 50% kernel utilization distributions during the non-breeding season and their respective gradient in (C) $\delta^{15}N$ and (D) $\delta^{13}C$ values of S8. Black squares: breeding colonies (Ilhéu Raso and Ilhéu de Cima)

their first primary feathers (P1), similar to those reported for other oceanic species, such as the Barolo shearwaters in several Macaronesian localities (Roscales et al. 2011, Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016), but also by Bulwer's and Fea's petrel in Cape Verde (Roscales et al. 2011). These results contrast with the importance of the continental shelf inferred for the Barolo shearwaters breeding on Salvagens (J. A. Ramos et al. 2015, Paiva et al. 2016) and also for Audubon's shearwaters breeding in the Caribbean (Precheur 2015, P. Jodice unpubl. data). Further studies using more accurate loggers are needed to confirm these results as this apparent neritic behaviour may just result from the latitudinal error of the geolocation method (Fig. S1).

After breeding, Boyd's shearwaters performed a longitudinal-oriented migration, heading westward to the oligotrophic waters of the central North Atlantic Ocean. Despite their short migration, Boyd's shearwaters constantly moved during the non-breeding season, covering on average more than 30 000 km. These movements may be a foraging strategy to increase the chances of finding prey in tropical oceanic waters, which typically show lower productivity and predictability of resources than upwelling systems (Weimerskirch 2007). However, distance calculations should be treated with caution as they may be overestimated due to the positional error. The longitudinal-oriented migration was noticeably consistent across years at coarse scale, wintering in the same area of the Atlantic (except 1 individual remaining around the Cape Verde Islands). All birds spending their non-breeding period in this area also showed clear oceanic habits. The lack of direct observations of Boyd's shearwaters from their migration and non-breeding grounds may be due to the lack of observers in those areas and/or to the problematic identification of the taxa at sea. To our knowledge, there are just a few sightings of individuals of the little shearwater complex of unknown provenance (RNBWS 2014), illustrating once again the enormous insights geolocation is providing into the spatial ecology of seabirds, particularly in closely related taxa with few morphological differences and unclear taxonomic status. In contrast with our results, previous tracking studies on Barolo shearwaters in the Azores and Salvagens mainly showed a dispersive behaviour after breeding (Neves et al. 2012, Paiva et al. 2016). In addition, there is no spatio-temporal overlap in distribution of the different taxa of the complex, pointing out substantial differences in their migratory behaviour and distribution and potential for lineage divergence, which deserves some attention when discussing the taxonomy within the little shearwater complex.

To understand year-round trophic ecology and study the existence of oceanic isoscapes through the analyses of stable isotopes in feathers it is essential to know the moulting patterns of the study model. Unfortunately, there is a lack of information about moult in Boyd's shearwater. Shearwaters usually show simple descendent moult that takes 3 to 5 mo to complete (Bridge 2006), starting with the innermost primary feather (P1), which in some species may be moulted even before the bird leaves the breeding area (Cramp & Simmons 1977, Monteiro et al. 1996). According to our geolocation data, birds spent on average 114 d outside of the breeding area, which theoretically should leave enough time to complete moult in the non-breeding area. Our SIA supports this hypothesis. P1 and R6 were isotopically similar, suggesting that they are moulted in the same area, probably near the breeding area at the end of the breeding and non-breeding period, respectively. These 2 feathers differed from the S1 and S8, which we inferred were moulted during the non-breeding period in the North Central Atlantic, since the isotopic values of the S8 showed a high correlation with the longitude of the centroid of the non-breeding area of each individual. We inferred P1 and R6 to be moulted in the same area (surroundings of the breeding colony), so we expected to find lower isotopic variability compared to S1 and S8, which were moulted in different non-breeding areas with potentially different baselines. Therefore, the larger range of isotopic values of the P1 and R6 than S1 and S8 may reflect the inter-individual variability in the phenology at the beginning and at the end of the moulting period, with some birds advancing or delaying their moulting patterns in relation to migration depending, for example, on their breeding success. Moreover, moulting pattern of rectrices is typically more asynchronic among and within individuals than the rest of the flight feathers (Ramos et al. 2009), adding variability in the timing of moult and in turn in the standard deviation and range of the isotopic values we found in R6.

The inter-annual variability in stable isotope values was low for nitrogen, but relatively high for carbon values. However, the broad pattern found in longitudinal gradients was similar over the years (Fig. S5). Baselines of nitrogen and carbon values are known to vary between seasons and years due to changing environmental factors (temperature) and/or productivity in marine environment (Goering et al. 1990, Rolff 2000, Graham et al. 2010). Inter-annual differences in stable isotopes were also found in Barolo shearwaters, but the origin is difficult to determine, since these differences may result from changes in diet, foraging areas and/or baseline conditions due to environmental factors, or a combination thereof (Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016).

Many seabird species cross the equatorial area of the Atlantic Ocean during their trans-equatorial migrations, but do not forage in this area for extended periods (González-Solís et al. 2007, Guilford et al. 2009, Hedd et al. 2012). So far, the only tracked species known to use the equatorial Atlantic waters as one of their main non-breeding areas is the Bulwer's petrel *Bulweria bulwerii* (Dias et al. 2015, R. Ramos et al. 2015), although in a different period than the Boyd's shearwater, since Bulwer's petrels breed during the non-breeding period of the Boyd's shearwaters. Temporal segregation in the breeding cycles of Bulwer's petrel and Boyd's shearwaters may suggest that this is driven by competition for food, but their segregation in trophic level, as indicated by the greater δ^{15}N in the former than in the latter (Roscales et al. 2011), would not support this interpretation. Instead, temporal segregation may partly result from competition for nesting sites (Fagundes et al. 2016). Indeed, previous studies on breeding seabirds of the tropical and subtropical Atlantic indicated that the trophic position of the Boyd's shearwater is the lowest among all pelagic seabirds, together with Barolo and Audubon's shearwaters (Roscales et al. 2011, Neves et al. 2012, Mancini et al. 2014, Paiva et al. 2016). No conventional dietary analysis of Boyd's shearwaters has been conducted so far (but see Bourne 1955), but its low trophic level indicates the consumption of small juvenile squid and fish and crustaceans, as found in the diet of the Barolo shearwater (Neves et al. 2012, J. A. Ramos et al. 2015). Previous studies have suggested seasonal changes in the diet of the Barolo shearwater (Neves et al. 2012, J. A. Ramos et al. 2015, Paiva et al. 2016), as indicated by an increase in δ^{15}N values in feathers moulted in the non-breeding season compared to those moulted in the breeding season, suggesting that shearwaters targeted prey with higher trophic level during the non-breeding season (Neves et al. 2012). We also found seasonal changes in the isotopic values quite consistent over 5 years, but changes in $\delta^{15}N$ were the opposite, i.e. we observed a decrease in $\delta^{15}N$ and an increase in $\delta^{13}C$ values from feathers moulted in the non-breeding (S1 and S8) compared to those grown in the breeding season (P1 and R6; Fig. 4). However, this opposite trend in $\delta^{15}N$ values and its significant correlation with longitude suggest that these changes just reflect baseline isotopic gradients in longitude (Fig. 5). Indeed, correlations between longitude of the non-breeding centroids with the isotopic values of feathers grown in this period broadly match isoscapes based on plankton samples from the same area (Somes et al. 2010, McMahon et al. 2013a). Spatial patterns indicating greater values of $\delta^{13}C$ and smaller in $\delta^{15}N$ in the central oligotrophic subtropical Atlantic Ocean were confirmed by a recent study on plankton biomass (Mompeán et al. 2013). Knowledge of baselines is also essential in any isotopic studies of trophic ecology, since baseline adjustment allows for the comparison of species from different geographical origin (Navarro et al. 2013). The strong longitudinal gradient in values of nitrogen and carbon found in this study suggests propagation of isotopic variability up to the food chain on a coarse scale. However, failure to find latitudinal gradients may be related to latitudinal error inherent to geolocation methodology. Another constraint in gradient models is the limitation in modelling techniques to incorporate all sources of uncertainty and error of location estimations. Furthermore, care should be taken, as the high isotopic variability among individuals and the reduction of the moulting area to a centroid may hinder the potential use of this isotopic gradient to infer the non-breeding areas of untracked birds. A study using data with more precise spatial resolution and more detailed knowledge about timing of moult would be required to create complex isoscapes and investigate the potential geographic assignment to foraging movements or non-breeding areas of top predators in the tropical Atlantic Ocean using SIA, but our results show some promising potential for this.

Overall, in this study we provided detailed information about the year-round distribution, trophic ecology, phenology and moulting patterns of Boyd's shearwater. The combined use of geolocators and SIA allowed us to bring new insights to the biology and ecology of a poorly known tropical species.

Acknowledgements. We thank all the people who helped us at several stages of fieldwork (S. Martins, R. Ramos, L. Zango). We are also grateful to the Direção Nacional do Ambiente of Cape Verde who provided logistical support and the necessary authorisations. Z.Z. was supported by a PhD grant (APIF) from the University of Barcelona (Spain) and T.M. by a PhD grant (SFRH/BD/47467/2008) from Fundação para a Ciência e Tecnologia (Portugal). This study was funded by the MICIN, Spain (CGL2009- 11278/BOS and CGL2013-42585-P) and Fondos FEDER. We are thankful to Sarah Saldanha for language corrections, Martin Stýblo for his encouragement and José Manuel Reyes-González for helpful discussions and comments on previous versions of the manuscript. We are also grateful to Steffen Oppel and an anonymous reviewer for their comments, which greatly improved the previous version of the manuscript.

LITERATURE CITED

Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. Mem Natl Inst Polar Res 58:227–233

Ainley DG, Ribic CA, Woehler EJ (2012) Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. Mar Ecol Prog Ser 451:231–243

Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus Nat Hist Yale Univ Bull 24

Austin JJ, Bretagnolle V, Pasquet E (2004) A global molecular phylogeny of the small puffinus shearwaters and implications for systematics of the little-audubon's shearwater complex. Auk 121:847–864

Ballance L (2007) Understanding seabirds at sea: why and how? Mar Ornithol 35:127–135

Ballance LT, Pitman RL (1999) Foraging ecology of tropical seabirds. In: Adams NJ, Slotow RH (eds) Proc 22 Int Ornithol Congr, Durban. BirdLife South Africa, Johannesburg, p 2057–2071

Bartoń K (2016) MuMIn: multi-model inference. https://cran.r-project.org/web/packages/MuMIn/index.html

BirdLife International (2015) *Puffinus lherminieri*. The IUCN Red List of Threatened Species 2015: eT45959182A 84678618

Booth A, Minot E, Imber M, Fordham R (2000) Aspects of the breeding ecology of the North Island little shearwater *Puffinus assimilis haurakiensis*. NZ J Zool 27:335–345

Bourne WRP (1955) The birds of Cape Verde Islands. Ibis 97: 508–555

Bourne WRP, Loveridge A (1978) Small shearwaters from Ascension and St. Helena, South Atlantic Ocean. Ibis 120:65–66

Bridge ES (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. Mar Ornithol 34:7–19

Brooke M (1990) The Manx shearwater. Academic Press, London

Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Camphuysen KCJ, Garthe S (2004) Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi-species associations. Atl Seabirds 6:1–32

Carboneras C (1992) Family Procellariidae (petrels and shearwaters). In: Del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, Vol 1. Lynx Edicions, Barcelona, p 216–271

Carboneras C, Jutglar F, Kirwan GM (2016a) Audubon's shearwater (*Puffinus lherminieri*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona

Carboneras C, Jutglar F, Kirwan G (2016b) Little shearwater (*Puffinus assimilis*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona

Catry T, Ramos JA, Le Corre M, Phillips RA (2009) Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. Mar Ecol Prog Ser 391:231–242

Catry T, Ramos JA, Catry I, Monticelli D, Granadeiro JP (2013) Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. Mar Biol 160:1189–1201

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cherel Y, Le Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar Ecol Prog Ser 366:281–291

Cramp S, Simmons KEL (1977) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, Vol I. Oxford University Press, London

Delong RL, Stewart BS, Hill RD (1992) Documenting migrations of northern elephant seals using day length. Mar Mamm Sci 8:155–159

Dias MP, Alho M, Granadeiro JP, Catry P (2015) Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel. J Ornithol 156: 955–962

Dubois PJ, Holmström N, Verneau A (2009) La péninsule du Cap-Vert à Dakar, Sénégal, est-elle la «Mecque» du seawatching? Ornithos 16:220–232

Ekstrom PA (2004) An advance in geolocation by light. Mem Natl Inst Polar Res 58:210–226

Fagundes AI, Ramos JA, Ramos U, Medeiros R, Paiva VH (2016) Breeding biology of a winter-breeding procellariiform in the North Atlantic, the Macaronesian shearwater *Puffinus lherminieri baroli*. Zoology 119:421–429

Freitas C (2012) argosfilter: Argos locations filter. R package version 0.63. https://cran.r-project.org/web/packages/argosfilter

Goering J, Alexander V, Haubenstock N (1990) Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a North Pacific Bay. Estuar Coast Shelf Sci 30:239–260

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 5:297–301

González-Solís J, Smyrli M, Militão T, Grémillet D, Tveraa T, Phillips RA, Boulinier T (2011) Combining stable isotope analyses and geolocation to reveal kittiwake migration. Mar Ecol Prog Ser 435:251–261

Graham BS, Koch PL, Newsome SD, McMahon CR, Aurioles-Gamboa D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson T, Tu KP (eds) Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping. Springer, New York, NY, p 299–318

Guilford T, Meade J, Willis J, Phillips RA and others (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc Biol Sci 276:1215–1223

Guilford T, Wynn R, McMinn M, Rodríguez A and others (2012) Geolocators reveal migration and pre-breeding behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. PLOS ONE 7:e33753

Hazevoet CJ (1995) The birds of the Cape Verde Islands. An annotated check list. British Ornitologists Union, London

Hazevoet CJ (1997) Notes on distribution, conservation, and taxonomy of birds from the Cape Verde Islands, including records of six species new to the archipelago. Bull Zool Mus Univ Amst 15:89–100

Hedd A, Montevecchi WA, Otley H, Phillips RA, Fifield DA (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. Mar Ecol Prog Ser 449:277–290

Hijmans RJ, Williams E, Vennes C (2012) Geosphere: spherical trigonometry. R package version 1.2-28. http://cran.r-project.org/web/packages/geosphere/geosphere.pdf

Hill RD (1994) Theory of geolocation by light levels. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkeley, CA, p 227–236

Hill RD, Braun MJ (2001) Geolocation by light level. In: Sibert JR, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Reviews: methods and technologies in fish biology and fisheries, Vol 1. Springer, Dordrecht, p 315–330

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Jaeger A, Lecomte VJ, Weimerskirch H, Richard P, Cherel Y (2010) Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. Rapid Commun Mass Spectrom 24: 3456–3460

Jaquemet S, Le Corre M, Weimerskirch H (2004) Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). Mar Ecol Prog Ser 268:281–292

Kuznetsova A, Brockhoff PB, Christensen RHB (2015) lmerTest: tests in linear mixed effects models. R package version 2.0-29. https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf

Liechti F (2006) Birds: blowin' by the wind? J Ornithol 147: 202–211

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol Evol 3:603–612

Mancini PL, Hobson KA, Bugoni L (2014) Role of body size in shaping the trophic structure of tropical seabird communities. Mar Ecol Prog Ser 497:243–257

McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct Sci 4:393–398

McMahon KW, Hamady LL, Thorrold SR (2013a) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697–714

McMahon KW, Hamady LL, Thorrold SR (2013b) Ocean ecogeochemistry: a review. Oceanogr Mar Biol Annu Rev 51:327–374

Mompeán C, Bode A, Benitez-Barrios VM, Dominguez-Yanes JF, Escanez J, Fraile-Nuez E (2013) Spatial patterns of plankton biomass and stable isotopes reflect the influence of the nitrogen-fixer *Trichodesmium* along the subtropical North Atlantic. J Plankton Res 35:513–525

Monteiro LR, Ramos JA, Furness RW, del Nevo AJ (1996) Movements, morphology, breeding, moult, diet and feeding of seabirds in the Azores. Colon Waterbirds 19: 82–97

Müller MS, Massa B, Phillips RA, Dell'Omo G (2014) Individual consistency and sex differences in migration strategies of Scopolis shearwaters *Calonectris diomedea* despite systematic year differences. Curr Zool 60: 631–641

Navarro J, Coll M, Somes CJ, Olson RJ (2013) Trophic niche of squids: insights from isotopic data in marine systems worldwide. Deep Sea Res II 95:93–102

Neves VC, Bried J, González-Solís J, Roscales JL, Clarke MR (2012) Feeding ecology and movements of the Barolo shearwater *Puffinus baroli baroli* in the Azores, NE Atlantic. Mar Ecol Prog Ser 452:269–285

Nilsson C, Klaassen RHG, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837–845

Nisbet ICT, Mostello CS, Veit RR, Fox JW, Afanasyev V (2011) Migrations and winter quarters of five common terns tracked using geolocators. Waterbirds 34:32–39

Paiva VH, Fagundes AI, Romão V, Gouveia C, Ramos JA (2016) Population-scale foraging segregation in an apex predator of the North Atlantic. PLOS ONE 11:e0151340

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272

Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160:795–806

Pinet P, Jaquemet S, Pinaud D, Weimerskirch H, Phillips RA, Le Corre M (2011) Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. Mar Ecol Prog Ser 423: 291–302

Precheur C (2015) Ecologie et conservation du puffin d'Audubon (*Puffinus lherminieri lherminieri*) de la Réserve Naturelle des Ilets de Sainte-Anne (Martinique). PhD thesis, Zoologie des vertébrés, Université des Antilles

Priddel D, Hutton I, Carlile N, Bester A (2003) Little shearwaters, *Puffinus assimilis assimilis*, breeding on Lord Howe Island. Emu 103:67–70

Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: a review and case study of the Wilson's storm-petrel. Mar Ecol Prog Ser 295:295–304

R Core Team (2016) R: a language and environment for statistical computing. Version 3.3.0. R Foundation for Statistical Computing, Vienna. www.r-project.org

Ramos JA, Fagundes AI, Xavier JC, Fidalgo V, Ceia FR, Medeiros R, Paiva VH (2015) A switch in the Atlantic Oscillation correlates with inter-annual changes in foraging location and food habits of Macaronesian shearwaters (*Puffinus baroli*) nesting on two islands of the subtropical Atlantic Ocean. Deep Sea Res I 104:60–71

Ramos R, González-Solís J, Ruiz X (2009) Linking isotopic and migratory patterns in a pelagic seabird. Oecologia 160:97–105

Ramos R, Sanz V, Militão T, Bried J and others (2015) Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). J Biogeogr 42:1651–1664

Ramos R, Ramírez I, Paiva VH, Militão T and others (2016) Global spatial ecology of three closely-related gadfly petrels. Sci Rep 6:23447

RNBWS (Royal Naval Birdwatching Society) (2014) World Database. www.rnbws.org.uk/search-2/ (accessed May 2, 2014)

Robb M, Mullarney K (2008) Petrels night and day: a sound approach. The Sound Approach, Dorset

Rolff C (2000) Seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ of size-fractionated plankton at a coastal station in the northern Baltic proper. Mar Ecol Prog Ser 203:47–65

Roscales JL, Gómez-Díaz E, Neves V, González-Solís J (2011) Trophic versus geographic structure in stable isotope signatures of pelagic seabirds breeding in the Northeast Atlantic. Mar Ecol Prog Ser 434:1–13

Somes CJ, Schmittner A, Galbraith ED, Lehmann MF and others (2010) Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem Cycles 24: GB4019

Spear LB, Ainley DG, Walker WA (2007) Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. In: Marti CD (ed) Studies in avian biology, No. 35. Cooper Ornithological Society, Camarillo, CA, p 1–99

Surman CA, Nicholson LW, Santora JA (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. Mar Ecol Prog Ser 454:147–157

Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standarized approach. Auk 101:567–577

Velasco MC (2013) Mystery shearwater in Canary Islands in December 2012. Dutch Birding 35:186–189

Warham J (1990) The petrels: their ecology and breeding systems. Academic Press, London

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res II 54:211–223

Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: November 8, 2016; Accepted: July 20, 2017
Proofs received from author(s): August 30, 2017

Reprinted by permission from Springer Nature: Springer Nature - Journal of Ornithology.
Becker, P. H., Schmaljohann, H., Riechert, J., Wagenknecht, G., Zajková, Z., & González-Solís, J. (2016)
Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding
period. *Journal of Ornithology*, 157(4): 927-940. License Number 4673200175200 (2016).
https://link.springer.com/article/10.1007/s10336-016-1346-2

J Ornithol (2016) 157:927–940
DOI 10.1007/s10336-016-1346-2

ORIGINAL ARTICLE

Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period

Peter H. Becker[1] · **Heiko Schmaljohann**[1,2] · **Juliane Riechert**[1] · **Götz Wagenknecht**[1] · **Zuzana Zajková**[3] · **Jacob González-Solís**[3]

Received: 15 January 2016 / Revised: 24 March 2016 / Accepted: 11 April 2016 / Published online: 26 April 2016

Abstract We studied the temporal–spatial distribution of Common Terns *Sterna hirundo* along the East Atlantic Flyway. In 2009 and 2010 experienced adults from a colony on the German North Sea coast were tagged with geolocators recording light intensity and saltwater contact. Main objectives were the inter-individual temporal–spatial variation of migration routes and wintering areas, wintering site fidelity, and time spent at sea across the annual cycle. Geolocators had no effects on various traits of breeders, but their reproductive output suffered from egg breakage. This can be avoided by artificially incubating the eggs. Twelve routes of nine individuals were tracked. Transponder readings at the breeding site showed that birds left the colony 4 weeks before starting autumn migration. In spring and autumn, Common Terns stopped over around the Canary Islands. Main wintering distribution was the upwelling seas alongside the West African coast and similar between years, but different among individuals. Three females wintered further north and more offshore than six males. Pair mates wintered at different locations. Spring migration was longer (56 ± 8 days) than autumn migration (37 ± 17 days). During both migration and wintering the terns spent more time on salt water than during breeding and post-breeding. In most individuals saltwater contact was higher during the day than at night, reduced at sunrise and sunset likely due to foraging, and peaked about noon possibly related to resting or thermoregulation. Detailed ecological and behavioral studies of common terns during wintering are needed to clarify the results based on geolocators.

Keywords Migration · Wintering · Light-level geolocation · Saltwater contact · *Sterna hirundo*

Zusammenfassung

Flussseeschwalben entlang des Ostatlantischen Zugweges: Raumzeitliche Verteilung außerhalb der Brutperiode

Wir untersuchten die raumzeitliche Verteilung von Flussseeschwalben *Sterna hirundo* entlang des Ostatlantischen Zugweges. 2009 und 2010 wurden erfahrene Brutvögel einer Kolonie an der deutschen Nordseeküste mit Geolokatoren versehen, die Lichtintensität und Salzwasserkontakt aufzeichneten. Ziele der Untersuchungen waren die interindividuelle raumzeitliche Variation der Zugrouten und Überwinterungsgebiete, die Winterortstreue und die Dauer des Seewasserkontakts im Jahreszyklus. Die Geolokatoren beeinträchtigten die Flussseeschwalben nicht, der Reproduktionserfolg jedoch war durch Bruch der Eier verringert, was durch Austausch und Ausbrüten der Eier in einem Inkubator vermieden werden kann. 12 Routen von 9 Individuen wurden verfolgt. Die Registrierungen der zusätzlich mit

---

Communicated by N. Chernetsov.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-016-1346-2) contains supplementary material, which is available to authorized users.

✉ Peter H. Becker
peter.becker@ifv-vogelwarte.de

[1] Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, 26386 Wilhelmshaven, Germany

[2] University of Alaska, Fairbanks, AK, USA

[3] Departament de Biologia Animal, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av Diagonal 643, 08028 Barcelona, Spain

Transpon-dern gekennzeichneten Vögel zeigten, dass sie den Koloniestandort vier Wochen vor Beginn der Herbstwanderung verließen. Im Frühjahr und Herbst legten einige Flussseeschwalben bei den Kanarischen Inseln einen Zwischenhalt ein. Die Hauptverbreitung im Winter erstreckte sich entlang der Westafrikanischen Küste und war ähnlich zwischen den Jahren, aber verschieden zwischen Individuen. Die drei Weibchen überwinterten weiter nördlich als die sechs Männchen und die Paarpartner an verschiedenen Orten. Der Frühjahrszug dauerte länger (56 ± 8 d) als der Herbstzug (37 ± 17 d). Während der Wanderung und Überwinterung verbrachten die Flussseeschwalben mehr Zeit auf dem Salzwasser als im Brutgebiet. Die meisten Individuen hatten tagsüber längere Salzwasserkontakte als nachts, die bei Sonnenaufgang und -untergang stark reduziert waren, vermutlich aufgrund der Nahrungssuche. Während der Mittagszeit waren Salzwasserkontakte besonders intensiv, möglicherweise bedingt durch Rasten oder Thermoregulation. Detaillierte Studien zu Ökologie und Verhalten im Winter sollten folgen, um die auf den Geolokatoren basierten Ergebnisse zu klären.

Introduction

Seabirds spend most of their non-breeding period far offshore at the oceans, e.g. Shaffer et al. (2006), Guilford et al. (2009), and Egevang et al. (2010). This makes it difficult studying their behavior during these times. By analyzing the stable isotope composition of feathers grown outside the breeding area, we gain information about the birds' diet composition and how this might affect other life-history stages, e.g. Sorenson et al. (2009). Ring recoveries might give us some indication about the birds' whereabouts during the non-breeding period, but these recoveries seem to be highly aged-biased in seabirds (Wendeln and Becker 1999; Bairlein et al. 2014). Although both methods can be used to study the ecology and the behavior of seabirds away from their breeding areas to a certain extent, different types of loggers offer the opportunity to estimate seabirds' behavior during migration and winter on a more precise scale. After recapture such loggers provide data about, e.g. GPS coordinates (Weimerskirch et al. 2002), light-level geolocations (Weimerskirch and Wilson 2000), three-dimensional acceleration (Sommerfeld et al. 2013), heart rate (Ropert-Coudert et al. 2006), water depth (Garthe et al. 2000), temperature (Wilson et al. 1992a), saltwater contact (Wilson et al. 1995), and others (Wilson et al. 2002). So far these studies have been limited to rather large seabirds, because neither the size nor the weight of the specific loggers have allowed deploying these devices to small seabirds, i.e., with body mass <100 g. Only little, therefore, was known about the whereabouts and their behavior during the migration and wintering period of such seabirds. The miniaturization of light-level geolocators now allows tracking also these smaller seabirds such as terns (e.g. Egevang et al. 2010; Nisbet et al. 2011a, b; Fijn et al. 2013; van der Winden et al. 2014).

Here we add to better knowledge about the ecology of seabirds during the non-breeding period by estimating the temporal–spatial distribution of European Common Terns (*Sterna hirundo*) along the East Atlantic Flyway. To do so we tagged adult Common Terns with data loggers at a breeding colony site in northwestern Germany (e.g. Becker et al. 2008) to record light levels and wet–dry conditions. The main objectives of this study were to estimate the inter-individual temporal–spatial variation of both their migration and wintering period, to explore potential sex-specific and within-pair differences of the wintering area, and to quantify the birds' behavior across the annual cycle in relation to the individual time spent on sea water.

Methods

Study site

Common Terns considered in this study bred at a monospecific colony of about 400 breeding pairs located at "Banter See" at Wilhelmshaven on the German North Sea coast (53°36′N, 08°06′E, Becker et al. 2001, 2008; Becker 2010). This colony is the focus of an integrated, long-term population study, and about half of the breeders are aged, sexed, and marked with transponders (e.g. Szostek and Becker 2012). The colony site consists of six rectangular concrete islands (10.7 × 4.6 m), surrounded by a wall of 60 cm height. The walls are equipped with 44 elevated platforms for terns to land and rest on. Each platform contains an antenna reading transponder codes every 5 s, and half of them contain an electronic balance (accuracy ±1 g). This allows reliable automatic and remote detection of the birds' presence at the colony site, arrival, and body mass (Limmer and Becker 2007), with a reencounter probability of almost 1 (Szostek and Becker 2012). Colony site fidelity is very high (adult local return rate ca. 90 %; Ezard et al. 2006; Szostek and Becker 2012). The first and last transponder reading of an individual in a season indicated that the bird had arrived and left the breeding colony, respectively (Becker et al. 2008). For simplicity birds are called by individual names. Reproductive performance and output was determined for each clutch including those of geolocator-marked parents using standard protocols (e.g. Becker and Wink 2003; Zhang et al. 2015). For chicks, maximum mass, mass at fledging (±1 g), and age at fledging (±1 day) were recorded (Becker and Wink 2003).

Capture and deployment of light-level geolocators

Experienced breeders (9–14 years old, in 2009 and 2010 both pair members; Table S1) were identified by the transponder with a nest antenna and caught on the nest with an electronically released drop trap (or spring trap in exceptional cases) during incubation, on average 12 days after laying the first egg (Table S1). Before catching the birds, their eggs were replaced by dummy eggs to avoid egg breakage. The captured adults were weighed (±1 g, digital balance), measured (head and bill length ±0.1 mm; wing length 0.5 mm), and tagged with light-level geolocators (Fig. S9). Total handling time was 3–6 min. Most individuals returned to the clutch a few minutes after release and started incubation soon [on average after 13±11 (2–38) min, $n = 11$]. No clutch was deserted owing to catching the breeders. In 2011 when light-level geolocators had to be only recovered, the eggs were removed immediately from the clutch after laying of the identified individuals, put in an incubator and were replaced by dummy eggs. Eggs remained in the incubator until light-level geolocators were retrieved from the adults to avoid any egg breakage. After that original eggs were exchanged again. Captures were performed earlier during incubation than in the previous years. Most individuals were captured in three successive years (Table S1).

Light-level geolocators

We used miniature light-level geolocators, Mk 10, from the British Antarctic Survey (BAS). They were fixed with layers of self-amalgamating tape to a plastic ring with cable tie (Fig. S9; 10 mm height, 5 mm internal diameter, 1.0 mm thickness). In 2010, three geolocators were attached to an aluminum ring for a Black-headed Gull (*Croicocephalus ridibundus*, 10 mm height). Mass of the ring and fixing materials was <1.7 g (about 1.3 % of Common Tern body mass). At recapture, the geolocator from the previous year was removed and replaced by a new one (Table S1). During the pre-calibration period light-level geolocators experienced the unhindered natural change in light conditions at the colony site for 7–19 days. After removal a post-calibration was conducted with each light-level geolocator for 5–18 days (in 2011 at the colony, in 2009 and 2010 at the Institute of Avian Research, 53°33′N, 08°06′E). Twelve of the 24 geolocators had failed (see Table S1); reasons for data loss were infiltrated water, non-realistic shift in longitude due to internal clock shifts (Fig. S8), or insufficient lifetime of batteries.

Light-level geolocators used in the present study archive maximum light intensity every 10 min. Sunrise and sunset times allow inferring length of day and night and the timing of midday and midnight, and finally estimate latitude and longitude twice a day (Wilson et al. 1992b; Hill 1994). As a matter of principle, latitude cannot be estimated on about 10 days around the equinoxes (Wilson et al. 1992b; Hill 1994; Lisovski et al. 2012). The general uncertainty of the estimated locations is generally on the order of magnitude of about 150 km (Phillips et al. 2004; Fudickar et al. 2012; Lisovski et al. 2012).

Light-level geolocation data were analyzed using the statistical software R 3.1.2 (R Core Team 2014) and the freely available *SGAT* package (https://github.com/SWotherspoon/SGAT). This packages combines tools of the R package *GeoLight* (Lisovski and Hahn 2012), which uses the threshold approach (Hill 1994; Ekstrom 2004), and the R package *tripEstimation* (Sumner et al. 2009), which uses the curve-fitting approach (Ekstrom 2004; Nielsen and Sibert 2007) to estimate the animals' locations. Here a threshold-based approach was used to estimate the birds' locations via an Estelle model. A probability distribution of these locations is derived from the Markov chain Monte Carlo method with a metropolis sampler. In comparison to other methods of estimating birds' locations from light-level geolocation data, here a priori knowledge can be used to estimate locations by considering (1) a species-specific movement model, which is described by a bird's ground speed, (2) a species-specific land mask model, and (3) that the errors in the twilight times, which follow a log normal distribution. Following these assumptions, probability distributions of the locations are estimated. The movement model defines the density distribution of travel speed, which is described here by a gamma distribution. As air speed of common terns is about 11 m/s (Bruderer and Boldt 2001; Pennycuick et al. 2013) and as terns in general exploit favorable wind conditions (Egevang et al. 2010), we arbitrarily set mean ground speed to 15 m/s. To determine the density distribution of ground speeds, all locations of a bird were initially estimated with the threshold-sensitivity twilight function *threshold.path* and used to estimate the ground speed for the initial track. This was on average 14.66 ± 1.05 m/s (mean ± SD; $n = 11$) and similar to the arbitrarily chosen ground speed. In a second step, we excluded extremely high speeds which are associated with erroneously estimated locations. The mean and SD of these remaining speed values were used to estimate both the shape parameter (1.51) and rate parameter (0.13) of the corresponding gamma distribution (Becker et al. 1988). This gamma distribution fitted well the density distribution of the ground speed during the tracking period (Fig. S1). The land mask model allows setting different probabilities for the bird being on land or on water. We set the probability of a Common Tern to be near or over water two times higher than being over land because Common Terns are typical seabirds (Harrison 1997; Nisbet et al. 2011a; Neves et al. 2015) and because the vast majority of ring recoveries from mid-European breeding populations comes from the West African coast and not from inland sites, indicating the wintering grounds to be on or even off the West African coast (Wernham et al. 2002; Bairlein et al. 2014). When sunrise and sunset events are not affected by artificial light, light cannot be detected before sunrise or after sunset by the light sensor. Hence, twilight errors are not normally distributed, but described by a lognormal distribution, as twilight error of recorded light cannot be negative (Fig. S2).

We considered these assumptions in our analyses of estimating birds' locations (for details and R-code see https://github.com/SWotherspoon/SGAT). The resulting estimates in respect of longitude and latitude and their corresponding 95 % confidence intervals are given for each individual in the electronic supplemental material (Fig. S3).

We defined departures and arrivals from stationary sites, i.e., breeding area, stopover sites, and wintering grounds, as obvious changes in longitude and/or latitude (Fig. S3). In the latter, changes were only considered outside 10 days before and 10 days after the equinoxes. Because of corrupt data and heavy outliers (Fig. S3) the "changeLight" function of the "GeoLight" R packages (Lisovski and Hahn 2012) to estimate the migration schedule did not work properly. The values describing the individual migratory schedules should be treated cautiously. The estimated start of spring migration, e.g. in Cornelia and Joachim (Table 1; Fig. S3) could also be attributed to the start of movements in the wintering area. Some light-level geolocators broke before detachment, and in some the internal geolocator clock drifted (Figs. S3, S8). The area that was visited during winter time was individually estimated based on light-level geolocation estimates (Fig. S3; Table S2). However, we did not consider location estimates derived before 1 November and after 28 February to minimize the influence of the equinoxes on the latitudinal estimates (Table S2). The centroid of the wintering ground for each individual was estimated as the mean ± SD of the estimated locations which are all shown in the corresponding figures. Stopover sites could only be determined for three individuals (Table S2). Kernel densities (45, 75, and 95 %; Epanechnikov kernel) were calculated for wintering grounds of different sets (sex, year) of individuals using the *kernelUD* function of the R-packages *adehabitatHR* (Calenge 2006). The ad hoc method was used for the smoothing parameter. The grid was set to 500. The same settings were applied when estimating kernel densities for stopover sites. The distance between the breeding area and the average wintering ground was calculated as the great circle distance between these locations.

Table 1 Departure and arrival dates (day–month) of common terns at the breeding and wintering area based on tracks by light-level geolocators and on remote identification by transponders at the colony site

Bird			Departure date at breeding area			Wintering area		Arrival date at breeding area		
Name	Sex	Year	Last record colony	Geolocator	Diff (days)	Arrival date	Departure date	Geolocator	First record colony	Diff (days)
Joachim	M	2009/10	02–09	02–09	0	22–10	18–02	27–04	28–04	1
		2010/11	02–09	21–09	−19	23–10	ND	ND	23–04	–
Moses	M	2009/10	31–07	12–09	−43	08–10	03–03	27–04	03–05	6
		2010/11	12–07	06–09	−56	28–10	ND	ND	ND	–
Kasimir	M	2009/10	12–07	12–09	−62	11–10	ND	28–04	25–04	−3
Cornelia	F	2009/10	28–07	28–07	0	08–10	ND	ND	26–04	–
		2010/11	22–07	22–07	0	29–07	19–02	14–04	14–04	0
Heiner[a]	M	2010/11	24–08	06–09	−13	01–11	15–02	11–04	18–04	7
Ayla[a]	F	2010/11	24–08	06–09	−13	25–10	15–02	18–04	14–04	−4
Ernst[a]	M	2010/11	07–08	21–09	−45	28–10	23–02	13–04	14–04	1
Wieland	M	2010/11	26–07	11–09	−47	12–10	08–03	23–04	ND	–
Marianna	F	2009/10	15–07	30–08	−46	21–10	ND	ND	25–04	–
Mean ± SD			04–08 ± 20	02–09 ± 19	−31[b] ± 23	13–10 ± 25	22–02 ± 8	20–04 ± 7	22–04 ± 7	1[b] ± 4

Twelve tracks of nine individuals were achieved. Pair mates are italicized

ND no data, not analyzed, *Diff* difference of date of first or last record at colony, date based on geolocator data given in days. Only three individuals had fledged young

[a] Care of juveniles on migration

[b] Calculated for the individual differences

Time spent on salt water

The Mk 10 BAS geolocators also recorded saltwater immersion every 3 s and stored number of positive records ranging from 0 (continuously dry) to 200 (continuously wet) at the end of each 10-min period ("wet–dry" information). Immersion data were available for eight individual tracks (two females, six males, Table S3). We estimated the average proportion of time spent on saltwater per hour (0–24 h, Greenwich Mean Time, GMT) and per day (in hours or % of 24 h, and for wintering at the latitude of Dakar, Senegal, we differentiated between daylight (7:30–18:45) and night hours (18:45–7:30).

Defining stages of the annual cycle

Based on the individual light-level geolocation data combined with data from transponders at the colony site (Table 1; Fig. S3) we defined for each individual six different annual stages:

Breeding stage: the bird was at the colony.

Post-breeding stage: the bird had left the colony, but remained in the vicinity of the German Bight and did not start its autumn migration.

Autumn migration: the bird was on the move, but had not reached its wintering area.

Wintering: the time after arrival at the wintering area and before spring migration.

Spring migration: the bird started its spring migration and had not reached the colony.

Pre-breeding: spring migration was finished, but the colony site not reached (sufficient data only in one individual, Table S3).

Defining these stages based on light-level geolocation data was a rough estimate, and small differences between these stages with respect to saltwater contact should be interpreted cautiously.

Statistics

Data were analyzed using the statistical software R 3.1.2 (R Core Team 2014). To assess whether individual birds being tracked for two consecutive winters showed significantly higher winter area fidelity than the population on average, we performed a randomization test, randomly selecting 10,000 pairs of mean wintering locations from our data set. We did not allow that a pair of mean locations consisted of the same locations. If the within-individual difference of the two tracked mean wintering locations were shorter than the 250 shortest distances between randomly selected pairs of mean wintering locations, birds were assessed more faithful than expected by chance.

We tested for seasonal differences in at-sea activity between stages (without the pre-breeding period, owing to insufficient data) using GLMRM (generalized linear model for repeated measurements, SPSS 22). The Mann–Whitney *U* test was applied when comparing non-parametric differences between two groups. The Wilcoxon signed-rank test was used as a non-parametric test for paired samples. If not otherwise stated values are reported as mean ± 1 SD.

Results

Retrieval of geolocators

Twenty-five out of the 29 tagged birds, i.e., 86 %, returned to the breeding colony the year after deployment. All individuals carrying a light-level geolocator bred in their returning year (Table S1). No bird showed any signs of leg injuries when light-level geolocators were removed. One female had lost her light-level geolocator (Table S1). Twelve of the 24 light-level geolocators contained analyzable data by nine adults (three females and six males, including three pairs).

Potential effects of geolocators

Carrying light-level geolocators did not significantly affect both arrival and laying date, mass at arrival, mass at catching, clutch size, body mass growth of chicks, and ability to fledge chicks (see chapter "Additional information about potential effects of geolocators on common terns" in Electronic Supplementary Material). However, we recorded a strong and significant deterioration of hatching success from 86 to 43 % reducing reproductive output of pairs marked with geolocators severely (Tables S5, S6). The reduced hatchability was caused by eggshell breakage owing to fine fissures increasing with time advancing of incubation by the marked individuals (Figs. S9, S10). In 2011, i.e., the last year of this study, reproductive success of geolocator-birds was successfully increased by exchanging pairs' original eggs with dummy eggs, and incubating the original eggs in an incubator until geolocators were retrieved. These measures had increased hatching success to 89 % (for details see Electronic Supplementary Material, Table S6).

General temporal–spatial distribution of Common Terns during the non-breeding period

As Common Terns mainly migrated during both equinoxes (Fig. S3), we dispensed with a detailed temporal–spatial analysis of individual movements between the colony and the wintering areas.

Birds left the colony on average on 4 August ±20 days (range 12 July–2 September) and abandoned the German Bight on 2 September ±19 days (22 July–21 September; Table 1). In general, the data suggested that common terns moved along the East Atlantic Flyway and that they predominantly used offshore migration routes (Fig. S3). The sea around the Canaries was identified as a stopover area (Fig. 1; Table S2): two individuals stopped there during autumn migration. One remained in this area approximately for 7 days (Moses in 2010) and the other slightly less than a month (Cornelia in 2009; Table 1, Table S2). Also, during spring migration one individual (Kasimir) stopped there (Table S2). Within 13 days after resuming migration from this stopover area the bird (Kasimir) reached the colony (Table 1, Table S2).

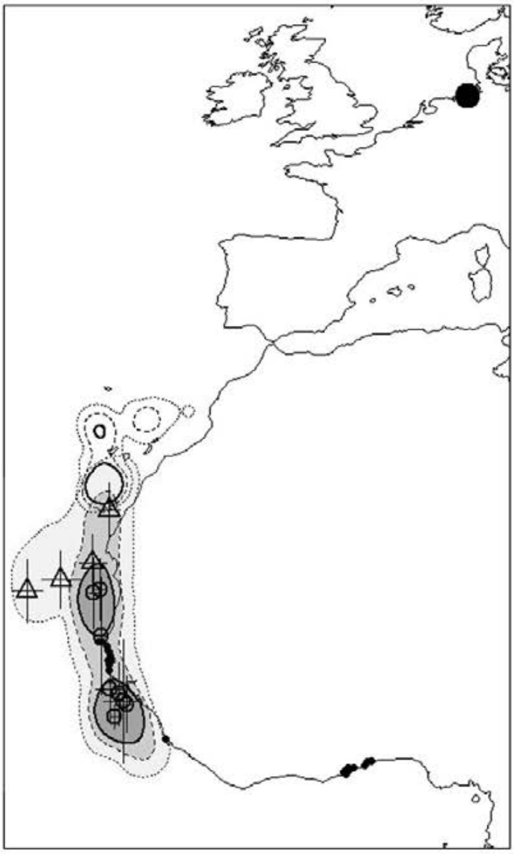


Fig. 1 Wintering and stopover locations at Canary Islands of 12 routes of nine Common Terns tracked with light-level geolocators between 2009 and 2011. Breeding site *large black dot*. *Large black triangles* (females) and *black circles* (males) mean winter locations ±SD. *Dotted lines* 95 kernel densities; *dashed lines* 75 kernel densities; *solid lines* 45 kernel densities. Kernel densities at wintering sites were highlighted in three different shades of *grey*. Birds migrated to their winter locations by flying mainly over water. *Small black dots* indicate African ring recoveries during December and January of adult common terns from northwest German breeding sites (Helgoland ringing center, $n = 30$; age at ringing older than 1 year or period between ringing and recovery date >3 years; cf. Bairlein et al. 2014). Map is Mercator projection

Common Terns arrived at the wintering areas on 13 October ±25 days (29 July–1 November, Table 1). Mean wintering period lasted 136 ± 34 days ($n = 7$, calculated by the individual differences, cf. Table 1). Their preferred wintering areas were the upwelling seas alongside the West African coast of Morocco, Western Sahara, Mauritania, Senegal, The Gambia, Guinea Bissau, Guinea, and Sierra Leone (Fig. 1). Mean great circle distance between the colony and the individual mean wintering locations was 4,782 ± 467 km (range 3,881–5,368 km, $n = 12$). In autumn, this distance was covered in 41 ± 17 days ($n = 12$, calculated by the individual differences, cf. Table 1). The mean distances covered per day during southward migration was 158 ± 132 km ($n = 12$). The four females spent the winter further north (females 20 ± 2.5°N, range 18–24°N, males 13 ± 3.8°N, range 9–19°N; Mann–Whitney U test: $U = 30$, $p = 0.016$; Fig. 1) and seemingly more offshore than the eight males (males 107 ± 57 km, range 30–217 km; females 293 ± 255 km, range 86–624 km; Mann–Whitney U test: $U = 44$, $p = 0.174$).

The winter distributions were not obviously different between the 2 years (Fig. S5). There was no indication for significant wintering site fidelity, however, as the within-individual distance of the tracked mean wintering locations were not shorter than expected by chance in comparison to the between-individual distance of the mean wintering locations (Figs. S4–S6).

In the three pairs for which light-level geolocation data were available for both partners (Table 1), the general wintering areas and the estimated mean wintering locations did not overlap between the sexes (Fig. 2). There was some spatial overlap of the general wintering area of Cornelia and Kasimir (Fig. 2), but they seemed to be temporally separated (Fig. S3). Distance of pair members' mean wintering locations was 897 ± 320 km (530–1,120 km, $n = 3$) and with longer than the median great circle distance (647 km) of the 10,000 randomly chosen mean wintering location pairs (Fig. S4). These sex-specific differences in the mean location of the general wintering areas within breeding pairs supported the general picture of females wintering further off-shore and unrelated to their mates.

Spring migration started on average on 22 February ±8 days (15 February–8 March, Table 1). Common terns arrived at the breeding grounds on 20 April ±7 days (11–28 April) so that total time of migration was about

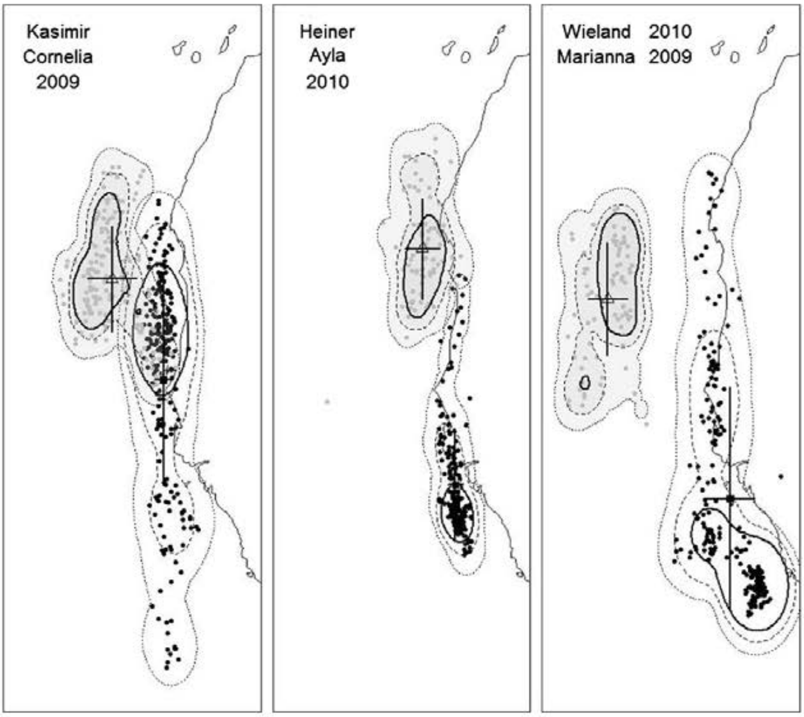


Fig. 2 Wintering areas of pair mates tracked during the same winter (Ayla, Heiner 2009/2010; Cornelia, Kasimir 2010/2011) or with male one winter later (Marianna 2009/2010, Wieland 2010/2011). *Grey dots* female; *black dots* male locations. *Symbols* and kernel densities (females highlighted in *grey*) as described in Fig. 1

56 ± 8 days (mean ± SD, $n = 7$) in spring. The mean distance covered per day during northward migration was 88 ± 20 km ($n = 7$). For these seven birds spring migration lasted significantly longer than autumn migration (autumn: 37 ± 17 days; Wilcoxon signed-rank test: $V = 0$, $p = 0.036$, $n = 7$). Common Terns spent about 117 ± 8 days ($n = 11$) at the breeding colony or in the vicinity of the colony during the reproductive season. Based on transponder data only the tracked common terns stayed 96 ± 23 days ($n = 16$) at the colony site.

The within-individual variation of the migration schedule between 2 years varied in general by a few days (Table 1). In 2009 Joachim and Cornelia and in 2010 only Cornelia left the colony and the breeding area on the same day, i.e., autumn migration started on the day individuals were last recorded at the colony by their transponder. Cornelia arrived at the wintering area in the beginning of October in 2009, but to the end of July in 2010. This between-year difference in the estimated arrival time at the wintering area was not explained by the between-year variation in the start of autumn migration (about 1 week).

The return of the young of Ayla, Heiner, and Ernst (Table 1) as prospectors to the colony 2 years later showed that post-fledging parental care of these parents was successful. The temporal patterns of Ayla's, Heiner's, and Ernst's autumn migration, however, were not distinctively different from the adults failing to produce fledglings (Table 1).

Arrival and departure dates at the colony site: a comparison of transponder data and light-level geolocation estimates

After leaving the breeding colony (transponder data) it took on average 31 days before Common Terns started their autumn migration (Table 1; Fig S3). Only two birds had left both the colony site and the breeding area on the same day (Joachim and Cornelia, Table 1; Fig S3). In spring, however, arrival date at the breeding colony detected with the transponder recording system was similar to the estimated arrival date by light-level geolocation data (Table 1).

Saltwater contact during the annual cycle

The proportion of time spent on salt water varied among individuals and stages (Fig. 3, Fig. S7; Table S3). The differences between the stages of the annual cycle were highly significant ($F = 10.228$, $p < 0.001$, $n = 6$; 3 stages, $F = 11.711$, $p = 0.002$, $n = 8$; Fig. 3). During breeding

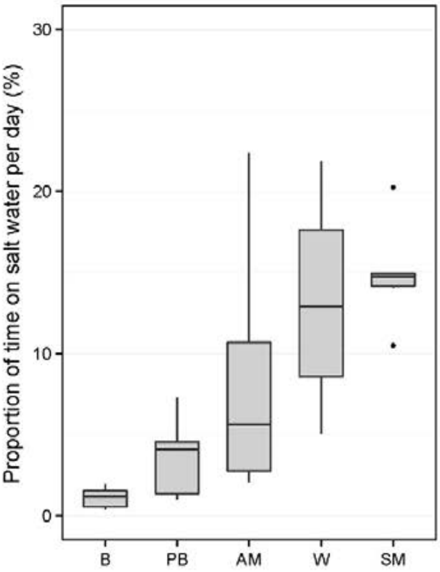


Fig. 3 Seasonal variation in the temporal proportion of saltwater contact across different stages of the annual cycle. Means of daily percentage of time eight common terns had contact with salt water recorded by using saltwater immersion data from geolocators (*B* breeding, *PB* post-breeding, *AM* autumn migration, *W* wintering, *SM* spring migration)

and post-breeding, common terns spent only a small proportion of time on saltwater (1.1–3.5 %). During autumn migration, wintering, and spring migration, however, individuals spent significantly more time on salt water (8.6–13.9 %; Fig. 3, Fig. S7; Table S3 with statistics among single periods). Inter-individual differences were consistent between stages: during all periods, e.g. Ayla or Joachim spent more time at sea than, e.g. Heiner and Moses (between subject effects, $F = 37.325$, $p = 0.002$, $n = 8$; Fig S7; Table S3). There was a tendency that individuals wintering more offshore had more water contact than birds wintering closer to the coast (correlation between proportion of time at sea water with distance from the coast, Pearson, $r = 0.624$, $p = 0.098$, $n = 8$). Furthermore, the daily proportion of time spent at seawater during winter was significantly and positively correlated with the latitude of mean wintering locations of the common terns studied (Pearson, $r = 0.743$, $p = 0.035$, $n = 8$).

The time spent with saltwater contact varied over the course of the day with respect to the stages of the annual cycle (Fig. 4). During both autumn and spring migration and during winter, Common Terns spent about 10–15 % of the time on salt water during the night. At times around sunrise and sunset proportion of water contact was minimal, but highest between these events (Fig. 4), peaking between 11 and 15 GMT. There was no clear daytime pattern for the other stages of the annual cycle (Fig. 4). With respect to day and night differences in winter, five out of seven individuals had more saltwater contact at daylight than during the night, for the other two individuals it was vice versa (Cornelia and Joachim, who also had most saltwater contact in total, cf. Table S3).

Discussion

Our results show that common terns from the breeding colony in Germany winter in the fish-rich upwelling off the West African coast (Grecian et al. 2016; Fig. 1). Females' wintering areas were situated further to the north by 7° than that of males. The proportion of time birds had direct contact with salt water varied between the different stages of the annual cycle: While at the breeding area saltwater contact was low, it was high during the migration and wintering periods (Fig. 3). This difference across the annual cycle might be explained by the daily variation of saltwater contact (Fig. 4).

Potential effects of geolocators

Despite the phenomenon of egg breakage (Fig. S10 and below) we found no adverse effects of birds being tagged at the tarsus with a light-level geolocator neither on return rate, body condition, nor arrival date after spring migration or laying date. Return rate to the colony was in the range known for this and other colonies of the common tern (Ezard et al. 2006; Szostek and Becker 2012; Nisbet and Cam 2002; Breton et al. 2014; Palestis and Hines 2015). Return rate of tagged birds was also similar to the rates as reported from other light-level geolocation studies of *Sterna* terns in general (Nisbet et al. 2011a; Fijn et al. 2013). Returned Common Terns equipped with geolocators were in good physical condition like Arctic Terns (*Sterna paradisaea*, Egevang et al. 2010; Fijn et al. 2013) and showed no reduction of body mass at arrival or when recaptured. This is in contrast to the findings of Nisbet et al. (2011a) in Common Terns and Mostello et al. (2014) in Roseate Terns *Sterna dougallii*. Neither arrival date of the birds repeatedly measured before, during, or after deployment of the geolocators nor laying date was affected (for further details see Electronic Supplemental Material). Thus, the various parameters recorded in the individuals tagged with light-level geolocators make us confident that the geolocators did not negatively affect the temporal–spatial distribution of the Common Terns during their non-breeding period.

After return all experimental birds produced normal clutch sizes (in contrast to Arctic Terns, Egevang et al.

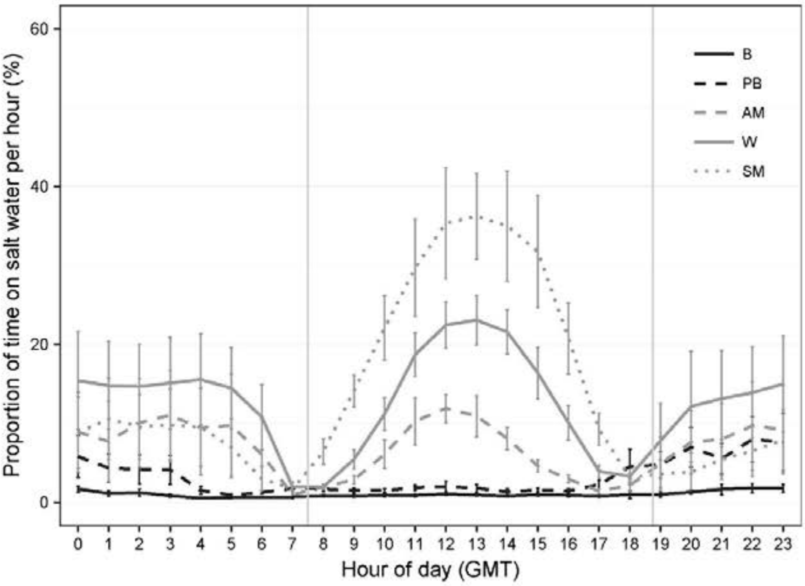


Fig. 4 Daily saltwater contact pattern. Mean hourly percentage of time spent on salt water ± standard error of seven common terns recorded using geolocation-immersion loggers during different stages of the annual cycle. Means of values were first calculated for individual birds, then averaged for all birds (without Ayla owing to clock shift, Fig. S8). *Vertical lines* refer to mean sunrise and sunset hour during wintering. Codes for stages as in Fig. 3

2010), but suffered from increased egg breakage (cf. Nisbet et al. 2011a). This was caused by the geolocator and dependent on the number of days the eggs were incubated by a parent carrying a geolocator. Thus, effects of geolocators on the individual fitness can be serious (cf. Scandolara et al. 2014 for barn swallows *Hirundo rustica*). This effect, however, can be minimized by exchanging natural eggs with dummy eggs soon after laying and by artificially incubating the natural eggs until deployment of the geolocator, or even until hatching.

General temporal–spatial distribution of common terns during the non-breeding period

In agreement with recoveries of adult Common Terns ringed during the breeding period in Germany, this study confirms that individuals from our study site mainly winter in coastal West Africa (Fig. 1). However, ring recoveries suggested that the wintering area of adults from eastern, but also from western Germany is further extended to the south of western Africa than pictured by the birds from Banter See colony (Fig. 1, cf. Neubauer 1982; Bairlein et al. 2014). Common Terns made use of the upwelling zone supplied by the cold Canary current off the northwest African coast (Brenninkmeijer et al. 2002), where primary productivity is higher than in other areas (McGregor et al. 2007; Arístegui et al. 2009). Accordingly, the coastline of about 2,200 km along Mauritania, Senegal, Gambia, Guinea Bissau, Guinea, Sierra Leone to Liberia is a very attractive and important wintering area for many seabird species (Grecian et al. 2016). To reach and leave this area, Common Terns might make use of stopover sites at the seas around the Canary Islands (Fig. 1), similarly to Black Terns *Chlidonias niger* (van der Winden et al. 2014). Like other tern species passing West African waters, Common Terns mainly use offshore migration routes (Figs. 3, 4, Figs. S3, S7), cf. Arctic Terns (Fijn et al. 2013) and Black Terns (van der Winden et al. 2014).

Wintering site fidelity is described for some seabird species (Phillips et al. 2005; Guilford et al. 2011; Dias et al. 2013). On average the three birds tracked for two seasons did not revisit the exact same wintering area (see “Results”), suggesting a low wintering site fidelity at a narrow spatial scale. However, this may result from a low sample size and indeed site fidelity varied substantially among individuals (Figs. S5, S6). The habitat which common terns seek for wintering is not fixed to a certain location, because biotic and abiotic environmental conditions are on the move with the actual currents. Hence, we do not predict a similar level of high winter site fidelity as found in terrestrial bird species, e.g. Salewski et al. (2000).

The general data indicate that Common Tern females wintered further north than males (Fig. 1), which was supported by within-pair data (Fig. 2). Causes are unknown, but could be related to different nutritional requirements between male and female Common Terns: Nisbet et al. (2002) showed that pair members of Common Terns breeding at Bird Island, MA, USA, had different diets in winter. Females were supposed to feed on a higher trophic level than males. A stable-isotope analysis of feathers from individuals whose gender and wintering site are known could enlighten these interesting findings. Based on our light-level geolocation data, we argue that pair mates do not meet during their wintering period and that in consequence they likely migrated separately from their mate to the colony. Similar results have been found for other seabird species, e.g. the Cory's Shearwater *Calonectris borealis* (Müller et al. 2015).

Time schedule of the annual cycle

The general timing of the stages within a year was similar between Common Terns on their East and West Atlantic Flyways (Table 1, cf. Nisbet et al. 2011a). In contrast to the more general pattern that avian spring migration is faster than autumn migration (Nilsson et al. 2013), Common Terns reached their seasonally appropriate migratory goal in on average 41 days in autumn, but 55 days in spring. This may be a consequence of prevailing winds, rotating clockwise in the North Atlantic and offering tailwind during autumn migration, but headwind during spring migration (Liechti 2006). For the few birds tracked along the West Atlantic Flyway, however, spring migration was faster than autumn migration (Nisbet et al. 2011a) again in agreement with prevailing wind directions. However, these results should be treated cautiously given the location error in light-level geolocation estimates and the low sample sizes.

Most adult Common Terns lingered for 4 weeks around the breeding area, as inferred by the time passed between the last detection at the colony site by the transponder system and the first sign of migration from geolocation. A similar pattern was described by Nisbet et al. (2011a) showing that adult Common Terns stayed about 100–200 km to the east or the west of the breeding colony before starting autumn migration. The reason for this behavior remains speculative. Possibly, adults care for their offspring, which they may guard and feed up to several weeks after fledging (Burger 1980; Becker and Ludwigs 2004; Nisbet et al. 2011b: at least until end of September; for other tern species see Ashmole and Tovar 1968). Parents may familiarize their offspring with the extended surroundings of the colony site or to reach more productive feeding grounds (cf. Fijn et al. 2013). Adults may also accumulate energy, in terms of fat and muscle mass, as a preparation for the upcoming migrations. Our light-level geolocator data indicated that the delay until the final departure of adults for migration was independent of sex (Table 1). This is in contrast to the findings of Nisbet et al. (2011a, b) showing that females started earlier than males presumably because the post-fledgling guarding is mostly provided by the fathers (Nisbet et al. 2011b).

Saltwater contact during the annual cycle

Common terns spent small proportions of time resting on saltwater during the breeding period (Figs. 3, 4). This saltwater contact was likely explained by bathing as Common Terns do not swim in the breeding area (PHB personal observations; Nisbet 2002; Nisbet et al. 2011a). During the non-breeding season, however, the birds spent more time on salt water, confirming observations of Common Terns from the West Atlantic Flyway (Nisbet et al. 2011a; Neves et al. 2015). The inter-individual differences in saltwater contact during both migration periods and wintering along the West African coast might be due to individual selection of habitats. In contrast to other individuals who spent most time resting at sea water during the day, Cornelia and Joachim showed high saltwater contact during the night, which they obviously had spent offshore (Fig. S8). Perhaps inter-individual variation in wintering habitat selection may be influenced by an extended parental care; hence, wintering on the coast might be beneficial if parents still care for their offspring (e.g. potentially in Heiner, Ayla and Ernst), so that juveniles in poor body condition can easily find sites for resting on beaches or sandbars (e.g. Bugoni et al. 2005; Blokpoel et al. 1982, 1984). Whether Common Terns care for their offspring at wintering sites is still unclear, but juvenile Royal Terns *Thalasseus maximus* were fed by adults during wintering in Peru in December and January, when they were about 7 months old (Ashmole and Tovar 1968).

Changes in the daily routines of Common Terns as suggested by the saltwater contact data could likely be explained to a certain extent by their daily foraging pattern. Radio-tracked Common Terns spending the non-breeding season in southern Brazil usually started foraging from roosting sites on the beach or sandbars in the morning or late afternoon (Bugoni et al. 2005). The low proportion of saltwater contact during sunrise and sunset (Fig. 4) is, therefore, likely to be related to the foraging behavior of Common Terns, considering that during the short plunge dives no saltwater contact was recorded, cf. in the breeding period (Figs. 3, 4). Another explanation of the high proportion of saltwater contact during the non-breeding period in common terns on the West (Nisbet et al. 2011a) and East Atlantic Flyways could be thermoregulatory necessities: during noon at areas close to the equator (Fig. 4) they may cool down their body temperature, which might be heated up considerably by the high solar irradiation. This is corroborated by the significant positive correlation of Common Terns' saltwater contact per day with higher latitude

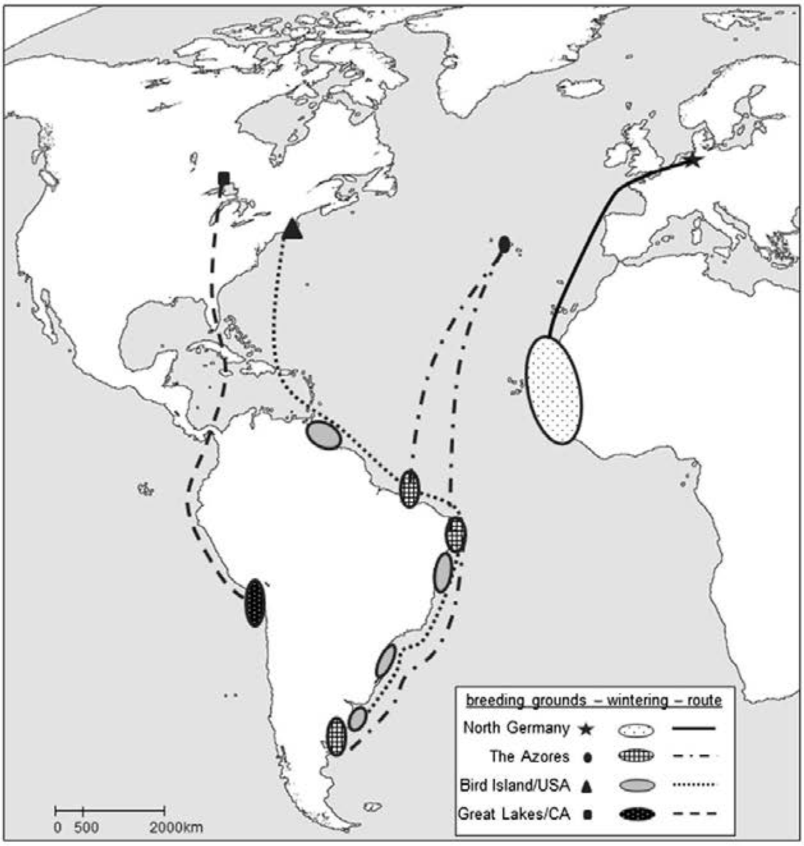


Fig. 5 Breeding grounds (indicated by *different symbols*), migration routes (*diverse lines*), and wintering areas (*differently shaded areas*) of Common Terns tracked with light-level geolocators. Migration routes are rough estimates. Data are from four populations of Common Terns breeding in north Germany (this study), on the Azores (Neves et al. 2015), at MA, USA (Nisbet et al. 2011a, b), and Great Lakes, Canada (Moore et al., personal communication)

of the wintering locations coming along with decreasing sea water temperatures. Moreover, water contact was highest during spring migration (Figs. 3, 4) when also sunshine duration is highest in Senegal and Mauretania, concomitant with lowest sea surface temperatures due to upwelling (19–20 °C, February and March; e.g. Hayward and Oguntoyinbo 1987; http://www.iten-online.ch/klima/afrika) that the temperature gradient between birds' legs and sea water should warrant body heat release. Another explanation of longer resting times at sea during noon (Fig. 4) may be related to winds, since wind speed is typically higher at midday than at sunrise and sunset, possibly handicapping the terns' flight. Gannets *Sula bassana*, too, wintering off West Africa spend more time on the sea water during daylight than conspecifics wintering at the Bay of Biscaya or the North Sea (Garthe et al. 2012). There is a need of detailed behavioral observations of terns and other seabirds in their wintering areas to clarify these speculations on persisting parental care and thermoregulation by offshore swimming.

General migration patterns of Common Tern populations studied by geolocation

Our study adds to the three investigations published to date of Common Tern migration based on light-level geolocators (Nisbet et al. 2011a, b; Neves et al. 2015; Moore et al., personal communication). Overall, these studies clearly show a strong east–west separation in their migration routes and wintering areas among breeding populations and connectivity at broad spatial scales (Fig. 5). Some studies on pelagic seabirds have also found a certain degree of migratory connectivity (e.g. Cory's Shearwater *Calonectris diomedea*, González-Solís et al. 2007, Bulwer's petrel *Bulweria bulwerii*, Ramos et al. 2015), but Common Terns are more coastal seabirds and their longitudinal change in migratory routes parallel those found in terrestrial birds of the Palearctic–Tropical and Nearctic–Neotropical migratory systems (e.g. Trierweiler et al. 2014; Hallworth et al. 2015). Such knowledge is important to understand migration strategies and for conservation concerns. Based on information about the migratory connectivity we can recognize and elucidate impacts of population-level threats during the non-breeding period, which may affect demographic rates or traits of migration timing (e.g. in Common Terns: Szostek and Becker 2015; Szostek et al. 2015). The differences in the wintering areas and migratory flyways of Common Terns breeding, in geographical terms, in relative close vicinity to each other are striking for seabirds. Common Terns breeding in northwest Germany and on the Azores are separated to a larger scale in winter when visiting the West African coast or the eastern South American coast, respectively, than in summer. A similar pattern exists for the breeding populations in North America: Common Terns from the northeast Atlantic coast (Bird Island) spent their winter along the eastern South American coast and mix with birds from the Azores breeding population, whereas Common Terns from the Great Lakes winter along the eastern Pacific coast in South America (Fig. 5). Ring recoveries suggest similar divergence of wintering sites for further common tern populations (Neubauer 1982; Bairlein et al. 2014; Cohen et al. 2014). The origin and causes of the population-specific migration patterns and wintering areas in Common Terns may be driven by geographical structures and barriers such as mountains, coastline courses, wind patterns, currents, water bodies, or oceans.

Acknowledgments We thank Christina Bauch, Alexander Braasch, Julia Spieker, Lesley Szostek, Katharina Weißenfels, Silas Wolf, and Christian Wolter for their help with field work. Simeon Lisovski helped with analyzing the light-level geolocation data. Kathrin Hüppop helped preparing the figures. We thank Dave Moore giving access to unpublished data of migration of common terns breeding at the Great Lakes and Olaf Geiter for providing ring recovery data of common terns. The manuscript was improved by helpful comments of Franz Bairlein and two anonymous reviewers. The studies were performed under license of the Nds. Landesamt für Verbraucherschutz und Lebensmittelsicherheit Oldenburg and of the Stadt Wilhelmshaven. H.S. is financed by the Deutsche Forschungsgemeinschaft (SCHM 2647/1-1) which also supported the project (BE 916/8 and 9).

References

Arístegui J, Gasol JM, Duarte CM, Herndl GJ (2009) Microbial oceanography of the dark ocean's pelagic realm. Limnol Oceanogr 54:1501–1529

Ashmole NP, Tovar HS (1968) Prolonged parental care in royal terns and other birds. Auk 85:90–100

Bairlein F, Dierschke J, Dierschke V, Salewski V, Geiter O, Hüppop K, Köppen U, Fielder W (2014) Atlas des Vogelzugs. AULA, Wiebelsheim

Becker PH (2010) Populationsökologie der Flussseeschwalbe: Das Individuum im Blickpunkt. In: Bairlein F, Becker PH (eds) 100 Jahre Institut für Vogelforschung "Vogelwarte Helgoland". Aula, Wiebelsheim, pp 137–155

Becker PH, Ludwigs J-D (2004) *Sterna hirundo* common tern. In: Parkin D (ed) BWP update, vol 6, nos 1/2. Oxford University Press, NY, pp 93–139

Becker PH, Wink M (2003) Influences of sex, sex composition of brood and hatching order on mass growth in common terns (*Sterna hirundo*). Behav Ecol Sociobiol 54:136–146

Becker RA, Chambers JM, Wilks AR (1988) The new S language. Wadsworth and Brooks/Cole, Belmont

Becker PH, Wendeln H, González-Solís J (2001) Population dynamics, recruitment, individual quality and reproductive strategies in common terns marked with transponders. Ardea 89(special issue):239–250

Becker PH, Dittmann T, Ludwigs J-D, Limmer B, Ludwig SC, Bauch C, Braasch A, Wendeln H (2008) Timing of initial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. PNAS 105:12349–12352

Blokpoel H, Morris R, Trull P (1982) Winter observations of common terns in Trinidad, Guyana, and Suriname. Colon Waterbirds 5:144–147

Blokpoel H, Morris R, Tessier G (1984) Field investigations of the biology of common terns wintering in Trinidad. J Field Ornithol 55:424–434

Brenninkmeijer A, Stienen EWM, Klaassen M, Kersten M (2002) Feeding ecology of wintering terns in Guinea-Bissau. Ibis 144:602–613

Breton AR, Nisbet ICT, Mostello CS, Hatch JJ (2014) Age-dependent breeding dispersal and adult survival within a metapopulation of common terns *Sterna hirundo*. Ibis 156:534–547

Bruderer B, Boldt A (2001) Flight characteristics of birds: 1. Radar measurements of speeds. Ibis 143:178–204

Bugoni L, Cormons TD, Boyne AW, Hays H (2005) Feeding grounds, daily foraging activities, and movements of common terns in Southern Brazil, determined by radio-telemetry. Waterbirds 28:468–477

Burger J (1980) The transition to independence and post fledging parental care in seabirds. In: Burger J, Olla BL, Winn HE (eds) Marine birds. Behavior of marine animals, vol 4. Plenum Press, New York, pp 367–447

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Cohen EB, Hostetler JA, Royle JA, Marra PP (2014) Estimating migratory connectivity of birds when re-encounter probabilities are heterogeneous. Ecol Evol 4:1659–1670

Dias MP, Granadeiro JP, Catry P (2013) Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. Anim Behav 86:359–364

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proc Natl Acad Sci 107:2078–2081

Ekstrom PA (2004) An advance in geolocation by light. Mem Natl Inst Polar 58:210–226

Ezard T, Becker PH, Coulson T (2006) The contributions of age and sex to variation in common tern population growth rate. J Anim Ecol 75:1379–1386

Fijn RC, Hiemstra D, Phillips RA, van der Winden J (2013) Arctic terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctica. Ardea 101:3–12

Fudickar AM, Wikelski M, Partecke J (2012) Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Methods Ecol Evol 3:47–52

Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit plunging by northern gannets (*Sula bassana*) "feeding on capelin (*Mallotus villosus*)". Proc R Soc B 267:1717–1722

Garthe S, Ludynia K, Hueppop O, Kubetzki U, Meraz JF, Furness RW (2012) Energy budgets reveal equal benefits of varied migration strategies in northern gannets. Mar Biol 159:1907–1915

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 5:297–301

Grecian WJ, Witt MJ, Attrill MJ (2016) Multi-species top predator tracking reveals link between marine biodiversity and ocean productivity. Biol Lett (in revision)

Guilford T, Meade J, Willis J, Phillips RA, Boyle D, Roberts S, Collet M, Freeman R, Perrins CM (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc R Soc B 276:1215–1223

Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic puffin and its implications for migratory navigation. PLoS One 6:e21336

Hallworth MT, Sillett TS, Van Wilgenburg SL, Hobson KA, Marra PP (2015) Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecol Appl 25:336–347

Harrison P (1997) Seabirds of the world. Princeton University Press, Princeton

Hayward DF, Oguntoyinbo J (1987) The climatology of West Africa. Hutchinson, London

Hill RD (1994) Theory of geolocation by light levels. In: Burney J, Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkeley, pp 227–236

Liechti F (2006) Birds: Blowin' by the wind? J Ornithol 147:202–211

Limmer B, Becker PH (2007) The relative role of age and experience in determining variation in body mass during the early breeding career of the common tern (*Sterna hirundo*). Behav Ecol Sociobiol 61:1885–1896

Lisovski S, Hahn S (2012) GeoLight—processing and analysing light-based geolocator data in R. Methods Ecol Evol 3:1055–1059

Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol Evol 3:603–612

McGregor HV, Dima M, Fischer HW, Mulitza S (2007) Rapid 20th-century increase in coastal upwelling off northwest Africa. Science 315:637–639

Mostello CS, Nisbet ICT, Oswald SA, Fox JW (2014) Non-breeding season movements of six North American roseate terns *Sterna dougallii* tracked with geolocators. Seabird 27:1–21

Müller MS, Massa B, Phillips RA, Dell'Omo G (2015) Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes? Anim Behav 102:267–276

Neubauer W (1982) Der Zug mitteleuropaeischer Flusseeschwalben (*Sterna hirundo*) nach Ringfunden. Ber Vogelwarte Hiddensee 2:59–82

Neves VC, Nava CP, Cormons M, Bremer E, Castresana G, Lima P, Azevedojun SM, Phillips RA, Magalhães MC, Santos RS (2015) Migration routes and non-breeding areas of common terns (*Sterna hirundo*) from the Azores. Emu 115:158–167

Nielsen A, Sibert JR (2007) State-space model for light-based tracking of marine animals. Can J Fish Aquat Sci 64:1055–1068

Nilsson C, Klaassen RH, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837–845

Nisbet ICT (2002) Common tern. Birds N Am 618:1–39

Nisbet ICT, Cam E (2002) Test for age-specificity in survival of the common tern. J Appl Stat 29:65–83

Nisbet ICT, Montoya JP, Burger J, Hatch JJ (2002) Use of stable isotopes to investigate individual differences in diets and mercury exposures among common terns *Sterna hirundo* in breeding and wintering grounds. Mar Ecol Prog Ser 242:267–274

Nisbet ICT, Mostello CS, Veit RR, Fox JW, Afanasyev V (2011a) Migrations and winter quarters of five common terns tracked using geolocators. Waterbirds 34:32–39

Nisbet ICT, Szczys P, Mostello CS, Fox JW (2011b) Female common terns *Sterna hirundo* start autumn migration earlier than males. Seabird 24:103–106

Palestis BG, Hines JE (2015) Adult survival and breeding dispersal of common terns (*Sterna hirundo*) in a declining population. Waterbirds 38:221–228

Pennycuick CJ, Åkesson S, Hedenström A (2013) Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. J R Soc Interface 10:20130419

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272

Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 86:2386–2396

R Core Team (2014) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Ramos R, Sanz V, Militão T et al (2015) Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). J Biogeogr 42:1651–1664

Ropert-Coudert Y, Wilson RP, Grémillet D, Kato A, Lewis S, Ryan PG (2006) Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. Mar Ecol Prog Ser 328:275–284

Salewski V, Bairlein F, Leisler B (2000) Recurrence of some palaearctic migrant passerine species in West Africa. Ringing Migr 20:29–30

Scandolara C, Rubolini D, Ambrosini R, Caprioli M, Hahn S, Liechti F, Romano A, Romano M, Sicurella B, Saino N (2014) Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. J Avian Biol 45:417–423

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Nat Acad Sci 103:12799–12802

Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013) The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. J Avian Biol 44:531–540

Sorenson MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that non-breeding diet quality influences reproductive success. J Anim Ecol 78:460–467

Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian estimation of animal movement from archival and satellite tags. PLoS One 4:e7324

Szostek L, Becker PH (2012) Terns in trouble: demographic consequences of low breeding success and recruitment on a common tern population in the German Wadden Sea. J Ornithol 153:313–326

Szostek KL, Becker PH (2015) Marine primary productivity in the wintering area influences survival and recruitment in a migratory seabird. Oecologia 178:643–657

Szostek KL, Bouwhuis S, Becker PH (2015) Are arrival date and body mass after spring migration influenced by large-scale environmental factors in a migratory seabird? Front Ecol Evol 3:42

Trierweiler C, Klaassen RGH, Drent RH, Exo K-M, Komdeur J, Bairlein F, Koks BJ (2014) Population specific migration routes and migratory connectivity in a long-distance migratory raptor. Proc R Soc B Lond 281:1471–2954 van der Winden J, Fijn RC, van Horssen PW, Gerritsen-Davidse D, Piersma T (2014) Idiosyncratic migrations of black terns (*Chlidonias niger*): diversity in routes and stopovers. Waterbirds 37:162–174

Weimerskirch H, Wilson RP (2000) Oceanic respite for wandering albatrosses. Nature 406:955–956

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp H-P (2002) GPS tracking of foraging albatrosses. Science 295:1259

Wendeln H, Becker PH (1999) Significance of ring removal in Africa for a common tern *Sterna hirundo* colony. Ringing Migr 19:210–212

Wernham CV, Toms MP, Marchant JH, Clark JA, Siriwardena GM, Baillie SR (2002) The migration atlas: movements of the birds of Britain and Ireland. T & AD Poyser, London

Wilson RP, Cooper J, Plötz J (1992a) Can we determine when marine endotherms feed? A case study with seabirds. J Exp Biol 167:267–275

Wilson RP, Ducamp JJ, Rees G, Culik BM, Niekamp K (1992b) Estimation of location: global coverage using light intensity. In: Priede IG, Swift SM (eds) Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood Ltd, Chichester, pp 131–134

Wilson RP, Weimerskirch H, Lys P (1995) A device for measuring seabird activity at sea. J Avian Biol 26:172–175

Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, Schäfer-Neth C, Scolaro JA, Bost C-A, Plötz J, Nel D (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar Ecol Prog Ser 228:241–261

Zhang H, Vedder O, Becker PH, Bouwhuis S (2015) Age-dependent trait variation: the relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. J Anim Ecol 84:797–807

ANNEX 2: Stable isotope analysis

Stable isotope analysis

Some chapters of this thesis include the use of stable isotopes. In the following lines I introduce and extend the basics about stable isotope analysis to ease reading for those who are not familiar with this technique.

Intrinsic markers, such as stable isotope analysis (SIA), have become an essential tool in ecological studies, allowing researchers to reveal aspects of animals' spatial and trophic ecology across different spatial and temporal scales (Ramos & González-Solís 2012). SIA allows to infer trophic relations between predators and prey across the food webs, since stable isotopes are directly transferred from prey to predator tissues throughout diet, which allows their traceability. As stable isotopes are already present in the sampled tissue and hold the information needed at the moment of sampling, there is no need to recapture the individual. In marine environments, carbon $\delta^{13}C$ values (the ratio 13C/12C) have been established as relevant indicator of inshore vs. offshore feeding distribution (Hobson et al. 1994). On the other side, nitrogen $\delta^{15}N$ values (the ratio 15N/14N) are used to infer trophic level position of consumers. This is especially relevant to study seabirds during the non-breeding season, when conventional diet analysis cannot be carried out. Therefore, SIA approach can provide information to infer potential changes in seabird diet and trophic position over the annual cycle.

In seabird studies, SIA of feathers have been commonly used, as they become metabolically inert and integrate information about when and where they were grown (Inger & Bearhop 2008). Moult represent a critical period for birds, as feather growth is energetically demanding and also reduce flight efficiency (Rayner and Swaddle 2000). Moulting pattern in many seabird species remains unknown because in most cases the replacement of feathers occurs during the non-breeding season, after birds leave their breeding grounds and thereafter become hard to observe in detail. However, differences and similarities in isotope values among feathers can be used to reveal the moulting sequence in relation to the annual cycle (Cherel et al. 2000). Moreover, the knowledge of the moult pattern of studied species is important to properly link the timing and area where feathers were grown and hence reveal movements within and between breeding and non-breeding grounds (Hobson 2005).

Isotopic values vary geographically according to baseline levels specific of each zone. The gradient of this values across space can be represented in 'isoscape' maps. While for terrestrial territories various isoscape maps are currently available (West et al. 2008, Hobson et al. 2012a, Hobson et al. 2012b), there exists a lack for such maps for seas and oceans (Somes et al. 2010, McMahon et al. 2013a). Such isoscape maps represent an important tool for linking movements of animals with the marine environment, and to examine migratory connectivity of different populations and species (Rubenstein & Hobson 2004, Hobson et al. 2010).

Overall, SIA can complement other techniques, such as animal tracking, opening new areas of research with potential for identifying foraging areas and potential prey of seabirds (Meier et al.

2017), spatial and trophic segregation of multiple species (Roscales et al. 2011, Navarro et al. 2013) or revealing moulting areas of seabirds (Cherel et al. 2016).

REFERENCES

Cherel, Y., Hobson, K. A. & Weimerskirch, H. (2000) Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia*, 122(2): 155-162.

Cherel, Y., Quillfeldt, P., Delord, K. & Weimerskirch, H. (2016) Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution*, 4: 3.

Hobson, K. A., Piatt, J. & Pitocchelli, J. (1994). Using Stable Isotopes to Determine Seabird Trophic Relationships. *Journal of Animal Ecology*, 63(4): 786-798.

Hobson, K. A. (2005) Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, 11(2): 157-164.

Hobson, K. A., Barnett-Johnson, R. & Cerling, T. (2010) Using isoscapes to track animal migration. In Isoscapes (pp. 273-298). Springer, Dordrecht.

Hobson, K. A., Van Wilgenburg, S. L., Wassenaar, L. I., & Larson, K. (2012a) Linking hydrogen (δ2H) isotopes in feathers and precipitation: sources of variance and consequences for assignment to isoscapes. *PloS one*, 7(4): e35137.

Hobson, K. A., Van Wilgenburg, S. L., Wassenaar, L. I., Powell, R. L., Still, C. J. & Craine, J. M. (2012b). A multi-isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) feather isoscape to assign Afrotropical migrant birds to origins. *Ecosphere*, 3(5): 1-20.

Inger, R. & Bearhop, S. (2008) Applications of stable isotope analyses to avian ecology. *Ibis*, 150(3): 447-461.

McMahon KW, Hamady LL & Thorrold SR (2013a) A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnol Oceanogr* 58: 697−714

Meier, R. E., Votier, S. C., Wynn, R. B., Guilford, T., McMinn Grivé, M., Rodríguez, A., ... & Trueman, C. N. (2017) Tracking, feather moult and stable isotopes reveal foraging behaviour of a critically endangered seabird during the non-breeding season. *Diversity and Distributions*, 23(2): 130-145.

Navarro, J., Votier, S. C., Aguzzi, J., Chiesa, J. J., Forero, M. G. & Phillips, R. A. (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PloS one*, 8(4): e62897.

Rayner, J. M. V. & Swaddle, J. P. (2000) Aerodynamics and behaviour of moult and take-off in birds. *Biomechanics in animal behaviour*, 125-157.

Ramos, R. & González-Solís, J. (2012) Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. *Frontiers in Ecology and the Environment*, *10*(5): 258-266.

Roscales, J. L., Gómez-Díaz, E., Neves, V. & González-Solís, J. (2011) Trophic versus geographic structure in stable isotope signatures of pelagic seabirds breeding in the northeast Atlantic. *Marine Ecology Progress Series*, 434: 1-13.

Rubenstein, D. R. & Hobson, K. A. (2004) From birds to butterflies: animal movement patterns and stable isotopes. *Trends in ecology & evolution*, 19(5): 256-263.

Somes, C. J., Schmittner, A., Galbraith, E. D., Lehmann, M. F., Altabet, M. A., Montoya, J. P., ... & Eby, M. (2010) Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochemical Cycles*, *24*(4).

West, J. B., Sobek, A., & Ehleringer, J. R. (2008) A simplified GIS approach to modeling global leaf water isoscapes. *PLoS one*, 3(6): e2447.

ANNEX 3: Outreach contributions

POSTER PRESENTED AT 22ND SPANISH CONFERENCE OF ORNITHOLOGY, MADRID, 2014

New insights into behavioural strategies and time cycles in a small oceanic seabird: Boyd's shearwater *(Puffinus boydi)*

Zuzana Zajková*, Santiago Guallar & Jacob González-Solís

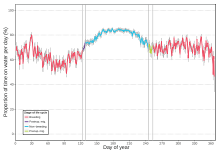
Institut de Recerca de la Biodiversitat (IRBio) and Dept Biologia Animal, Universitat de Barcelona, Barcelona, Spain
**E-mail: zuzulaz@gmail.com*

Introduction

Many aspects of seabird behaviour at sea remain unknown. Recently miniaturized devices that combine different kind of sensors allow us to reveal the movements and at-sea behaviour of highly pelagic species in more detail than ever before. Salt-water immersion sensors provide continuous data during long periods that can be used as a proxy to infer activity patterns. In combination with light geolocation positioning we have revealed the phenology, migratory movements and ***behaviour of Boyd's Shearwater for the annual cycle****.*

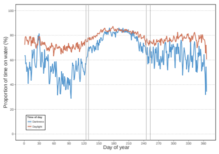
Results

(1) Activity during year



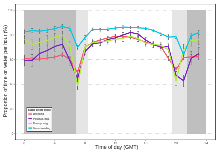
The proportion of time spent on the water during the day varied between different stages of life cycle ($p < 0.01$). Birds spend more time on water during non-breeding than during other stages. During the breeding period they are more active (less time on water, more time flying), probably due to foraging effort related to breeding duties.

(2) Activity by daylight & darkness



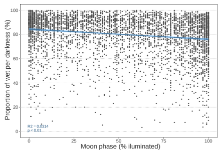
When we split up the time spent on water by darkness and daylight for every day, we find out Boyd's Shearwater to be a slightly nocturnal species ($p < 0.01$). Comparing between daylight and darkness, birds spend more time on the water during daylight.

(3) Activity by 24-hours



Activity daily patterns show clear differences among phenological phases. Birds consistently are more active during sunrise and sunset for the whole year since they spend more time in flight (i.e. less time on water).

(4) Activity by moon phase



Birds do not show an increase in activity (i.e. time flying) in relation to the moon phase during the non-breeding stage. This finding, that differs to previous publications about relation between other seabird species and the moon, may be related to a highly use of the sit-and-wait foraging strategy, which implies less time flying.

Conclusions

Our results show Boyd' Shearwater:

- spends non-breeding period in oligotrophic waters of Central North Atlantic Ocean,
- is more active (i.e. invest more time in flying) during breeding period,
- is slightly more active during darkness along the year,
- is more active in twilight periods of day,
- presents inter-individual differences in activity which may reflect individual specialization in different foraging strategies.

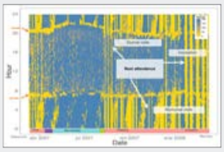
Material & Methods

- Boyd's Shearwater *(Puffinus boydi)*
- Cape Verde Islands (Ilhéu Raso, Ilhéu de Cima)
- Six years of tracking (2007-2013)
- Data from 37 geolocators (BAS & Biotrack) with salt-water immersion sensors of 30 individuals. Raw immersion data in 10 minutes blocks range from 0 (**dry**) to 200 (**wet**).

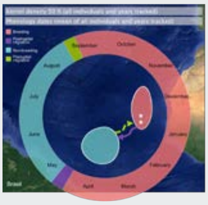
As a measure of activity for each individual we calculated **percentage of time spent on the water**:

- per day (consecutive light and dark period)
- per day that occured during daylight and darkness
- per hour within 24 hours

Time calculations excluded periods spent in burrows (whole daylight or whole darkness duration).



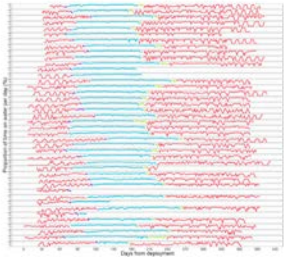
Distribution & Phenology



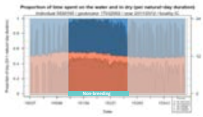
Analysis of spatial data revealed Boyd's shearwater is a species with oceanic distribution all year round. After the breeding, in the beginning of May, shearwaters migrated on average 1 482 km to oligotrophic waters in the Central North Atlantic Ocean (5 – 15º N/ 30 - 40º W), where they spent aprox. 115 days. Birds started the prenuptial migration on 2nd of September, but because of equinox effect, exact route remains unknown.

(5) Behavioural strategies at individual level

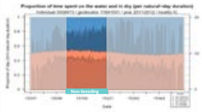
(5a)



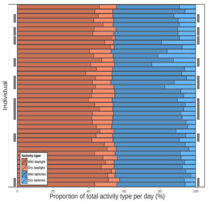
(5b)



(5c)



(5d)



Analysis of activity at individual level, presented by line graphs corresponding to individual and year (5a, colours correspond to phenological phases), remarks differences in phenology and behaviour during the annual cycle.

Activity during non-breeding stage compared among individuals shows clear differences (example of two individuals in 5b, 5c; all individuals in 5d), especially regarding the nocturnal activity.

Differences are present even at intra-individual level among years (individuals marked with a grey rectangle). Since the whole population winter in oligotrophic waters where marine productivity (and its variability) is low, these individual differences suggest a possible specialization in foraging strategies at individual level.