

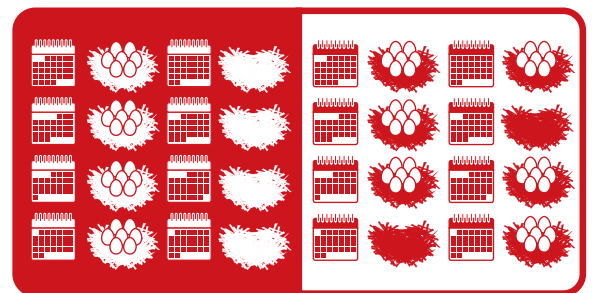
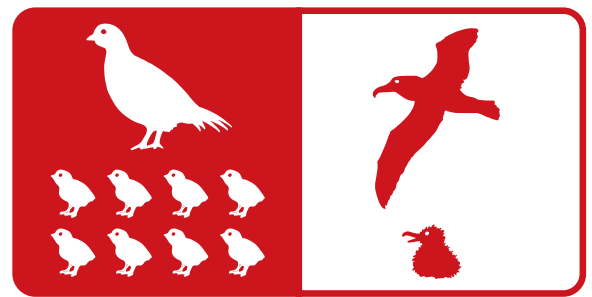


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LIFE HISTORY, BEHAVIOUR AND RESPONSES TO ENVIRONMENTAL CHANGES

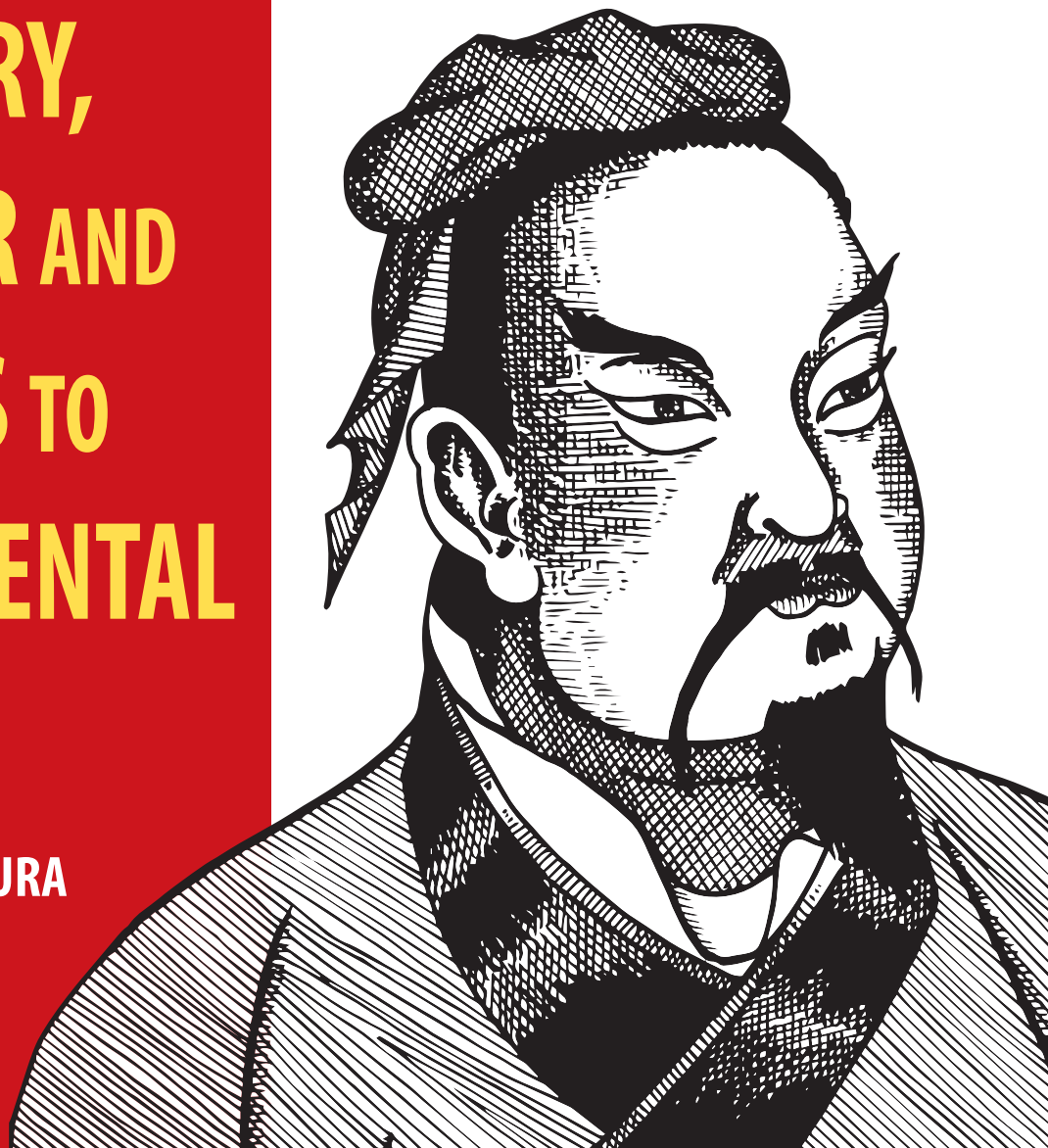
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Ph.D. Thesis

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Universitat Autònoma de Barcelona
Centre de Recerca Ecològica i Aplicacions Forestals
DOCTORAT EN ECOLOGIA TERRESTRE

Life History, Behaviour and Responses to Environmental Changes

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Can Maspons de la Vall
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Resum

A la natura trobem una extraordinària diversitat d'estratègies vitals, les diferents maneres en què les espècies optimitzen els seus recursos limitats en els diferents components de l'eficàcia biològica, com ara la reproducció, el desenvolupament o la supervivència. En un món canviant com el nostre, oimés en un context de canvis ambientals ràpids induïts pels humans, és de vital importància entendre com les espècies poden adaptar-se a les noves condicions tenint en compte les restriccions de l'evolució dels trets i als balanços entre els diferents trets. El marc teòric de les estratègies vitals permet veure de forma integrada l'evolució dels trets de les espècies en funció de les pressions de selecció de l'ambient. En el cas dels animals, un mecanisme alternatiu per fer front als canvis és mitjançant la plasticitat del comportament. Malgrat que tradicionalment les respostes comportamentals i d'estratègies vitals s'han analitzat per separat, evidències recents suggereixen que es poden lligar en el què anomenem síndromes del ritme de vida.

L'objectiu d'aquesta tesi és contribuir a entendre com les espècies responen als canvis i quin paper hi juguen les estratègies vitals i el comportament. En el primer capítol, descriu els principals eixos de variació de les estratègies vitals en ocells, posant èmfasi en els efectes demogràfics de l'eix ràpid-lent (*fast-slow* en anglès) i descrivint altres eixos menys estudiats com ara la iteroparitat o la mida relativa dels ous (Capítol 2). A continuació, exploro els efectes i les interaccions entre les estratègies vitals i el comportament en un context de canvi ambiental mitjançant un model estocàstic basat en individus que mostra que els beneficis de l'aprenentatge són contingents a l'estratègia vital (Capítol 3). Finalment, descriu l'existència d'interaccions entre estratègies vitals i el comportament en facilitar la resposta a entorns alterats pels humans, que mostren que les espècies de vida lenta tendeixen a prendre menys riscos i, alhora, aquest comportament és flexible i es pot ajustar quan es troben en nous ambients com ara àrees urbanes (Capítol 4).

Abstract

In nature, we find an extraordinary diversity of life history strategies, the different ways in which species optimize their limited resources in different components of the fitness, such as reproduction, development or survival. In a changing world like ours, even more in a context of human-induced rapid environmental change, it is vital to understand how species can adapt to the new conditions taking into account the constraints and trade-offs between different traits. The framework of the life history theory allows us to view the evolution of species traits in an integrated way as a function of the selection pressures from the environment. In the case of animals, an alternative mechanism to deal with changes is through the plasticity of behaviour. Although behavioural and life history responses have traditionally been analysed separately, recent evidence suggest that they could be linked in what we call peace of life syndromes.

The aim of this thesis is to contribute to understanding how species respond to changes and what is the role of the life histories and behaviour. In the first chapter, I describe the main axes of variation of life history in birds, emphasising the demographic effects of the fast-slow axis and describing other less studied axes such as the iteroparity or the relative egg size (Chapter 2). Then, I explore the effects and the interactions between life history and behaviour in a context of environmental change using a stochastic individual based model, showing that the benefits of learning are contingent on life history (Chapter 3). Finally, I describe the existence of interactions between life history and behaviour in facilitating the response to human-altered environments, showing that slow-lived species tend to be more risk-averse and, at the same time, this behaviour is plastic and can be adjusted in new environments like urban areas (Chapter 4).

Article references

- **Chapter 2:**
Maspons, J. & D. Sol. 2022. Revisiting the fast-slow continuum of life history variation in birds. Manuscript in preparation.
- **Chapter 3:**
Maspons, J., R. Molowny-Horas, & D. Sol. 2019. Behaviour, life history and persistence in novel environments. *Phil. Trans. R. Soc. B* 374:20180056. doi:10.1098/rstb.2018.0056
- **Chapter 4:**
Sol, D., J. Maspons, A. Gonzalez-Voyer, I. Morales-Castilla, L. Z. Garamszegi, A. P. Møller. 2016 Risk-taking behavior, urbanization and the pace of life in birds. *Behav. Ecol. Sociobiol.* 72, 59. doi:10.1007/s00265-018-2463-0



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Cover image by © 2021 **Jordi Roura Solà**. The drawing of Sun Tzu is inspired by a public domain resource from an unknown author of the time of the Qing dynasty. Sun Tzu was the author of the Art of War, a text from the 5th century BC about military tactics and strategies, but throughout history it has served as an inspiration for all kinds of competitive systems, from the economy to sport and, why not, also in ecology.

The \LaTeX code to generate this document is available at <https://github.com/jmaspons/Thesis>.

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1.1 Life history and responses to environmental changes

At the most fundamental level, the persistence of population hinges on the fate of individuals surviving and reproducing in their environments (Sol and Maspons, 2016). If individuals are able to reproduce at a higher rate than they die, the population will increase in numbers and persist over time; if the balance is negative, however, the population will decrease over time and end up extinct. Because the rates of birth and death are ultimately determined by how organisms allocate their limited time and energy to reproduction and survival (Stearns, 1992), life history theory has long been deemed essential to understanding the dynamics of populations (Sæther et al., 2004; Sol et al., 2012*b*).

Concern over the loss of biodiversity associated with human-induced rapid environmental alterations has generated an urgent need to understand why organisms differ in their response to environmental changes.

Box 1: Life History

Life history strategies are the different ways in which organisms allocate the limited resources among different components of fitness such as reproduction, survival and development (Stearns, 1992; Roff, 2002). Thus, each strategy is defined by a combination of life history traits such as clutch size, broods per year, age at first breeding or lifespan (Violle et al., 2007). Mechanisms that generate the trade-offs explaining the observed covariance among traits include resource partitioning, correlational selection between traits and antagonistic pleiotropy (Roff and Fairbairn, 2007; Stearns, 1989). Incompatible physiological states mediated by the endocrine system (Ricklefs and Wikelski, 2002) generate another source of mechanisms linking life history traits mediated by behaviour (Réale et al., 2010).

There is a consensus on the general features of a plausible explanation for the evolution of life history traits (Stearns, 2000*b*): (1) life histories are shaped by the interaction of extrinsic and intrinsic factors, (2) the extrinsic factors are ecological impacts on survival and reproduction; (3) the intrinsic factors are trade-offs among life history traits and lineage-specific constraints on the expression of genetic variation.

Despite the solid foundations and appealing logic behind the life history theory, no conclusive patterns linking the live history and the responses to environmental changes have been described. This is one of these strongholds that science has

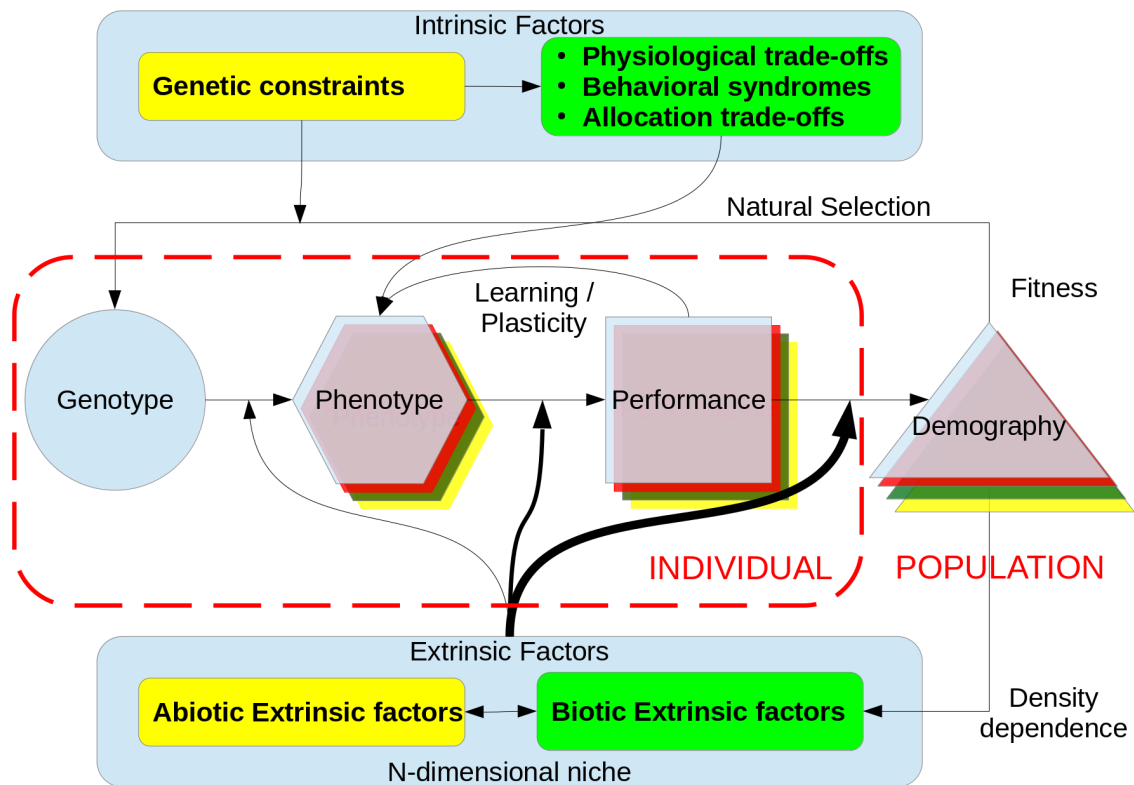


FIGURE 1.1: Schematic representation of the life history theory framework with the different levels of organisation and their relations. The life history of an individual depends on a series of steps from the genotype to the phenotype, which then interacts with the environment resulting in a specific performance in terms of reproduction and survival. The effect of the environment exerts a greater influence at each step modifying the phenotype and the performance of the individuals and ultimately, at the population level, modifying the fitness and the age structure. At the same time, differential fitness among genotypes changes their frequency in the population by natural selection resulting in evolutionary change. A second feedback in the system is the influence of organisms and population on the environment by modifying the population density for the same species or other species being relevant such as preys or predators. Any change modifying the age-specific mortality will result in a change in the optimum life history strategy. Inspired by Ricklefs and Wikelski (2002).

laid siege to, but has never completely conquered and perhaps a more holistic approach can help to overcome (Levins and Lewontin, 1985, p. 269–274). Life history theory covers a huge range of levels of organisation, from genetics at individual level to demography, including the effects of the environment and other species in the ecosystem. Furthermore, life history affects and is affected by the processes at each level of organisation (see figure 1.1). Most of the works framed in the life history theory focus on few levels (reviewed in Stearns (2000b)).

Despite the seductive philosophy described by Levins and Lewontin (1985), pragmatism and the need to put limits to this thesis impose to focus on a subset of the framework. I choose to focus on phenotype and demography. To characterise the phenotype I use life history traits, individual traits with direct effects on fitness such as clutch size, age at first breeding or number of broods per year. I do not consider intraspecific variation, but the traits were aggregated at species level

throughout this thesis. The demographic traits are the population level features affecting the growth rate such as age-specific mortality rate or average fecundity and also were aggregated at species level. Neither evolution nor temporal variation were considered for the life history traits or for demographic traits. Regarding the environmental change, I used data to compare urban and non-urban areas (Chapter 4) and simulated the effects of unknown new habitats or resources with better or worst juvenile or adult survival (Chapter 3).

1.2 Life history and behaviour

Behaviour mediates how animals interact with their environment and, by virtue of their plastic nature, it can modify the nature of these interactions, shaping the biotic and abiotic pressures that act upon them (Futuyma and Moreno, 1988; Losos et al., 2004; Lapiedra et al., 2013). The idea that behaviour, through cognitive and neural machinery, allows behavioural solutions to unusual or new problems to be devised is known as the cognitive buffer hypothesis (Allman et al., 1993; van Schaik and Deaner, 2003; Sol, 2009*a,b*).

Box 2: Behavioural Plasticity

Behaviour can be defined as the actions or inactions of organisms that change their relation with the environment as a response to external or internal stimuli. As such, it is a form of phenotypic plasticity. We can distinguish two types of behavioural plasticity: activational and developmental plasticity.

Activational Plasticity

Activational plasticity refers to the expression of behaviour and describes the innate response to stimuli that triggers a shift to an alternative behaviour through the activation of a neural network (Snell-Rood, 2013). Because of its immediacy and reversibility, such forms of plasticity allow individuals to rapidly respond to environmental uncertainties by enabling rapid modulation of, or transitions between, behaviours as a function of the individuals' needs (Snell-Rood, 2013; Sol et al., 2013*b*). This kind of pre-established responses can be maladaptive if the individuals face new conditions for which no evolutive selection has taken place, leading to a so called ecological traps (Kokko and Sutherland, 2001).

Developmental Plasticity

Animals can confront novel challenges, like the need to obtain new types of food or avoid unfamiliar predators, by modifying or inventing new behaviours, a process known as developmental behavioural plasticity (Snell-Rood, 2013). Developmental behavioural plasticity is not so immediate as activational plasticity, because it involves changes in the nervous system that alter motor responses. However, it has the advantage that it allows animals to construct responses to unfamiliar or novel problems. One of the main mechanisms behind developmental behavioural plasticity

is learning, the acquisition of new information influencing performance in behaviour (Dukas, 1998). Instead of consistently expressing the same behaviour to a particular stimulus, learning allows animals to devise innovative behavioural responses or to improve already established behaviours on the basis of experience (Lefebvre et al., 1997; Dukas, 1998; Reader and Laland, 2002; van Schaik and Deaner, 2003; Ricklefs, 2004). Learning is particularly relevant in facilitating the responses to environmental changes, including new resources, predators or habitats.

As I argue in this thesis, if we want to fully understand how life history affects the population dynamics of animals exposed to environmental changes, we need to explicitly consider the role of behaviour. The argument for the need to better integrate behaviour into life history theory is founded upon three main principles. The first is the fact that behavioural responses are part of the adaptive machinery of animals to cope with uncertainties and evolutionary disequilibria of novel environments. While the idea is not new (Mayr, 1965), recent theoretical and empirical advances provide a strong foundation for moving forward (Sol et al., 2020; Ducatez et al., 2020). The second argument is the growing evidence that behaviour affects and is affected by life history, which implies that both are part of a same adaptive strategy (Ricklefs and Wikelski, 2002; Réale et al., 2010; Sol and Maspons, 2016; Sol et al., 2016). When behaviour changes the relations of the individuals with the environment, the age-specific mortality and therefore the optimum life history strategy also change. Thus, when we examine how life history affects population dynamics, including extinction or colonization, we are considering not only life history mechanisms but also mechanisms related to behavioural responses to novel environments (Sol and Maspons, 2016). The third and last argument is that behaviour mediates some life history mechanisms of response to novel environments, particularly those related to environmental uncertainty and adaptive mismatch. For example, to breed or not to breed is a behavioural decision with direct effects in the number of eggs produced in a year. By clearly delineating these mechanisms, we can better infer when it is necessary to consider behaviour to understand how life history affects the response to environmental changes.

1.3 Objectives

In my thesis I addressed fundamental unresolved questions about the interaction of life history and behaviour in facilitating or impeding the response to rapid environmental changes. Chapter 2 describes the main axes of life history traits variation in birds using a demographic approach within a phylogenetic comparative framework. Chapters 3 and 4 explore the links between life history and behaviour, the first using a theoretical model focused on the process of colonization of novel environments to better understand the mechanisms, and the second analysing empirical data using comparative methods from urban and non-urban populations looking for patterns relating life histories and behaviour. The specific goals of the chapters are:

- **Chapter 2: To describe the axes of life history variation in birds**

Not all combinations of life history traits exist in nature. Traits covary due to trade-offs and are organized among different axes. A major axis of variation of the life history traits is the so-called fast-slow continuum, which mainly reflects a fecundity-survival trade-off. However, defining and quantifying the fast-slow axis has proven to be difficult and at least 18 studies have attempted to characterise the fast-slow axis in the last 40 years with no clear consensus regarding the life history traits that best define it. I tried to address this problem by giving a demographically meaningful definition to the axis and identifying the combination of traits that better describe the underlying trade-off. In this chapter, I defined the fast-slow axis that better predicts the elasticity of the adult survival and generation time from available demographic models and a large dataset of life history traits of birds, and describe other less studied axes of life history from the remaining variation such as the degree of iteroparity, the relative egg size or the lifelong productivity. Then, I generated a global dataset for birds with the position of each species along the new fast-slow axis, which then can be used for comparative analyses (see Chapter 4 for example).

- **Chapter 3: To explore the mechanisms linking life history and behaviour**

I developed a theoretical individual based model simulating the introduction of a species with different life histories in a new environment with different habitat options characterized by different degrees of habitat mismatch that affects adult or juvenile mortality and evaluate how the life history and behaviour could interact and affect the persistence of the population under stochastic and maladaptive scenarios. Specifically, I tested 6 different behaviours representing activational plasticity affecting preferences for the best habitat or the worst (ecological trap) or skipping a reproductive event when individuals are on the worst habitat, and behaviours representing developmental plasticity by increasing the probability to change habitat when there is a breeding failure or by learning by exploring, and a neutral choice behaviour.

- **Chapter 4: To analyse the effects of life history and behaviour in the ability to colonize urban habitats**

By means of a comparative analysis of flight initiation distances (i.e., the distance at which an animal takes flight when a human being is approaching) across >300 bird species distributed worldwide, I show the existence of a peace-of-life syndrome (POLS) predicted by theory where slow-lived species tend to be more risk-averse than fast-lived species. Furthermore, the POLS structure vanishes in urbanized environments due to slow-lived species adjusting their flight distances based on the perception of risk. The results shows that slow species have a more plastic behaviour which can potentially facilitate the adaptation to environmental changes.

I believe that this thesis will contribute to develop a new way to understand how life history influences population growth in novel or changing environments, potentially contributing to a more predictive theory. Such a theory may be useful to help prevent and mitigate the ecological and economic impact of biological invasions (Kolar and Lodge, 2002; Vall-llosera and Sol, 2009; Leung et al., 2012). The new theory should also be of great importance in predicting extinction risk associated with human-induced rapid environmental changes like habitat destruction and climate change (Sæther and Bakke, 2000; Sih et al., 2011).

Revisiting the fast-slow continuum of life history variation in birds

2

Abstract

Despite overwhelming evidence that the life history of organisms has diversified in a broad variety of combinations of reproduction rate, age at maturity and longevity, it is still uncertain what combinations of life history traits are possible in nature. Here, we use an unusually large dataset of life history information for birds to demonstrate that not all combinations of life history traits are possible. Rather, much of life history variation is structured along the fast-slow continuum, defined on the basis of elasticity analyses and estimations of generation time derived from demographic models. The fast-slow continuum may be best described by ~ 70 (elasticity) or ~ 500 (generation time) out of 7527 possible trait combinations, is only weakly correlated with body mass and exhibits substantial phylogenetic signal. After extracting the fast-slow continuum, the remaining life history variation is structured along other less studied axes defined by the number of reproductive bouts and the quality-quantity trade-off in egg production. Describing the fast-slow continuum based on demographic analyses avoids the vagueness of the concept and allows integrating it with other axes of variation, providing a more solid basis to continue investigating the causes and consequences of life history variation through broad comparative analyses.

Keywords: Life history axes, Fast-slow, Iteroparity, Offspring quality-quantity, Traits' covariation

2.1 Introduction

Life history defines how organisms allocate their limited time and energy to reproduction and survival (Stearns, 1992). Early works demonstrated that the life history of organisms has diversified in an extraordinary variety of combinations of reproduction rate, age at maturity and longevity, reflecting the existence of trade-offs and constraints. However, it is still uncertain what combinations of life history traits are possible, and why some strategies have achieved greater evolutionary success. Documenting how life history varies across organisms is of interest in itself, and also because population dynamics ultimately depend on how organisms allocate their limited time and energy to reproduction and survival (Stearns, 1992). Consequently, life history traits have a great potential to influence key ecological and evolutionary processes, such as the likelihood of colonising new areas, the risk of extinction and the rate of evolutionary change (see Stearns (1992); Roff (1992, 2002)).

The challenge of understanding what combinations of life history traits are possible is exemplified by the unsettled controversy about how to quantify the fast-slow continuum axis of life history variation, a term first used by Stearns (1983). The fast-slow continuum aligns organisms along an axis from a “high reproductive-short life expectancy” (fast-lived) strategy at one end to a “low reproductive-long life expectancy” (slow-lived) strategy at the other end. The fast-slow continuum has attracted considerable attention because it is predicted by the age-specific mortality theory of life history evolution (Stearns, 1977; Charlesworth, 1980) and because it has implication in understanding how organisms respond to environmental changes (Sæther and Bakke, 2000; Forcada et al., 2008; Sol et al., 2012*b*). Despite being one of the most studied and influential axes of life history variation, there are notorious discrepancies regarding how to define and quantify it across species. Indeed, at least twelve different life history traits have been used to this purpose either alone or in combination often being chosen based on data availability rather than on biological significance. For example, many studies describe the fast-slow continuum based on surrogates of fecundity like clutch, litter size or productivity, ignoring that a high reproductive effort has high costs in terms of survival (Adler et al., 2014). Inconsistencies in the treatment of body size in previous studies have also been shown to profoundly affect the quantification of the fast-slow continuum (Jeschke and Kokko, 2009). Although many life history traits scale with body size, it is unclear whether body size should be considered part of the fast-slow continuum (e.g. because being larger improves survival) or should instead be factored out because it merely represents constraints (e.g. it takes longer for larger organisms to develop than it does for smaller organisms). The vagueness of the fast-slow continuum makes the concept and its ecological and evolutionary implications difficult to evaluate (Jeschke and Kokko, 2009), and limits our capacity to identify independent axes of life history variation.

The difficulties regarding how to define the fast-slow continuum across species may come as a surprise given that early works are clear in describing it as the result of the impossibility to simultaneously maximize survival and fecundity (Stearns, 1983; Sæther, 1988). This means that the fast-slow continuum needs to be understood in the context of the full life cycle of a species. The assessment

of the relative sensitivity (i.e. elasticity) of population growth to changes in fecundity and adult survival may be useful for this purpose, as it helps describe the fecundity-survival trade-off (Salguero-Gómez et al., 2016b). Thus, a slow-lived strategy should be characterised by high elasticities to the adult survival and low elasticities to fecundity, the contrary being true for fast-lived species. According to Gaillard et al. (1989), the fast-slow continuum can also be represented as a time scale gradient ranking species according to turnover (see also Jeschke and Kokko (2009); Sæther et al. (2013); Adler et al. (2014)). Under this view, the fast-slow should be better characterised by estimating generation time, where a long generation time is a distinctive feature of slow-lived strategies.

While demographically-derived approaches to the fast-slow continuum represent important advances (Salguero-Gómez et al., 2016b), resulting in metrics that are more accurate and demographically meaningful, the paucity of information of species' life cycles limits their application to broad comparative analyses that are geographically and taxonomically representative. This in turn limits our capacity to discern what combinations of life history traits are possible in nature. One way to overcome this limitation is to use a demographically-derived approach to identify the combinations of life history traits that best predict either generation time or the fecundity-survival trade-off (i.e. elasticities to fecundity and adult survival), and then use the best combinations of traits to estimate the position in the fast-slow continuum of species for which information of the full life cycle is not available.

In the present paper, we use this framework to characterise the fast-slow continuum of birds, a group that has played a pivotal role in developing life history theory but for which characterizing the fast-slow continuum has proved particularly difficult (Martin, 2004). We first estimate elasticities to the fecundity and generation time for a subset of species for which demographic data are available. We then explore the extent to which all the combinations of the 14 life history traits most commonly used to describe the fast-slow continuum predict variation in elasticities and generation time. Once the best combinations of traits are identified, we use them to classify >1000 species along the fast-slow continuum. We finally investigate the life history variation that remains once variation in the fast-slow continuum is factored out, and describe three extra axes related to iteroparity, development time, and the offspring quality-quantity trade-off.

2.2 Methods

Life history traits

We assembled published information on the 14 life history traits most often used to describe the fast-slow continuum (Table 2.1). These traits describe adult quality (LFS, RLS, AFB), juvenile quality (DP, INC, FLE, EMR, OV), the investment in offspring (FEC, CS, PRO, PEP), iteroparity (BV), and body mass (BM). Correlation between life history traits and BM were always <0.7 except for egg mass. We found information of the 14 life history traits for >6700 species (full life history dataset;

Table 2.1: Life history traits considered in the present study. Sample size is the number of species for which information is available.

Trait	Abbreviation	Definition	Sample size
Maximum lifespan	LFS	Maximum recorded lifespan	1583
Maximum reproductive lifespan	RLS	LFS - AFB	1088
Age at first breeding	AFB	Age at which individuals start reproducing	1205
Developmental period	DP	Period from egg laying to fledging (INC + FLE)	1907
Incubation	INC	Period from egg laying to hatching	2577
Fledging	FLE	Period from hatching until fledging	1980
Egg mass residual	EMR	Relative egg mass, estimated as a log-log phylogenetic regression of egg mass against body mass.	4074
Fecundity	FEC	CS multiplied by the number of broods per year	1633
Clutch size	CS	Number of eggs in a given clutch	6551
Productivity	PRO	Egg mass * fecundity / body mass	1582
Potential Egg Production	PEP	$PRO * RLS$	901
Brood value	BV	$\log_{10}\left(\frac{1}{broods \cdot RLS}\right)$	909
Offspring value	OV	$\log_{10}\left(\frac{1}{FEC \cdot RLS}\right)$	909
Body mass	BM	Weight	6462

see Table 2.1 for details), and complete information for 797 species (restricted life history dataset). All traits were log-transformed except BV, OV and EMR.

Restrictions in the life history traits space

With our life history dataset, we first investigated which portion of the dimensional trait space is occupied by birds. We restricted this analysis to nine life history traits (LFS, EMR, BM, DP, FLE, AFB, CS, FEC, BV), to avoid redundancies and to reduce the computational cost, and used them to compute a nine-dimensional convex hull volume containing 95% of the observed combinations of the traits to control for outliers (Díaz et al., 2016). The volume of the hull was compared with mean hypervolumes generated from 4 null models randomised 999 times (Hv_{nm} hereafter), following Díaz et al. (2016). Hypervolumes in Hv_{nm1} to Hv_{nm3} assume that the traits vary independently. Null model 1 assumes that any combination of trait values can exist with equal probability, each trait having a uniform distribution approximating an hypercube. Null model 2 assumes that extreme trait values

are selected against during evolution and each trait has a normal distribution, with Hv_{nm2} approximating an hypersphere. Null model 3 imposes no assumptions about trait distributions but instead allows each trait to be distributed as observed and assumes traits are independent of each other. Null model 4 assumes that extreme values are selected against (i.e., normally distributed) and maintains the observed correlation structure among traits. Relative to null models 1 to 3, null model 4 collapses the multidimensional trait-space occupied by birds (Hv_{nm4}) into an elongated hyperellipsoid.

Identifying the life history traits that best describe the fast-slow continuum

We used the COMADRE Matrix Database Version 4.20.11.0 (Salguero-Gómez et al., 2016a) to obtain age-structured population models that incorporate accurate information on the rates of survival, growth, and reproduction for 174 bird populations belonging to 78 species (demographic dataset, hereafter). For each species we selected population matrices from wild, unmanipulated populations with complete data instead of pooled from different populations if available ($n = 42$). See figure 2.1 to compare the distribution of the life history traits using the restricted dataset and the subset with demographic data from the population matrices.

From each population matrix model, we calculated 2 demographic traits (Caswell, 2001; Stubben and Milligan, 2007): generation time and elasticity to the fecundity. The elasticity matrices show the proportional effects on population growth rate for each demographic trait (de Kroon et al., 2000). We selected elasticities to the fecundity and to adult survival as a measure of the importance of these components on the life history strategies. However, both elasticities were strongly correlated (correlation coefficient = -0.63) and we only used the elasticities to the fecundity.

To assess how well life history traits correlate with the estimated demographic traits, we used the 14 life history traits previously described (Table 2.1), which were available for the 30 species. The estimated elasticities and generation times were modelled as a function of life history traits by means of phylogenetic least square regressions (with Pagel's λ estimated by means of maximum likelihood), as implemented in the R package "phylolm" (Ho and Ané, 2014). The traits were tested alone and combined with other traits by means of phylogenetic principal component analysis (PPCA), with maximum likelihood estimates of λ , as implemented in "phytools" (Revell, 2009). The phylogenetic analyses were run with two consensus trees from Jetz et al. (2012), one for the Ericsson and one for the Hackett backbones. The PPCAs were obtained using the restricted life history dataset ($n = 797$). We assembled all combinations of traits with the only rule that a PPCA should include at least a trait related to adult quality, juvenile quality and the number of offspring. A total of 10080 combinations of traits were used in the PPCAs, from which 2464 were discarded due to unsatisfactory convergence, resulting in 7616 trait combinations with a proper PPCA. For each PPCA, we selected the Principal Component (PC) that better matched the demographic

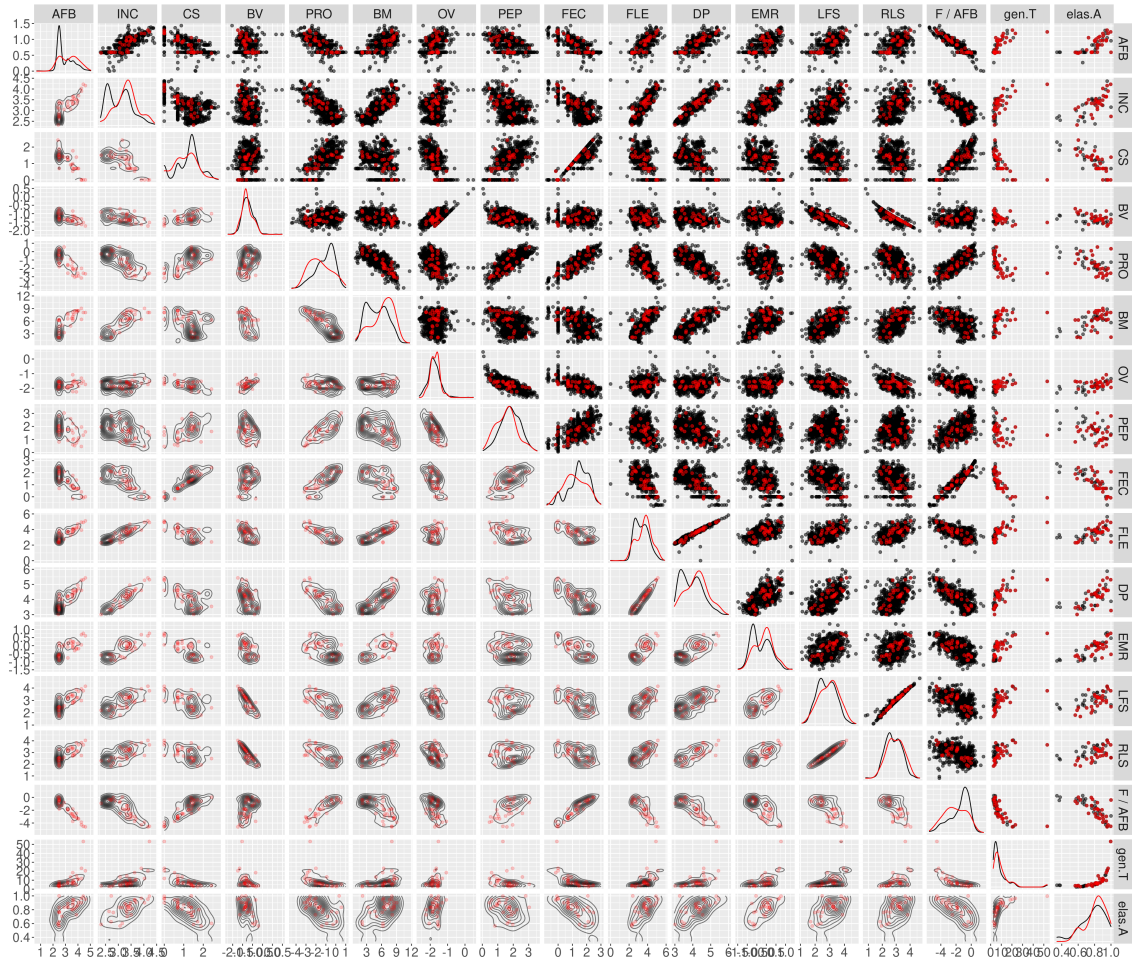


FIGURE 2.1: Biplots (upper triangle) and density plots (lower triangle) of the traits. Black for species with either demographic or traits data and red dots for species with both demographic (gen.T for generation time and elas.A for elasticities to the fecundity) and life history traits data (see table 2.1 for details).

traits ($\Delta AIC = 0$) and flipped the axis when needed, multiplying the PC scores and loadings by -1 in order to sort the species from fast (negative values) to slow (positive values).

From all the studied traits, whether alone or combined in a PC, we considered those that better explain variation in elasticities or generation time as corresponding to the fast-slow axis. We tested their relative importance by estimating the AIC based weight of each regression, considering the best models as those with 2 units difference from the model with the lowest AIC ($\Delta AIC < 2$).

Defining species position on the fast-slow axes

Because we found that the combination of some life history traits accurately predicted variation in elasticities and/or generation time, we used these traits to estimate the position in the fast-slow continuum of species for which demographic data were unavailable. We defined the position of the species in the fast-slow axis as the mean scores of the PCs weighted by the AIC based weights of the

elasticity models (FSe) and generation time models (FSgt). We did the same using all selected PCs and using only the PCs of the best models only ($\Delta AIC < 2$).

Our finding that to accurately predict elasticities and/or generation time you only need a few life history traits, not all of them, opens the possibility to assess the position in the fast-slow continuum for many more species than those with full information on the 14 key life history traits. Therefore, we repeated each of the PPCAs identified as best predictors of elasticities and generation time in the previous analyses, but now including all the species for which information on the underlying life history traits was available, regardless that other traits were missing. As before, we defined their position as the mean scores of best PCs weighted by the AIC based weights of the elasticity and generation time models (FSe and FSgt).

Our extrapolations to estimate the fast-slow axes assumes that the studied subsets of species are representative of the observed variation in the fast-slow continuum. This assumption is supported by two analyses. First, the phylogenetically corrected correlation (Revell, 2009) of the relevant PCs estimated with the demographic, restricted and full life history datasets was >0.99 in all cases. Second, the mean values of each PC estimated for our subsets of species (i.e. the demographic and restricted datasets) do not significantly differ from those expected by randomly sampling the same number of species from the full life history dataset.

Other axes of life history variation

We analysed the remaining 9500 (from 9385 to 9604 depending on the life history dataset and phylogeny) significant PCs (eigenvalue >1) not selected as components of the fast-slow axes to explore potentially different axes of variation. To identify relevant axes, we used the correlation among the scores of the PCs to build clusters using different minimum absolute correlations (0.7 – 0.9), discarding clusters containing less than 5% of the PCs and removing duplicated clusters in different correlation thresholds. Every cluster represents a potential axis of life history variation. We grouped clusters with a correlation on averaged loadings >0.95 for visualisation purposes.

Characterisation of the life history axes

For the fast-slow and rest of life history axes, we calculated the mean and the standard deviation of the loadings and the relative frequency of the traits for the corresponding PPCAs, assuming that the loadings of missing traits in a PPCA is 0. As the frequencies of the traits were not the same for each cluster, we also estimated the relative weight of each trait as:

$$Relative\ weight = \frac{|L|}{\sum |L|} - \frac{Freq}{\sum Freq}$$

Where L is a vector with the mean loadings of each trait and $Freq$ is a vector with the number of PPCAs from the cluster that contain the trait. The relative weight of the traits ranges from -1 to 1, where negative values means that the absolute

value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait. For the fast-slow axes, we weighted the former metrics by the AIC based weight from all the models and also including only the best models.

For each axis defined, we averaged the scores of each species to generate a data base of life history for birds. Again, for the fast-slow axes we weighted the PCs scores by the AIC based weight for all models and also using the scores of the PCs selected in the best models only ($\Delta AIC < 2$). The averaged scores of the fast-slow axes were then used to predict elasticities to the fecundity and generation time to compare the performance against the scores of single PCs.

2.3 Results

The observed hypervolume based on the nine non-redundant life history traits is much smaller than the hypervolumes predicted by the null models (p-value = 0.001, see table 2.2). The closest null model, Hv_{nm4} , is the one that imposes a correlation among traits as observed but is still seven times larger than the hypervolume of the observed data. The smaller size and aggregation in the hypervolume indicate that not all trait combinations are possible, consistent with the existence of constraints and trade-offs in life history evolution. The observed aggregation of species is greater for the observed traits than the expected for each Hv_{nm} (table 2.2). Thus, the existing diversity of life history strategies seems restricted to certain combinations of correlated traits and shows a greater concentration in the trait space than expected under multivariate normality.

From the 7631 trait combinations, including single traits, the selected PCs scores from the PPCAs combining sets of traits, and other metrics used to describe the fast-slow continuum in the literature, 104 were among the ones that better predict elasticities to the fecundity ($\Delta AIC < 2$), while for predicting generation time 468 trait combinations were among the bests. All the best predictors involve combinations of three or more life history traits (5.9 ± 1.3 traits for fecundity elasticities and 6.2 ± 1.3 for generation time) except for the single trait CL that alone is also part of the best predictors for the elasticity to the fecundity. The

Table 2.2: Observed vs expected hypervolume based on nine non-redundant life history traits. N10 and N50 are the minimum number of cells within nine-trait multivariate space (divided in 10^6 cells) needed to respectively cover 10% (N10) or 50% (N50) of the observed hypervolume (Hv_{obs}) based on four different null-model hypervolumes simulated by means of 999 permutations. See main text for details.

Hypervolume	N10	N50	Volume
Hv_{obs}	9	71	4.3
Hv_{nm1}	131	354	1030450
Hv_{nm2}	131	397	10808.4
Hv_{nm3}	131	394	8187
Hv_{nm4}	131	312	30.6

adjusted R^2 indicates the PCs explain $55\% \pm 0.008$ of the elasticities to the fecundity and $48\% \pm 0.008$ for generation time (see also table A.2.1).

Although single traits are often used as surrogate for the fast-slow axis, only CL appears among the best models for elasticity to the fecundity ($\Delta AIC = 0.6$) and no single trait for generation time (see FS_modelSelection.xlsx in the ESM). The ratio FEC / AFB, which has also been suggested to accurately describe the fast-slow axis (Oli, 2004), is not among the best traits, alone or in combination, that better explains adult survival elasticities ($\Delta AIC = 85.6$) nor generation time ($\Delta AIC = 10.2$).

Figure 2.2 shows the loadings of each life history trait in the best fast-slow axes, for both elasticities and generation time. In both cases, the life history traits with higher and consistent weights include CS and AFB. However, there are two main differences. First, INC is more influential for the axis based on generation time than for those based on elasticities. Second, FEC seems more important for PCs selected to predict generation time. Traits in selected PCs are less consistently associated with the axes (see SD bars in figure 2.2). Other traits commonly included in the fast-slow axis such as LFS or BM seems unrelated to the fast-slow axes defined by our methodology.

One advantage of combining all PPCA in single weighted-average axes is that it allows to estimate the position of a species in the fast-slow axis even when some scores cannot be estimated due to missing data. We thus estimated the fast-slow continuum for all the species from the the extended dataset with information on the relevant life history traits (i.e. up to 1516 species). The PCs representing the fast-slow continuum explains around 30% of the variation in life history traits (0.35 ± 0.07 for FSgt, 0.34 ± 0.06 for FSgt best AIC, 0.35 ± 0.07 for FSe and 0.29 ± 0.05 for FSe best AIC), highlighting that this is a main axis of life history variation. The two estimated fast-slow axes (FSe and FSgt) are correlated with each other (phylogenetic correlation = 0.85 and 0.74 for all or models with $\Delta AIC < 2$ only). Both fast-slow axes are only weakly correlated with body mass (phylogenetic correlations = 0.34 for the axes averaging PC scores with $\Delta AIC < 2$ and 0.5 for axes averaging all PCs). The difference on the correlation between FSgt and FSe when includes all or only the best PCs, suggest that BM decrease the accuracy of the PCs on predicting generation time or the elasticity to the fecundity. In fact, there is zero PPCA containing BM among the best models for FSe and only 3 from 487 for FSgt. The correlation among other axes than FS, is quite low except for the lifelong productivity axis and FSgt (-0.76) and for the lifelong productivity axis and iteroparity axes (mean correlation 0.76 ± 0.11). See table A.2.8 for detailed correlations among axes and traits.

However, substantial variation still remains to be explained. To explore this variation, we extracted all the PCs with Eigenvalue > 1 (Kaiser-Guttman criterion) among the PCs not selected as descriptors of the fast-slow continuum, and classified them in groups based on a cluster analyses of the species scores (figure 2.3). These clusters classify together PCs that represent similar life history axes, which may then be interpreted by examining the loadings of their traits. The averaged loadings of these groups suggest at least three axes of life history variation that are independent of the fast-slow continuum.

The most important one in terms of variance explained ($37 \pm 0.09\%$, see table

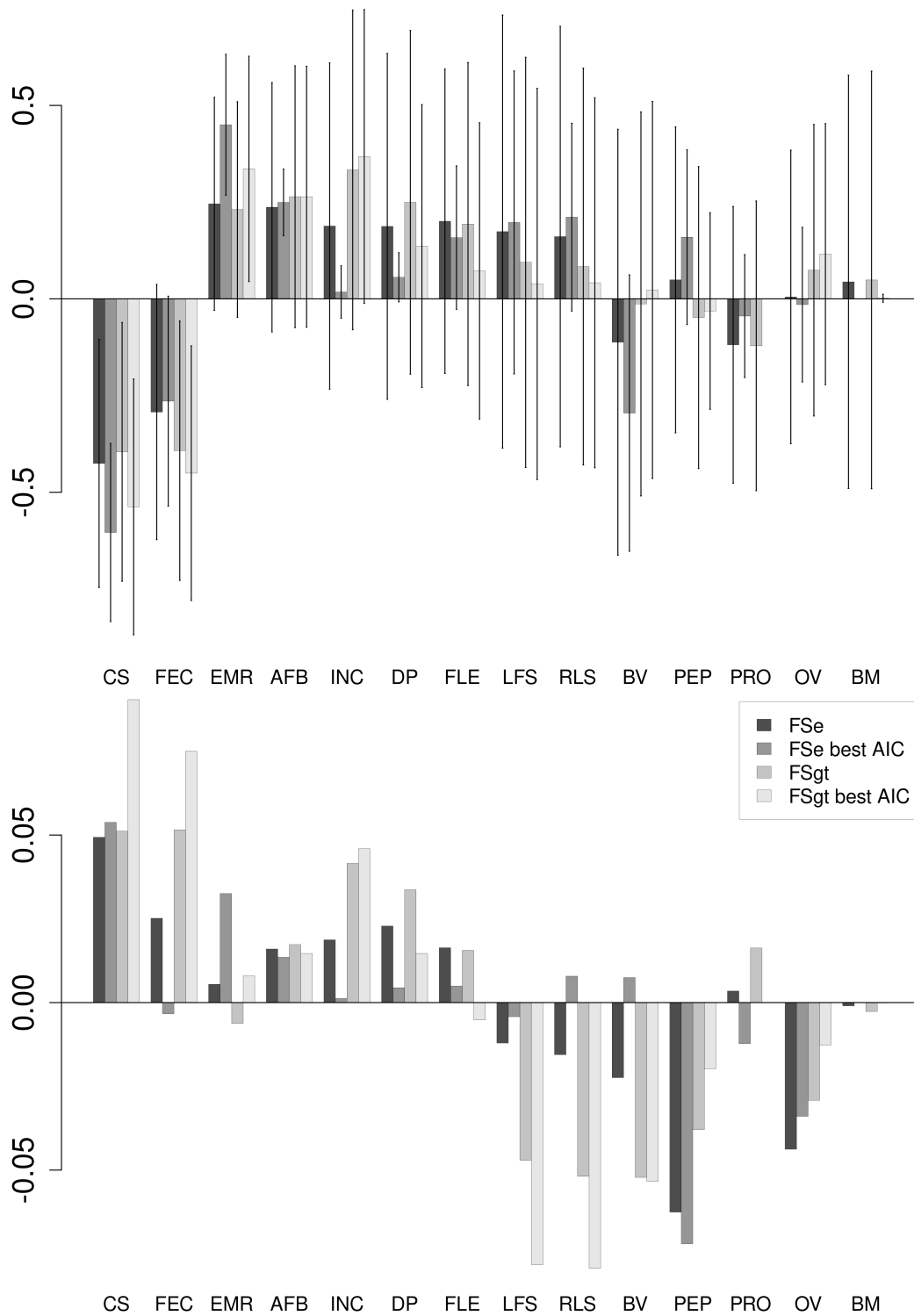


FIGURE 2.2: Importance of the traits describing the fast-slow continuum. Top panel: Loadings mean \pm standard deviation of the selected PCs combining sets of life history traits that better describe the fast-slow axis. Bottom panel: Relative weight of the life history traits in the fast-slow continuum. Values range from -1 to 1, where negative values means that the absolute value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait in the selected PPCAs (see main text for details). The loadings and frequencies come from the selected PCs that better predict elasticities to the fecundity (FSe) or generation time (FSgt), weighted by the AIC based weight of the models taking all or only the models with $\Delta AIC < 2$ (best AIC).

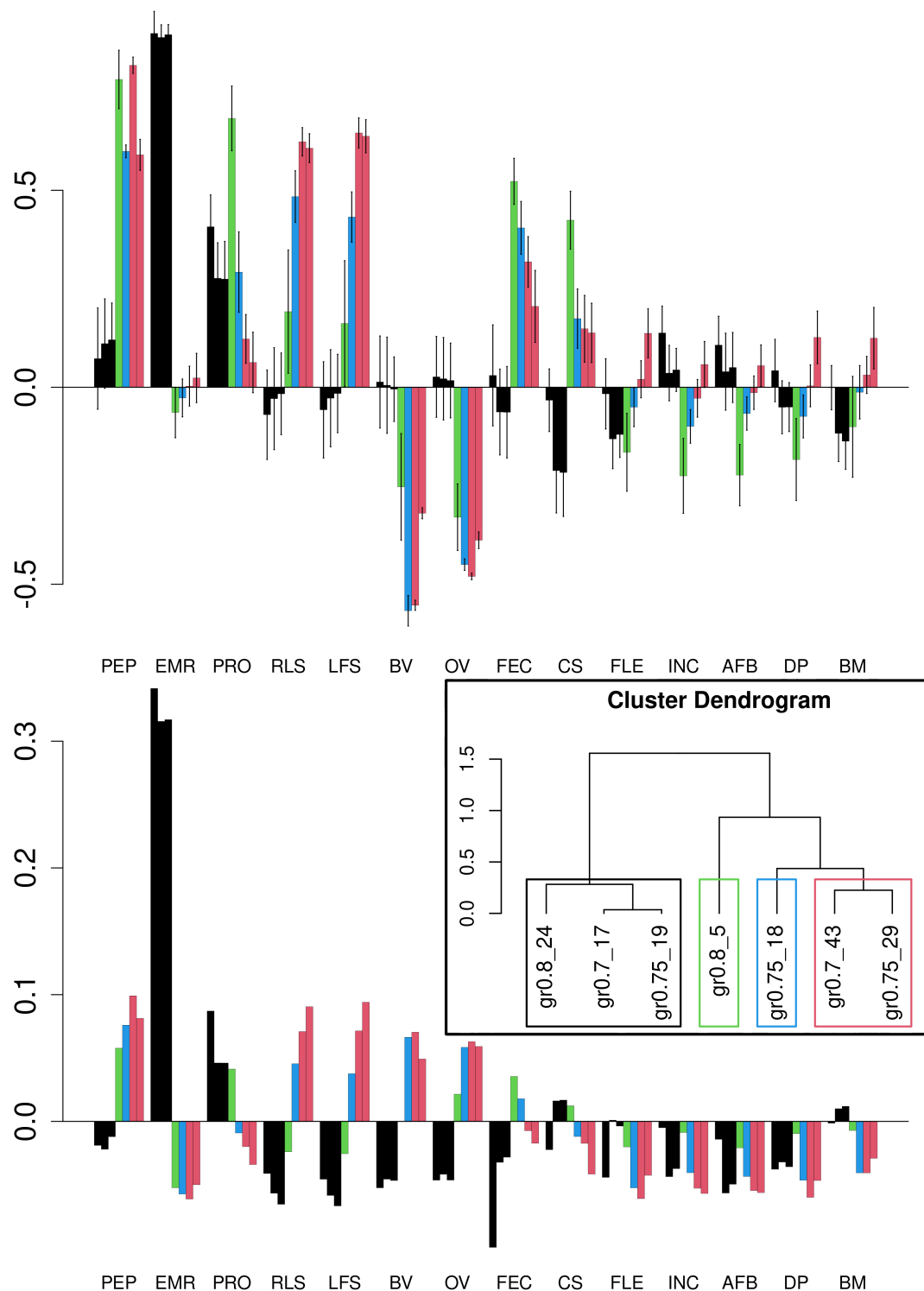


FIGURE 2.3: Importance of the traits for clusters of similar significant PCs not selected for the fast-slow axes. Each group contains PCs with scores correlation greater than the correlation specified in the group name in the inset dendrogram (e.g. gr0.8 means correlation >0.8). Boxes include clusters with a correlation among averaged loadings >0.95 and can be conceptualized as a offspring quality-quantity trade-off in black, lifelong productivity in green and iteroparity in blue and red. Top panel: Loadings mean \pm standard deviation for the traits of each group of PCs. Bottom panel: Relative weight of the life history for each group of PCs (see figure 2.2 for details).

A.2.4 for the variance explained by each cluster, number of traits and number of PCs) is related to the degree of iteroparity (gr0.75_18, gr0.7_43 and gr0.75_29 in figure 2.3), quantified as the brood value index (Bókony et al., 2009), which represents whether reproductive effort is allocated into a few reproductive events (i.e. high brood value as each brood has high contribution to fitness) or instead the effort is distributed into many attempts (low brood value), whether in a same breeding season or in different ones. Brood value is highly correlated with RLS (-0.89), LFS (-0.87), OV (0.92) and PEP (-0.8), thus they often appear loading together on the same PCs. Another life history axis that consistently appears in the analyses is the offspring quality-quantity trade-off (gr0.8_24, gr0.7_17 and gr0.75_19 in figure 2.3), with species laying few eggs yet relatively large at one extreme and species laying many eggs of small size at the other extreme. The PCs in this group explains 0.15 ± 0.02 % of the variance and the main trait in this axis is EMR, followed by PRO and CS. The third axes, gr0.8_5 in figure 2.3 is related to PEP, PRO, FEC and OV and reflects the lifelong productivity of the species in terms of offspring number and egg mass produced relative to body size.

The axes described appears consistently regardless of the phylogeny and dataset used (see tables A.2.2, A.2.3, A.2.5, A.2.6 and figures A.2.1, A.2.2, A.2.3, A.2.4, A.2.5 for the details of the extended dataset and Ericson backbone based phylogeny). Most of the described axes exhibit high phylogenetic signal (Pagel's $\lambda > 0.9$) except for the axes from the iteroparity group with Pagel's $\lambda = 0.66 \pm 0.09$ and the lifelong productivity group with Pagel's $\lambda = 0.89 \pm 0.01$ (see table A.2.7 for details).

2.4 Discussion

Our finding that not all combinations of life history traits are possible is at first sight unsurprising, given the existence of overwhelming evidence of life history trade-offs and constraints. Demonstrating it is however important because our empirical evidence is based on an unusually large and representative sample of species. We therefore can largely exclude the possibility that the observed pattern results from sampling biases.

The Fast-Slow continuum emerged as a major axis structuring life history variation in birds, confirming and generalising previous studies (Sæther, 1987; Gaillard et al., 1989; Sæther and Bakke, 2000; Jeschke and Kokko, 2009). Our empirically-derived estimates of the fast-slow continuum reflect well the fecundity-survival trade-off, are strongly correlated among each other and are largely independent of body size. Although a variety of life history traits contribute to define the continuum, CS, FEC and AFB appear particularly relevant in line with some previous suggestions (Stearns, 1983; Sæther, 1987; Gaillard et al., 1989; Oli, 2004; Dobson and Oli, 2007; Jeschke and Kokko, 2009). However, these life history traits are not good surrogates of the continuum when alone, but only when combined with other life history traits.

Although the fast-slow continuum is widely considered the most important axis of life history variation, growing evidence suggest the existence of other relevant axes (Stearns, 1983; Read and Harvey, 1989; Gaillard et al., 1989; Promis-

low and Harvey, 1990; Dobson and Oli, 2007; Bielby et al., 2007). By accurately quantifying the fast-slow continuum, we could investigate the remaining axes of life history variation. Our analyses identified an important axis of variation related to the timing of reproductive bouts. This axis, the so-called brood value (Bókony et al., 2009) or semelparity-iteroparity (Gaillard et al., 1989), represents the extent to which all reproductive effort is allocated into a few reproductive events (i.e. high brood value) or instead the effort is distributed into many attempts (low brood value), whether in a same breeding season or in different ones. Many species in our dataset only breed once per year, therefore the brood value is highly correlated with the reproductive lifespan and this explain why both often load together on the same PC. However, a low brood value may also be achieved by reproducing multiple times during a same breeding season, a strategy that is used by some pigeons and starlings.

Other previously suggested life history axis that appear consistently in mammals once the fast-slow continuum is factored out is related to the trade-off between offspring quantity and quality (Promislow and Harvey, 1990; Bielby et al., 2007; Dobson and Oli, 2007). We found a similar axis in birds, but clutch size weight is not as important as the relative egg mass, perhaps because PPCA impose the orthogonality among PCs and the fast-slow axis already includes part of the variance in clutch size. Another explanation may be that the offspring quality-quantity trade-off in birds is embedded in the fast-slow axes, as found by Jeschke and Kokko (2009), with fast lived species investing in many and low quality offspring while slow species invest in few but high quality offspring. Although our results suggest that this axis is largely independent of the fast-slow continuum, we note that egg mass residual and offspring development duration also have some weight in the fast-slow axis.

Much of the ecological relevance of the fast-slow continuum resides in its influence on population dynamics under challenging conditions, an issue particularly relevant in the current context of global environmental change (Ricklefs and Wikelski, 2002; Forcada et al., 2008; Réale et al., 2010; Sol et al., 2018; Maspons et al., 2019). Species at the fast extreme have a higher potential to rapid population grow than those at the slow extreme, which may facilitate recovering from a population crash. When population size is low, however, they also tend to be more susceptible to populations fluctuations associated with demographic stochasticity. The relevance of these mechanisms can only be investigated by properly defining and accurately quantifying the fast-slow continuum based on the entire life cycle.

Moreover, the influence of other life history axes needs also to be considered. A low brood value has been suggested to favour geometric population growth under environmental stochasticity through mechanisms such as bet-hedging (Stearns, 2000a) and the storage effect (Cubaynes et al., 2011). The finding that brood value and the fast-slow continuum are different life history axes but share critical life history traits opens the possibility to life history strategies that facilitate a rapid population growth when conditions are favourable and reduce the costs of a reproductive failure when conditions are unfavourable. For example, brood value seems a significant trait to adapt to new environments in introduced species or species colonising urban habitats (Sol et al., 2012b, 2014).

Despite having solid foundations, life history theory has surprisingly achieved

little success in predicting the response of organisms to rapid human-induced environmental alterations such as habitat loss, climate change and biological invasions. This is paradoxical considering that some proposed mechanisms were proposed more than 50 years ago. A more integrative and mechanistic view of life history variation can contribute to develop a more predictive body of theory regarding how life history and the possible interactions with behaviour (Ricklefs and Wikelski, 2002; Réale et al., 2010; Sol et al., 2018; Maspons et al., 2019) affects the response to environmental changes. The provided axes of life history variation can open further studies to elucidate the links between environmental condition and the evolution of life history strategies.

Electronic Supplementary Material

Scores for all described axes and the results of the models to select the best PCs describing the fast-slow axes are available online at <https://github.com/jmaspons/Thesis/tree/master/ESM/chapter02>.

Abstract

Understanding what affects population growth in novel environments is fundamental to forecast organisms' responses to global change, including biological invasions and land use intensification. Novel environments are challenging because they can cause maladaptation, increasing the risk of extinction by negative population growth. Animals can avoid extinction by improving the phenotype–environment match through behavioural responses, notably matching habitat choice and learning. However, the demographic consequences of these responses remain insufficiently understood in part because they have not been analysed within a life-history context. By means of an individual-based model, we show here that matching habitat choice and learning interact with life history to influence persistence in novel environments. In maladaptive contexts, the likelihood of persisting is higher for life-history strategies that increase the value of adults over the value of offspring, even at the cost of decreasing reproduction. Such a strategy facilitates persistence in novel environments by reducing the costs of a reproductive failure while increasing the benefits of behavioural responses. Our results reinforce the view that a more predictive theory for extinction risk under rapid environmental changes requires considering behavioural responses and life history as part of a common adaptive strategy to cope with environmental changes. This article is part of the theme issue “Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation”.

Keywords: Biological invasions, Extinction risk, Demographic stochasticity, Cognitive ecology, Habitat selection, Urbanization

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3.1 Introduction

Most organisms experience serious difficulties when exposed to novel environments. Novel contexts often generate mismatches between the phenotype and the environment, leading to maladaptation and extinction through negative population growth (Bell, 2017). Maladaptation is one of the reasons why translocations of species from their native ranges to novel environments generally fail to establish self-sustaining populations (Sol and Maspons, 2016; Sakai et al., 2001), and it is also a primary cause of extinction by land use intensification (Sih et al., 2011). Given that biotic exchanges and land use intensification are becoming increasingly frequent as a result of human activities, there is an urgent need to understand the mechanisms that influence population persistence in novel environments.

Several processes can allow organisms to improve the matching of their phenotypes to new contexts and hence facilitate persistence in novel environments. Natural selection—the most obvious process—can contribute to reconstitute the phenotype–environment match through genetic changes, a process known as evolutionary rescue (Bell, 2017). However, an evolutionary rescue is less effective in animals with long generation time, such as many birds and mammals, which exhibit slow evolutionary responses to selection. In these animals, behavioural responses are an alternative to reduce the phenotype–environment mismatch (Sih et al., 2011; Klopfer, 1981; Sol, 2003; Tuomainen and Candolin, 2011; Kokko and Sutherland, 2001). Individuals may, for instance, improve fitness in novel environments by choosing the habitats where they live and reproduce that best fit their phenotype, a process known as matching habitat choice (Nicolaus and Edelaar, 2018; Stamps and Swaisgood, 2007; Greene and Stamps, 2001; Schmidt et al., 2010). Animals can also decide when is best to reproduce, and skip reproduction when conditions are unfavourable (Williams, 1966).

The choice of where and when to live and reproduce can express activational plasticity, that is, an innate response to environmental cues (Snell-Rood, 2013; Sol et al., 2013*b*). In a novel environment, however, individuals must often take decisions with insufficient information and using cues that may have changed relative to those from the old environment, which can lead them to settle in poor-quality habitats (ecological traps) (Kokko and Sutherland, 2001). Yet, animals can improve decision-making, and hence avoid extinction, through learning (Grieco et al., 2002; Kawecki, 2010). Learning can modify decision-making based on previous experiences of the individual (Baudains and Lloyd, 2007; Eliassen et al., 2007)—for example, changing habitat after a reproductive failure—or by using public information generated by more experienced conspecific or heterospecifics (Doligez et al., 2002). Evidence is accumulating that species which readily adjust behaviours to novel contexts are better able to survive and reproduce in a novel environment than species that persist with the behaviours of their old environments (Kawecki, 2010; Dukas, 2008).

While the importance of behaviour in the response to environmental changes is widely recognized, we still lack a general theory regarding how such processes influence population growth in novel environments (Sol and Maspons, 2016). One important reason is that behavioural responses have rarely been investigated within a life-history context (Sol and Maspons, 2016; Ricklefs, 2004). Life

history—defined as the way organisms distribute their limited time and energy into growth, reproduction and survival (Stearns, 1992)—is relevant because it affects how populations increase and fluctuate over time. The demography of the organism is particularly influenced by its position in the fast–slow continuum of life-history variation (Stearns, 1983). Species at the fast side of the continuum have short life expectancy but mature early and show high fecundity, which give them a high potential for rapid population growth under favourable conditions. Growing fast may confer advantages during the invasion of novel environments by reducing the period that the population remains small and hence vulnerable to extinction by demographic stochasticity. Species at the slow side of the continuum have delayed maturity and low fecundity, and hence cannot increase in number so fast when the population is small. Yet, their long life expectancy (and long generation time) buffers their populations from fluctuations driven by demographic and environmental stochasticity that can lead to extinction (Sæther et al., 2013, 2004). A slow strategy also reduces the fitness costs of a reproductive failure, as individuals have higher chances of breeding again in the future. This offers advantages in novel environments by spreading the risk of reproductive failure over several breeding attempts (a type of bet-hedging) and by allowing individuals to skip a reproductive event (and hence improve their survival) when conditions are unfavourable (Sol et al., 2012*b*).

Thus, when we analyse how behavioural responses affect the demography of animals in novel, stochastic environments, we need to be aware that these responses will be affected by the organism's life history. This is relevant because the position of the animal in the fast–slow continuum can alter the benefits and costs of gathering environmental information and constructing appropriate behavioural responses (Forcada et al., 2008; Sæther and Bakke, 2000; Lewontin and Cohen, 1969; Sæther et al., 2005; Starrfelt and Kokko, 2012). The net benefit should generally be higher in slow animals, which are less constrained by time to explore and learn, and can use the learned behaviours for longer periods. The costs of delaying reproduction when conditions are unfavourable should also decrease in slow species, as individuals can reproduce again in the future, increasing the opportunities for acquiring environmental information and, through learning, improve the match of the phenotype to the novel conditions (Sol et al., 2012*b*). The demographic consequences of behavioural responses in novel, stochastic environments are also expected to vary depending on whether the phenotype–environment mismatch mainly affects offspring or adult survival. This is because fast and slow strategies differ in their sensitivity to changes in the demographic parameters, with fast strategies being highly sensitive to changes in fecundity and slow strategies to changes in adult survival (Gaillard et al., 2000). Thus, understanding how behavioural responses contribute to population persistence in novel, stochastic environments requires us to consider the position of the animal in the fast–slow continuum (Sol and Maspons, 2016).

While the demographic consequences of behaviour have been previously modelled by several authors (Kokko and Sutherland, 2001; Cressman and Křivan, 2013; Kisdi, 2002; Kawecki, 1995; Strasser et al., 2012), it remains to be seen to what extent behavioural responses influence population growth in novel, stochastic environments as a function of the position of the animal in the fast–slow contin-

uum. Here, we use an individual-based simulation model to address this issue. The behavioural responses that we investigate include innate preferences for habitats that better matches the organism's phenotype, learning rules to reduce the preference for inadequate habitats and decisions about skipping a reproductive event when individuals stay in a habitat that does not match their phenotype. We use the model to illustrate how considering life-history variation refines predictions of classic theory regarding the role of behaviour in facilitating population persistence in novel environments.

3.2 Model description

Building on previous studies (Cressman and Křivan, 2013; Kawecki, 1995), we envision a species that is introduced in a novel region with two habitats. Individuals are allowed to survive, reproduce and move between habitats, and the likelihood that the population persists in the novel region (establishment success) is estimated through simulations (figure A.3.2.1). Establishment success is estimated through a stage-structured population-based model (which allows us to compare the outcome for species differing in life history), in scenarios varying in the degree of phenotype–environment mismatch (causing negative population growth) and demographic stochasticity (causing extinction by demographic accidents). The introduced species has a particular life-history strategy that positions it along the fast–slow continuum, fixing the values of its onset of first reproduction, average fecundity and age-specific survival of individuals (see details below). Behavioural responses are studied by assessing how modifying the probabilities of changing habitat and skipping reproduction affects establishment success. Below, we briefly summarize the main features of the model. For further details about specific parts of the model and about its inner workings, we refer the reader to the electronic supplementary material. The model was built using the R language (R Core Team, 2018), and an accompanying R package implementing the model, with its corresponding tutorial, is also offered as the electronic supplementary material at <https://dx.doi.org/10.6084/m9.figshare.c.4546955>.

a) Stage-classified population

We chose a stage-classification approach to account for the complex life cycle of our simulated populations. Based on pre-breeding census, we classify the population into three individual classes: juveniles, subadults (only for strategies with age at first reproduction greater than 1 year) and adults. In turn, adults are divided into non-breeder (i.e. adults that decide not to breed in a given year) and breeders. Finally, breeding individuals are split at each brooding step into successful or failed breeders, distinguishing whether breeding yields viable juveniles or not, respectively. Only females are considered.

b) Demographic model set-up

Our population model includes the main processes that must be considered when evaluating the life cycle of a stage-classified population, namely survival, growth and reproduction (table 3.1):

- (i) *survival*: each stage-class (juveniles, subadults, non-breeding adults and breeding adults) is defined by an annual survival rate. In addition, juvenile survival is decomposed into individual survival and brood survival, the latter affecting all individuals in the same brood (e.g. as a result of nest predation). Data about the sources of juvenile mortality are scarce, and hence, we fixed the brood level mortality to account for 50% of the juvenile mortality;
- (ii) *growth*: individuals can be promoted to the next stage if they survive to the next year. Individuals only remain 1 year in the juvenile class, after which they move up to the subadult or adult class. After they reach adulthood, they remain in that condition until they die; and
- (iii) *reproduction*: each year, the algorithm determines which proportion of adults becomes non-breeders or breeders, and also which proportion of the latter may successfully breed. Only adults that are classified at each step as breeders can reproduce during a year.

c) Implementation of the demographic model

Each simulation starts with the introduction of a particular number of adults with an evolved life-history strategy along the fast–slow continuum. This cohort of adults is equally distributed between both habitats (labelled h). After the introduction phase, the growth of the population from year t to $t + 1$ is determined by the number of births and deaths within each habitat. The cohort of adults in each habitat is first divided into non-breeder and breeder adults with a probability p_h^b . Then the model enters the breeding phase, which consists of a loop within which m breeding episodes take place. At each step within that loop, breeder adults are randomly split between failed and successful breeders (p_h^{bf}), and only the latter give rise to viable juveniles. The number of juveniles per successful breeding attempt is the product of the clutch size (q) and probability for a juvenile to survive (p_{h,s_j}). After each reproductive event, breeders (failed or successful) may change habitat with a probability $p_{1 \rightarrow 2}^x$ (if they move from habitat 1 to habitat 2) or $p_{2 \rightarrow 1}^x$ (if they move from habitat 2 to habitat 1), with $p_{1 \rightarrow 2}^x = 1 - p_{2 \rightarrow 1}^x$. Once the breeding loop has finished, non-breeder adults and subadults are allowed to change habitats and, finally, all individuals are promoted to the next class after their survival is evaluated (table 3.1).

d) Demographic stochasticity

Demographic stochasticity is implemented both in the survival probability of each age class and in the probability of a brood failure (table 3.1) by means of

Table 3.1: Notation followed to describe the stochastic population model.

Symbol	Definition
q	Number of offsprings per brood in habitat h
m	Number of broods per year
n_{Sa}	Number of sub-adult stages
x	Labels for adult breeder type, $x = \{nb, b, b_s, b_f\}$. Label nb identifies adults that skip breeding and label b indicates adult individuals that try to breed. In turn, the latter can be divided into those which breed successfully (labelled b_s) or those which fail to do so (labelled b_f)
y	Labels for survival, $y = \{j, sa, nb, b\}$, where labels refer to juveniles, subadults, non-breeder and breeder adults, respectively
h	Index for habitat type, $h = \{1, 2\}$
r	Label for subadult stage, $r = \{r_1 \cdots r_{n_{Sa}}\}$
t	Subindex for time steps, measured in years, $t = \{1 \cdots 50\}$
p_h^b	Probability for an individual to become a breeder (successful or not) in habitat h
$p_h^{b_f}$	Probability of complete brood failure for a breeder in habitat h
p_{h,S_x}	Probability of survival in habitat h for individuals x
p_{h,S_y}	Probability of survival in habitat h for individuals of type S_y
$p_{1 \rightarrow 2}^x$ $p_{2 \rightarrow 1}^x$	Probability for an adult to move from habitat type 1 to 2, or vice versa
$p_{1 \rightarrow 2}^r$ $p_{2 \rightarrow 1}^r$	Probability for a stage- r subadult to move from habitat type 1 to 2, or vice versa

binomial distributions defined by each probability and population size, obtaining random deviates from the mean value. The number of individuals introduced defines the extent to which the population is exposed to demographic stochasticity. We consider population growth to be density-independent (i.e. we assume that during the establishment phase, the population is far from its carrying capacity) and little influenced by Allee effects (Kawecki, 1995).

e) Environmental scenarios to simulate maladaptation

The degree of match between the phenotype and the environment is modelled by varying the costs of selecting a habitat where the species can be viable but maladapted (Kisdi, 2002), defined by the following scenarios:

- (i) *high phenotype–environment match* , simulated by defining the two habitats as identical and without penalties (scenario 1). Therefore, fecundity and survival rates attain their maximum values, as defined by the species' life history;

- (ii) *insufficient phenotype–environment match penalizing adult survival* (p_{h,s_x}), simulated by imposing an increase in adult mortality of either 50% (scenario 2.1) or 100% (scenario 2.2) in habitat 2 (low-quality habitat, hereafter); and
- (iii) *insufficient phenotype–environment match penalizing offspring survival*, simulated by increasing the probability of a brood failure ($p_h^{b_f}$) by either 50% (scenario 3.1) or 100% (scenario 3.2) in habitat 2 (low-quality habitat).

f) Behavioural responses

To investigate how behavioural responses influence persistence in the different environmental scenarios, we first explore what happens when individuals are not allowed to take decisions (i.e. their behaviour is ‘neutral’). Thus, we assume that the probability of changing from one habitat to the other is the same ($p_{1 \rightarrow 2}^x$ and $p_{2 \rightarrow 1}^x = 0.25$) and all individuals reproduce after achieving adulthood ($p_h^b = 1$). To incorporate behavioural responses, we modify these parameters as follows:

- (i) *matching habitat choice* (abbreviated *GoodChoice*) is an innate preference for the habitat that better matches the organism’s phenotype (i.e. the high-quality habitat), which reduces either adult or offspring mortality depending on the environmental scenarios previously defined. To do so, the preference for habitat 1 is either doubled (moderate response) or quadrupled (strong response) in each simulation;
- (ii) *habitat mismatching choice* (*WrongChoice*) describes an innate preference for the habitat that does not match the organism’s phenotype (low-quality habitat), thereby increasing either adult or offspring mortality depending on the environmental scenario. Habitat mismatching choice simulates ecological traps (Kokko and Sutherland, 2001). To do so, $p_{1 \rightarrow 2}^x$ is either doubled (moderate response) or quadrupled (strong response) in each simulation;
- (iii) *reproductive skipping* (*ReprSkip*) refers to the decision about skipping or not a reproductive event when the individual is in the low-quality habitat. This simulates the storage effect (Warner and Chesson, 1985) by which adults improve survival by skipping reproduction when conditions are inadequate. To achieve it, the probability to breed in habitat 2 is reduced to either 0.5 (moderate response) or 0.25 (strong response) in each simulation. Non-breeding adults are given a 50% increase relative to breeding adults in the probability to survive from t to $t + 1$;
- (iv) *learning through exploration* (*LearnExpl*) refers to a decreased preference for the low-quality habitat after exploring any of the two habitats. This describes the process of gathering information to make more informed decisions (Eliassen et al., 2009). To do so, the preference for the high-quality habitat once the individual has explored the low-quality habitat is either doubled (moderate response) or quadrupled in each simulation (strong response), while the probability of moving from the best to the worse habitat ($p_{1 \rightarrow 2}^x$) is

set to zero, except for breeders that failed to reproduce. In this latter case, $p_{1 \rightarrow 2}^{b_f}$ is doubled or quadrupled; and

(v) *learning from a breeding experience (LearnBreed)* is the decision about changing habitat or not according to the result of the past breeding attempt. Regardless of the habitat, a reproductive failure in the habitat makes it more likely that individuals change the habitat in the next breeding attempt. Thus, $p_{1 \rightarrow 2}^x$ and $p_{2 \rightarrow 1}^x$ is 0 when the reproduction is successful (i.e. at least one offspring is produced), and the probability of shifting habitat in each simulation is either doubled (moderate response) or quadrupled (strong response) after a failed reproduction.

g) Simulations

The probability of persisting in the novel environment was estimated for different initial population sizes (N_0 from 2 to 100) as the proportion of populations that avoid extinction after 50 years, based on 10 000 replicates. This allowed us to describe the curves relating the likelihood of establishment with N_0 for each possible combination of life-history strategy, behavioural response and environmental scenario (see details below). As an integrative measure of the likelihood of population persistence, we used the initial population size that allows 50% of the populations to persist during the 50 years ($N_0P_{50\%}$). The value of each $N_0P_{50\%}$ was estimated through a lineal search testing different initial population size.

h) Exploration of the parameters

The exploration of the parameters was carried out by crossing all combinations of life-history traits with the behavioural responses and environmental scenarios. To obtain all combinations of life-history traits, we first defined regular sequences for each life-history trait within the ranges found in birds, based on published information (Sol et al., 2012b, 2018). The traits and ranges included adult survival (0.1–0.95), number of broods per year (1–2), number of offspring per brood (1–20) and age at first reproduction (1–4). For subadult stages, we used the same survival as for the adults. Next, we created all the possible combinations of life-history traits and fixed the deterministic growth rate λ from 1.05 to 1.2 by adjusting juvenile mortality rate, solving the Euler–Lotka equation (see the electronic supplementary material for details). Strategies with juvenile survival lower than 0.1 or higher than adult survival were discarded. The total number of life-history strategies resulting from the combination of life-history traits was 3612.

To evaluate the impact of these life-history strategies on the persistence of the populations in the novel environment, we first tested the sensitivity of $N_0P_{50\%}$ to λ , fecundity, age at first reproduction and age-specific survival by means of partial rank correlation coefficients (PRCC) (Saltelli et al., 2004). This method measures the association between two variables while accounting for the effect of other variables, and has the advantage of being little affected by collinearity and non-linear relationships. In addition, we also compared how $N_0P_{50\%}$ varies

between fast and slow strategies as a function of behavioural responses and maladaptive scenarios. The position of each life-history strategy along the fast–slow continuum was assessed as the relative sensitivity (i.e. elasticity) of population growth to changes in fecundity. Given that the fast–slow continuum describes a fecundity–survival trade-off (Stearns, 1992), any combination of life-history traits characterizing slow species should be related to high elasticities for adult survival and low elasticities for fecundity, the contrary being true for fast species. We classified life-history strategies as slow when their elasticities for fecundity were in the first quartile and as fast when their elasticities for fecundity were in the uppermost quartile (using elasticities for adult survival gives qualitatively similar results).

3.3 Results

a) Behavioural responses in stochastic, maladaptive scenarios

We first illustrate the results of the model by presenting the simulations for two species with the same maximum deterministic growth rate ($\lambda = 1.05$) but striking differences in life history, one being at the fast extreme of the fast–slow continuum and the other at the slow extreme. Figure 3.1 presents the simulated probability that these species thrive in a novel environment as a function of initial population size (N_0), according to different behavioural responses and scenarios of maladaptation (see also the electronic supplementary material, figure A.3.2.2). In all the scenarios, the likelihood of establishment increases with N_0 until reaching a threshold above which the probability of population persistence is 1 (i.e. all simulated populations become established). This pattern, which has also been found empirically (Blackburn et al., 2013; Sol et al., 2013a), reflects the pervasive effect of demographic stochasticity at small population sizes.

In the absence of behavioural responses (red line), the curve relating the probability of persistence and N_0 becomes flatter under maladaptation (figure 3.1, scenarios 2.1, 2.2, 3.1 and 3.2) relative to scenarios where there is phenotype–environment match. This is because the population not only suffers from demographic stochasticity but also from the negative population growth of the fraction of the population settled in the low-quality habitat. The new route towards extinction largely reduces population persistence, notably in scenarios where the phenotype–environment mismatch is higher (electronic supplementary material, figure A.3.2.2, scenarios 2.2. and 3.2).

When individuals are allowed to take decisions, either based on inherited or learned preferences, the probability of persistence experiences substantial changes relative to the situation where their behavioural responses are neutral (figure 3.1; electronic supplementary material, figure A.3.2.2). Matching habitat choice and learning both contribute substantially to increase the likelihood of persistence in a context of maladaptation. Learning is generally not so efficient as an innate choice based on perfect knowledge. When knowledge is imperfect, however, innate responses can increase extinction risk by leading individuals to choose an inappropriate habitat. Likewise, the decision of skipping a reproductive event

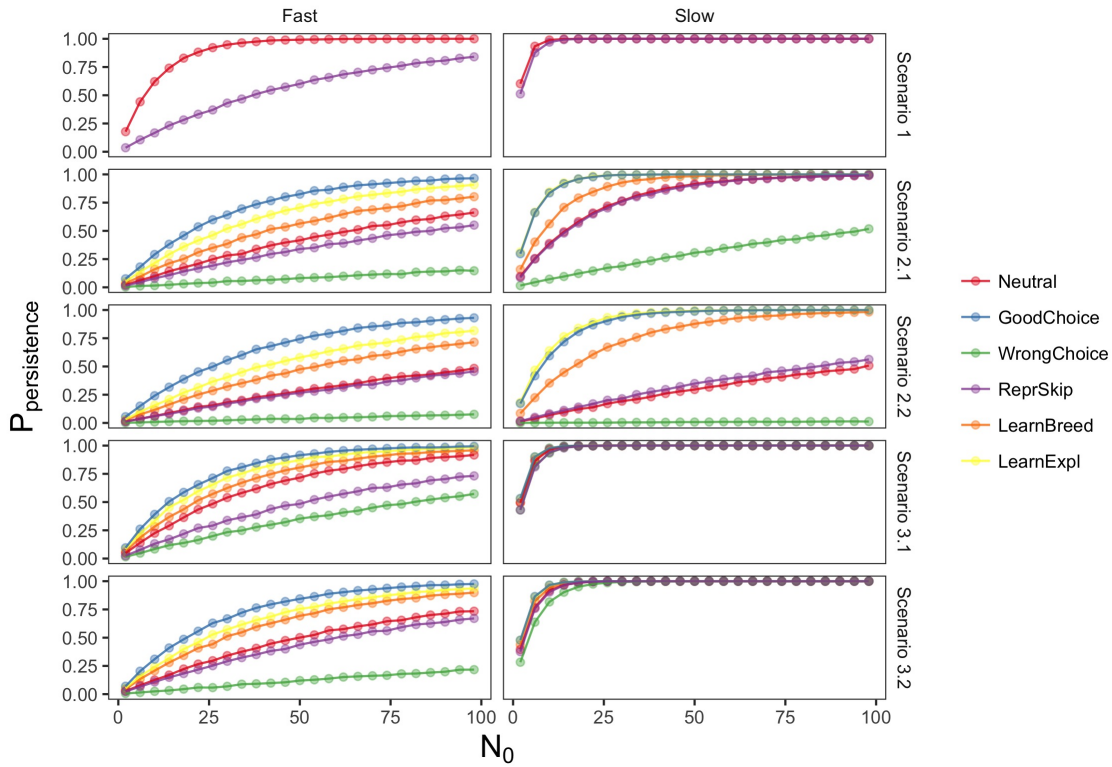


FIGURE 3.1: Simulations of probability of population persistence for 10 000 replicates as a function of behavioural responses (*Neutral*, random behavioural responses; *GoodChoice*, matching habitat choice; *BadChoice*, habitat mismatching choice; *ReprSkip*, reproductive skipping; *LearnExpl*, learning through exploration; *LearnBreed*, learning from breeding experience) for different initial population sizes according to different life histories (fast and slow). Simulations have been run with the same deterministic growth rate (λ) of 1.05 and moderate behavioural responses, under the five different scenarios: phenotype – environmental matching (scenario 1) and phenotype – environmental mismatch causing moderate increases of adult mortality (scenario 2.1), extremely high adult mortality (scenario 2.2), moderate increases of juvenile mortality (scenario 3.1) and extremely high juvenile mortality (scenario 3.2). Simulations with strong behavioural responses are shown in the electronic supplementary material, figure A.3.2.2. The fast strategy is characterized by early onset of first reproduction (1 year old), high annual fecundity ($q = 8$) and low adult survival ($p_{1,s_b} = 0.4$), while the slow strategy exhibits delayed onset of reproduction (3 years old), low fecundity ($q = 8$) and delayed onset of first reproduction but high adult survival ($p_{1,s_b} = 0.85$). Note that in scenario 1, the two habitats are the same, and therefore, all behavioural responses except reproductive skip are equivalent to the neutral behaviour.

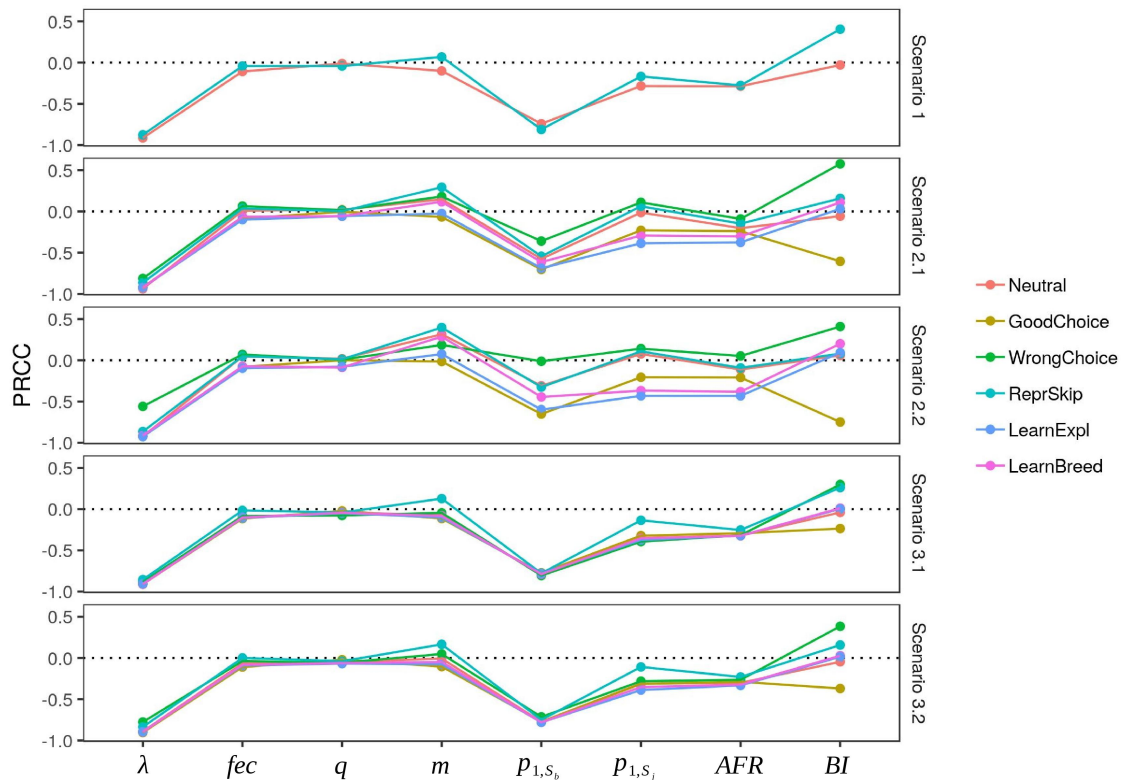


FIGURE 3.2: Sensitivity of the probability of population persistence to life-history traits for different behavioural responses and maladaptive scenarios, based on PRCC. Population persistence is measured as $N_0P_{50\%}$, the initial population that give a 50% chance of persistence. Notation not shown in table 3.1 is as follows: λ is the deterministic growth rate; fec is fecundity expressed as the number of offspring produced annually ($m \cdot q$); AFR , is the age at first reproduction; BI is the intensity of the behavioural responses, i.e. either moderate or strong. Analyses are based on 3612 combinations of life-history traits distributing species along the fast–slow continuum.

when conditions are unfavourable often entails important fitness costs, reducing the probability of establishment.

b) Integrating behavioural responses and life-history strategies

Figure 3.1 suggests that the way behavioural responses influence persistence in the novel environment differ according to the position of the species in the fast–slow continuum. To formally explore this, we repeated the simulations for the 3612 life-history strategies resulting from all combinations of life-history traits with λ between 1.05 and 1.2 (see the section Exploration of the parameters for details). For each life-history strategy, we then estimated $N_0P_{50\%}$ to describe the likelihood that the species persists in the novel scenario as a function of their behaviour. Sensitive analyses across all scenarios and behavioural strategies show that λ is the most important factor facilitating population persistence in the novel environments (figure 3.2). Life-history strategies with higher λ show lower $N_0P_{50\%}$, implying that they need fewer individuals to become established. However, adult survival is the life-history trait with greater influence in population persistence,

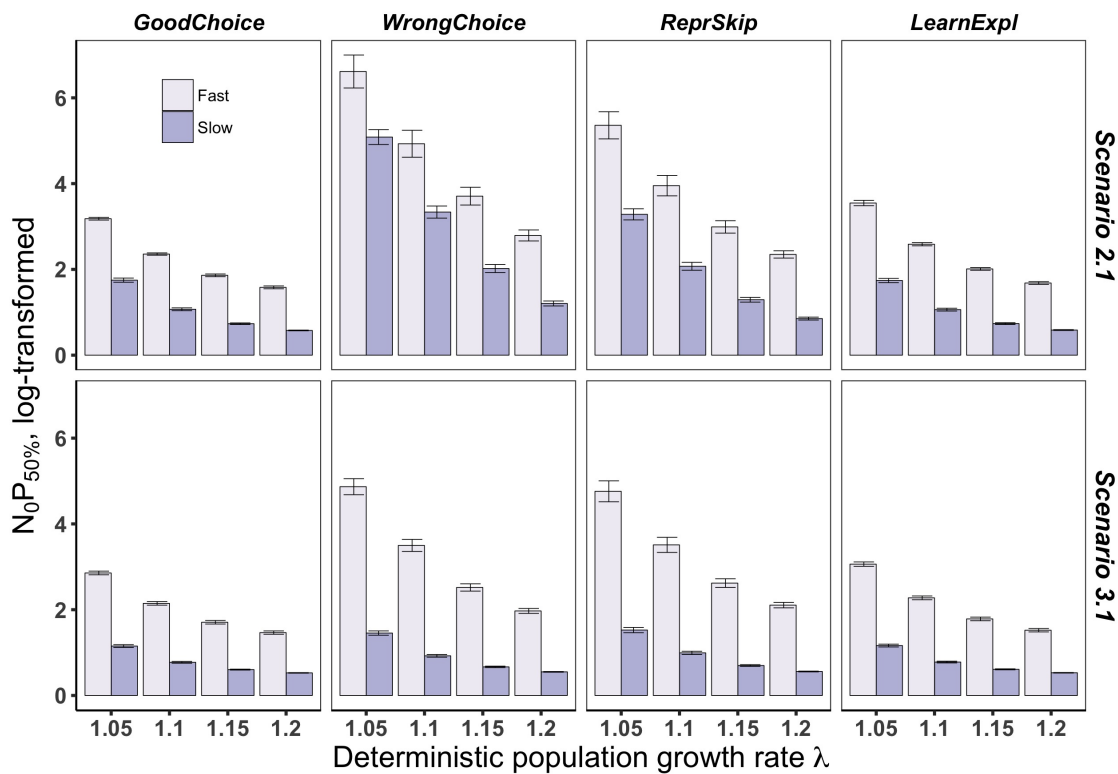


FIGURE 3.3: Effects of behavioural responses on population persistence in novel environments as a function of the position of the animal along the fast–slow continuum. Population persistence is estimated as $N_0P_{50\%}$ and behavioural responses are moderate (for strong responses, see the electronic supplementary material, figure A.3.2.4). For details on abbreviations, see figure 3.1.

suggesting that slow strategies have generally higher chances than fast strategies to persist in novel environments (figure 3.2). The high persistence of slow species in novel environments does not merely result from the individuals initially introduced being able to survive the entire simulation period. The explored life-history trait combinations rarely allow individuals to survive 50 years, and in most cases, the final population is higher than the initial one (electronic supplementary material, figure A.3.2.3).

c) Costs and benefits of behavioural responses in fast and slow strategies

To further investigate the interaction between behaviour and life history, we compared life-history strategies positioned either at the fast or slow extremes of the fast – slow continuum (see the section Exploration of the parameters for details). The results confirm that slow strategies generally need a lower $N_0P_{50\%}$ than fast strategies to persist in the novel environments (figure 3.3). To reach a success similar to that of slow strategies, fast strategies must have values of λ substantially higher (often more than 15% higher) than those of slow strategies.

Under maladaptive scenarios, the probability of persistence depends on whether the phenotype–environment mismatch mainly affects offspring or adults, as fast

and slow strategies differ in their sensitivity to changes in fecundity and adult mortality. Thus, although the general tendency of slow species to be superior invaders is consistent across environmental scenarios, slow species are particularly affected by scenarios increasing adult mortality and fast species by those affecting offspring mortality.

The benefits and costs of the behavioural responses are also contingent to the position of the species along the fast – slow continuum (figure 3.3; electronic supplementary material, figures A.3.2.6–A.3.2.10). In slow species, the gains of learning are substantial when maladaptation increases adult mortality, while the gains are almost negligible when maladaptation affects offspring because they are already well protected for their life history. Because slow strategies have more opportunities to reproduce in the future, they are less penalized than fast species by mistakenly choosing an inappropriate habitat to reproduce. Likewise, the decision of skipping a reproductive event when conditions are unfavourable, which is generally costly (figure 3.1), has a negligible impact on the demography of slow species when the risk of reproductive failure is high.

For fast species, learning through exploration and an innate preference for the high-quality habitat tend to improve population persistence in all scenarios, although the gains are modest and rapidly decrease at higher λ values (figure 3.3; electronic supplementary material, figures A.3.2.6 and A.3.2.8). Learning from a reproductive failure is marginally beneficial only when phenotype–environment match increases offspring survival, even though the risk of extinction remains high (electronic supplementary material, figure A.3.2.9). The costs of preferring a low-quality habitat or skipping a reproductive event are also generally high in most scenarios, compared to those of slow species, and generally cannot be compensated by increasing λ (electronic supplementary material, figure A.3.2.7).

3.4 Discussion

Our results show strong support for the notion that behavioural responses interact with life history to influence persistence in novel environments. Under maladaptive scenarios, where the match of the phenotype to the environment is insufficient, the simulations suggest that it pays to have a slow life history that increase the value of adults over the value of offspring even at the cost of decreasing reproduction. This is in part owing to the demographic consequences of the life-history strategy itself and in part owing to the added benefits of behavioural responses. Thus, a slow strategy represents a strong buffer against maladaptation causing high offspring mortality, indirectly affecting adult survival and hence the opportunities for future reproduction. Instead, behavioural responses primarily buffer individuals against maladaptation causing high adult mortality. As novel environments are likely to increase both adult and offspring survival, the complementary effects of behavioural responses and life history make slow animals particularly well equipped to cope with sudden changes in the environment.

The notion that slow animals exposed to novel environments generally gain greater benefits from behavioural responses has been suggested in previous studies. Animals at the ‘slow’ extreme of the fast–slow continuum are generally be-

lieved to explore more accurately the environment and exhibit better performance in learning than those at the ‘fast’ extreme (reviewed in Sol and Maspons (2016)). Eliassen et al. (2007), for instance, developed a model to investigate how foragers benefit from using a simple learning rule to update estimates of temporal changes in resource levels; the model showed that as lifetime expectancy decreases, learners invest less in information acquisition and show lower foraging performance when resource level changes through time. Our simulations generally align with these studies, even though we did not explicitly consider cognitive differences in learning between fast and slow animals. Although it is likely that including these differences accentuate the superiority of slow species in contexts of maladaptation, this will depend on costs that are difficult to estimate. Our model assumes some costs of behavioural responses, such as imperfect information leading to choose a low-quality habitat and a loss of breeding opportunities. However, there are other costs not considered, such as those related to the need to invest time and energy to produce and maintain the neural and cognitive functions needed to acquire and respond to environmental information.

A particularly intriguing question is to what extent innate preferences and learning interact to influence the realized preferences for habitats. Kawecki (2010) argued that an individual with no clear innate preference will be more amenable to changing its preference as a result of experience than an individual that already shows a strong innate preference, even when it means choosing a low-quality resource. Thus, it may be that some species primarily rely on matching the environment to the phenotype through habitat matching choice, while others rely more on improving the match of the phenotype to the new environment through learning. Several factors might contribute to favour one strategy over the other. Natural selection on heritable variation in habitat preferences should be more efficient in fast species, whose short generation times increase mutation rates and changes in allele frequency. Instead, in slow species that respond more slowly to selection, learned preferences would outperform genetically determined preferences (present study, see also Kokko and Sutherland (2001)). Learning might also be particularly favoured in ecological generalists. A generalist strategy selects against local adaptation (Kisdi, 2002), and frequently exposes individuals to new challenges that require learned responses (Sol et al., 2016; Ducatez et al., 2015). Our simulations suggest an additional factor that might contribute to favour learning over phenotype matching choice: the degree of novelty in the environment. We find that learning does not avoid extinctions as efficiently as perfect knowledge, but in terms of population persistence, it avoids the risk of falling into an ecological trap. Learning seems thus to be a better strategy than matching habitat choice to thrive in environments that are very different from the ancestral environments or that change too fast to provide reliable cues for habitat choice. One example could be urban environments. These environments expose animals to a variety of challenges that are drastically different from those found in nature, such as the need to confront frequent disturbances by people or avoid risks associated with traffic and buildings. Growing evidence indicate that urban animals tend to be more proficient in learning than non-urban animals (Sol et al., 2013b).

Our results contribute to the debate over whether successful invaders should

be characterized as fast or slow, an issue of high relevance to predict and prevent the spread and impact of biological invasions. Although life history has long been deemed essential to understanding the success of invaders (Lewontin and Cohen, 1969), confidence in theoretical arguments has been undermined by a perceived lack of empirical support (Sol et al., 2012*b*). The dissociation between theoretical and empirical work has in part been attributed to the excessive focus on the ‘small population paradigm’ (Sol and Maspons, 2016), which assumes that demographic stochasticity is the main driver of extinction in introduced populations. This has led to the widespread belief that successful invaders are characterized by high fecundity that reduces the risk of stochastic extinctions by facilitating rapid population growth from small initial populations. While this process has received some empirical support (Allen et al., 2017; Capellini et al., 2015), our results align with theoretical and empirical work suggesting that it mainly applies when the organism’s phenotype matches well with the environment (Sol et al., 2012*b*; Jeppsson and Forslund, 2012). Yet, under maladaptive scenarios our simulations indicate that fast strategies are more affected by ecological traps and are only superior to slow strategies when their population growth rate is substantially higher. Moreover, this superiority is only noticeable when the phenotype mismatch with the environment increases adult mortality, reflecting that population growth of fast species is less sensitive to changes in adult mortality than in fecundity. Given the importance of parental care in many animals, however, it is unrealistic to assume that a high adult mortality will not be accompanied by increased offspring mortality (Santema and Kempnaers, 2018). The crucial question is therefore to what extent fast animals can maintain high population growth rates in a context of maladaptation. Current evidence in birds and mammals does not indicate that fast species have higher population growth rates in the wild than slow-lived species (electronic supplementary material, figure A.3.2.11). To properly clarify this issue on empirical grounds, however, we would need field estimations of population growth rate for fast and slow populations exposed to different degrees of phenotype–environment mismatch. Unfortunately, this type of information is currently unavailable.

As any model, ours is a simplified representation of the reality. An issue that remains insufficiently resolved is how different behavioural responses affect establishment success when acting in concert. In our simulations, we have investigated behavioural mechanisms separately, to be able to disentangle their effects, but in reality, it is likely that they act in concert, either synergically or antagonistically. The challenge here is to parametrize the models in a way that is realistic enough to avoid biasing the simulations, but this requires a better understanding of mechanisms. Another issue that will need further attention in the future is the possibility that other mechanisms in addition of those analysed here also influence the response to environmental changes. We have previously suggested that producing several broods in the same breeding season can afford high benefits when the chances of a reproductive failure are high, as it provides the advantage of a high annual fecundity while reducing the costs of a reproductive failure (Sol et al., 2012*b*). Future models will also have to consider Allee effects, that is, the decline in the rates of reproduction and/or survival at low population densities. These effects are not only highly relevant during the early stages of the invasion

process, but may also be tied to the life history and behavioural strategies of the species (Leung et al., 2004). A preference for a low-quality habitat is indeed a type of Allee effect, as it slows population growth at low densities (Kokko and Sutherland, 2001), but other types of Allee effects could also be relevant (Reznick et al., 2002). Allee effects are expected to be particularly relevant in highly social animals that rely more on social and public information to take decisions and learn. Advancing in all these themes will offer a more complete picture of how animals cope with environmental changes.

Although organisms that are slow-lived relative to the rate of environmental fluctuations often exhibit enhanced learning abilities (Sol et al., 2016), the evolutionary causes are less well understood. It has been suggested that the causal link between learning and longevity could be bi-directional (Eliassen et al., 2007; Ratikainen and Kokko, 2019; Sol, 2009b). The possibility of constructing behavioural responses to ecological challenges might directly affect the evolution of life histories by buffering individuals from extrinsic mortality. The evolved combination of life-history traits might in turn alter the fitness benefits and costs of behavioural responses, as suggested here. However, the covariation between learning and life history can also result from correlated evolution (Sol et al., 2016). Our results reinforce this latter view, suggesting that the environments which favour slow life-history strategies are similar to those favouring learning. Thus, behavioural plasticity and slow life histories might be dimensions of a same pace-of-life syndrome to cope with sudden environmental changes (Sol et al., 2016).

We have shown that considering variation in life-history species is relevant when predicting the influence of behaviour on the probability of persisting in novel environments. Although the interplay between behaviour and life history is still insufficiently understood, our results highlight that to continue advancing, we need to acknowledge that both may be part of a broader adaptive system of organisms to cope with rapid environmental changes.

Risk-taking behavior, urbanization and the pace of life in birds ¹

4

Abstract

Despite growing appreciation of the importance of considering a pace-of-life syndrome (POLS) perspective to understand how animals interact with their environment, studies relating behavior to life history under altered environmental conditions are still rare. By means of a comparative analysis of flight initiation distances (i.e., the distance at which an animal takes flight when a human being is approaching) across >300 bird species distributed worldwide, we document here the existence of a POLS predicted by theory where slow-lived species tend to be more risk-averse than fast-lived species. This syndrome largely emerges from the influence of body mass, and is highly dependent on the environmental context. Accordingly, the POLS structure vanishes in urbanized environments due to slow-lived species adjusting their flight distances based on the perception of risk. While it is unclear whether changes in POLS reflect plastic and/or evolutionary adjustments, our findings highlight the need to integrate behavior into life history theory to fully understand how animals tolerate human-induced environmental changes.

Significance statement

Animals can often respond to changing environmental conditions by adjusting their behavior. However, the degree to which different species can modify their behavior depends on their life history strategy and on the environmental context. Species-specific perception of risk is a conspicuous example of adjustable behavior tightly associated with life history strategy. While there is a general tendency of higher risk aversion in rural than city-dwelling birds, it is dependent on the species' life history strategy. Slow-lived species are more prone to adjust their flight initiation distances based on the perception of risk, allowing humans to approach closer in urban than rural environments. Behavior must therefore be taken into account together with life history to reliably assess species' vulnerability at the face of ongoing environmental change.

Keywords: Life history theory, Phenotypic plasticity, Human-induced rapid environmental changes, Learning

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4.1 Introduction

Behavior is widely considered one of the main mechanisms through which animals cope with changes in the environment (Bogert, 1949; Klopfer, 1962; Mayr, 1965). Unlike other phenotypic features, behavior can often be rapidly modified to solve new ecological problems, thus contributing to reduce the uncertainties and adaptive mismatches that arise when environmental conditions change (Huey et al., 2003; Price et al., 2003; Estrada et al., 2016; Sol and Maspons, 2016). A growing number of studies has for instance documented that animals living in urban environments differ in behaviors related to resource use, disturbance avoidance, and communication from those inhabiting little urbanized environments (reviewed in Shochat et al. (2006); Evans et al. (2012); Lowry et al. (2013); Sol et al. (2013*b*)). Evidence is also accumulating that these behavioral differences primarily reflect plastic adjustments, although some may also result either from selection or from a non-random sorting of individuals by behaviors that affect colonization success (reviewed in Sol et al. (2013*b*)).

Despite the plastic nature of most behaviors, some animals exhibit strong consistencies in how they behave across time and contexts (reviewed in Sih et al. (2004); Réale et al. (2007)). These behavioral consistencies are expressed among individuals within species, as well as among individuals of distinct species (e.g., Møller (1994); Verbeek et al. (1994); Koolhaas et al. (1999); Gosling (2001); Greenberg (2003); Sih et al. (2004); Réale et al. (2007)). An example is a behavioral syndrome where some animals are risk-averse whereas others are risk-prone across a range of situations regardless the actual risks (Sih et al., 2004, 2012). This syndrome has attracted considerable interest of behavioral ecologists because the inability of individuals to adjust their behavior to the actual level of risk can entail important costs, such as greater exposure to predators, reduced foraging opportunities and increased energetic expenditure (Sih et al., 2004, 2012). However, the reasons why some animals readily adjust their behavior in response to novel situations while others persist with their behavior, even when maladaptive, remains unresolved (Sih et al., 2004). Recently, it has been suggested that the striking consistencies in risk-taking behavior observed across individuals of a given species, but not in members of other species, can be understood if we consider behavior and life history as dimensions of a same pace-of-life syndrome (POLS) (Wolf et al., 2007; Réale et al., 2010).

The POLS theory argues that animals experiencing different environmental conditions should diverge in a suite of behavioral and physiological traits according to their life history (Ricklefs and Wikelski, 2002; Tieleman et al., 2005; Hau et al., 2010; Réale et al., 2010). A central premise of this theory is the existence of a fast-slow continuum of life history variation (FS hereafter), which reflects the impossibility to simultaneously maximize survival and fecundity (Stearns, 1983; Sæther, 1988). The FS aligns organisms along a pace-of-life (POL) axis from a “highly reproductive” (fast-lived) strategy at one end to a “survival” (slow-lived) strategy at the other end. As slow-lived animals prioritize future over current reproduction (Stearns, 2000*b*), they should generally be more risk-averse compared to those at the fast extreme (Martin et al., 2000; Wolf et al., 2007; Hau et al., 2010; Møller and Garamszegi, 2012; Møller and Liang, 2013). In contrast, fast-lived

animals should prioritize behaviors that enhance current reproductive effort, even when doing so involves taking some risks. Therefore, the POLS theory explicitly verbalizes the classic idea that selection should favor behaviors ensuring higher adult survival in slow-lived animals and behaviors that enhance reproductive effort in fast-lived animals.

Despite the existence of theoretical predictions, empirical support for the existence of a risk-taking POLS is currently scarce (Hille and Cooper, 2015; Charmantier et al., 2017). A number of factors may indeed prevent the detection of such a POLS. One is the extent to which risk-taking behaviors can be modified by learning. Slow-lived species have less cognitive and time constraints to gather new environmental information and accommodate their behavior accordingly by means of learning (van Schaik and Deaner, 2003; Sol, 2009*b*; Sih and Del Giudice, 2012; Sol et al., 2016). If plastically modifying FID depends on the position of the animal in the fast-slow continuum, the POLS may vanish in contexts where the perception of risk is low.

Another factor that makes the demonstration of POLS challenging is the low heritability of life history traits (Price and Schluter, 1991). The analysis of individual variation within populations is fundamental to disentangle the importance of plasticity and genetic processes, as well as being of interest in itself (Réale et al., 2007). However, the low heritability of life history traits reduces the likelihood of detecting POLS at the individual level. An obvious alternative is to examine POLS across populations or species, as they have had more opportunities to diverge in behavioral and life history traits, yet such a level of analysis is more rarely used.

Here, we investigate if risk-taking behaviors are a defining part of a POLS syndrome in birds, and ask to what extent the syndrome can be relaxed according to the environmental conditions. We focus on behavioral and life history differences across species exposed to contrasting degrees of human disturbances. Our measure of risk-taking behavior is the flight initiation distance (FID), defined as the distance at which an individual takes flight when approached by a human. Previous work in birds has shown that FID within and across species is shorter in urbanized than in non-urbanized environments (Møller, 2008; Carrete and Tella, 2011; Sol et al., 2012*a*), indicating that the perception of risk is context-dependent. We take advantage of these previous findings to address two main expectations of POLS theory regarding risk-taking behavior. The first is the expectation that slow-lived species should exhibit longer FID than fast-lived species when the perception of risk is high. Although FID has been found to be positively related to certain vital rates in birds, like fecundity (Blumstein, 2006; Møller and Garamszegi, 2012), the fast-slow continuum is better characterized in the context of the full life cycle of a species (Adler et al., 2014). We operationally defined the continuum as the combination of life history traits that better predicts the fecundity-survival trade-off (Caswell, 2000; Oli and Dobson, 2003; Oli, 2004). We then used information on >11,000 measures of FID belonging to >300 avian species to ask whether flight distances vary depending on the position of the species in the fast-slow continuum. To this purpose, we used phylogenetic Bayesian mixed models that allow the integration of species-level information generated by observations of multiple individuals. As theoretical and empirical evidence suggests that both

the fast-slow continuum (Stearns, 1992) and FID (Møller, 2015) are positively correlated with body size, we also examined whether body size may be one of the factors underlying the FID-FS association.

The second expectation of POLS theory is that slow-lived species can better accommodate their FID to the perception of risk than fast-lived species. This expectation derives from the supposed higher behavioral plasticity of slow-lived species (Sol, 2009a), which would allow them to habituate faster to human presence, and from constraints in fast-lived species to adopt risk-averse strategies due to the need to prioritize reproduction. We validated this prediction by investigating how FIDs change between urban and rural habitats as a function of the position of the species in the fast-slow continuum, again using phylogenetic Bayesian mixed models. Following suggestions that behavioral differences between urban and non-urban birds might be linked to brain size and learning capabilities (Kark et al., 2007; Maklakov et al., 2011; Sol et al., 2011), we also verified whether a larger brain size contributes to explain why slow-lived species should be better able to accommodate FID to risk perception (Sol, 2009b,a).

4.2 Material and methods

Measuring FID

A total of 11,863 FID observations were recorded by one of the authors (APM) during February–September 2006–2014, using a standard experimental field procedure (Hediger, 1934; Hemmingsen, 1951; Blumstein, 2006). All estimates were collected blindly with respect to the hypotheses being tested here, thereby preventing any conscious or unconscious bias. The observations were made in an area of 100 km² in Orsay (48° 42' N, 2° 11' E, France), 800 km² in Northern Jutland (57° 12' N, 10° 00' E, Denmark), 500 km² in Oslo (59° 54' N, 10° 45' E, Norway), and 500 km² on Hainan Island (19° 12' N, 109° 42' E, Southern China). In most regions, observations were carried out in both urban habitats (i.e., areas with multistory buildings, single-family houses, roads, and urban parks) and rural habitats (i.e., open farmland and woodland lacking continuous urbanized areas). Therefore, our distinction between urban and rural habitats essentially separates environments very frequented by humans from those less frequented.

To record FIDs, the observer located an individual bird with binoculars and subsequently moved at a normal walking speed towards the individual, while counting the number of steps (which approximately equals the number of meters (Møller, 2008)). The FID was the horizontal distance at which the individual took flight. The starting distance (i.e., the distance from where the observer started walking up to the bird) was in most cases (>98% of all observations) fixed at ca. 30 m to avoid confounding FID with starting distance. If the bird was located in the vegetation, the height above ground was also recorded to the nearest meter using the observer as a yardstick. This method is reliable when cross-validated using a laser Bushnell® Elite 1500. FID was then estimated as the Euclidean distance, which equals the square-root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein, 2006). When possible, sex ($n =$

4958 observations), age ($n = 10,887$), and flock size ($n = 1387$) were also recorded to be included as confounds in the models. Although the FID of some individuals was measured twice, we only used the first measure in the analyses. All FID data are available as supplementary material.

Measuring POL

To estimate the fast-slow continuum, we searched for published information on six life history traits: (1) clutch size, (2) number of broods per year, (3) maximum lifespan (years), (4) incubation period (days), (5) nestling period (days), and (6) age at first reproduction (years). We found information of all six traits for 765 avian species (see Sol et al. (2016)). As originally defined, the fast-slow continuum results from the existence of a fecundity-survival trade-off (Stearns, 1992). Consequently, we empirically defined the fast-slow continuum as the combination of life history traits that better predicts the relative sensitivity (i.e., elasticity) of population growth to changes in adult survival (Caswell, 2000; Oli and Dobson, 2003; Oli, 2004). To this purpose, we used the COMADRE Matrix database (Salguero-Gómez et al., 2016a) to obtain age-structured population matrices that incorporate accurate information on the rates of survival, growth, and reproduction from natural populations. We removed four matrices for which elasticities did not sum up to 1, which could reflect mistakes in the data, and for the remaining matrices ($n = 53$ from 49 species), we estimated the elasticity for adult survival. To combine the life history traits, we conducted phylogenetic principal component analyses (PPCA) (Revell, 2009) based on the 765 species, including a minimum of three traits in each analysis (i.e., 42 PPCAs). The species scores of each PPCA was then used as predictor of elasticities in a phylogenetic least square models (PGLS) (Orme et al., 2013), and the best models were classified according to AICc. The combination of life history traits that best predicted variation in elasticity for adult survival included lifespan, clutch size, and fledging period. We therefore defined the position of each species in the fast-slow continuum by extracting the scores of this PPCA. In our best PPCA, species with high scores (i.e., high adult survival elasticities) were slow-lived and those with low scores (i.e., high fecundity elasticities) were fast-lived. We note that the results of our approach based on adult survival elasticities are similar to those based on estimates of elasticities for fecundity or on generation time extracted from the demographic matrices (see Chapter 2).

Modeling FID

To model variation in FID, we used Bayesian phylogenetic mixed models (BPMM) with Gaussian error structure, as implemented in the R package “MCMCglmm” (Hadfield and Nakagawa, 2010; Hadfield, 2010). FID was log transformed before analyses to improve model convergence. As our units of analysis were the FID observations, species identity was included as a random factor together with phylogeny. The phylogeny was a maximum clade credibility phylogeny (CCP) consensus tree based on a sample of 1000 phylogenies from the pseudo-posterior distribution in Jetz et al. (2012), built with the TREEANNOTATOR software

(Drummond et al., 2012). When appropriate, country was also included as a random factor to better account for data heterogeneity (see results for details). We first ran models without predictors to estimate FID consistency within species and phylogenetic heritability by means of a variance components analysis (Housworth et al., 2004). Then, we added predictors as fixed effects to explain variation in FID. To demonstrate the existence of POLS, we modeled FID as a function of the fast-slow continuum, including habitat (i.e., rural or urban), sex, age, flock size, and height at which the bird was observed as possible confounding effects. Using non-informative priors, the MCMC chains were run for 330,000 iterations with a burn-in interval of 30,000 and sampling each 300 iterations to ensure satisfactory convergence.

As we found evidence for a link between FID and FS, we tested whether this was caused by their common association with body size. To this purpose, we used phylogenetic path analyses on species' trait averages (von Hardenberg and Gonzalez-Voyer, 2013; Gonzalez-Voyer and Von Hardenberg, 2014). The minimal set of conditional independencies for each path model (von Hardenberg and Gonzalez-Voyer, 2013) was tested using PGLSs models as implemented in the package *ape* (Paradis et al., 2004) in R. Models were run estimating an evolutionary parameter (λ) simultaneously with model fit that adjusts the variance-covariance matrix to adequately fit the model of evolution, in our case a Brownian motion model (Freckleton et al., 2002). The fit of a given path model to the data was estimated via the C statistic. The C statistic tests whether the minimum set of conditional independencies of a model is fulfilled by the observational data, thus it provides an estimate of the goodness of fit of the model to the data (Shipley, 2013). A significant C statistic indicates that the model is a poor fit to the data. We employed an information theoretical approach and compared the different path models using the C statistic information criterion (CICc; analogous to the Akaike information criterion; von Hardenberg and Gonzalez-Voyer (2013)).

We finally investigated whether changes in FID between urban and rural habitat were larger in slow-lived species than in fast-lived species, using the same BPMM approach described above. To do so, we averaged the FID values of each species per habitat and then estimated FID difference as

$$\log(\text{meanFID}_{\text{rural}}) - \log(\text{meanFID}_{\text{urban}})$$

We therefore only used species present in both habitats for the analyses. FID differences were then used as response variable in a BPMM with the fast-slow continuum as fixed effect and the phylogeny as a random factor. Unlike previous models, the level of analysis here was the species instead of FID observations. Thus, the conclusions could be sensitive to the sample size used to estimate FID differences. We tackled this limitation in two ways. First, in the BPMM we weighted FID differences by $1/(n3)$, being n the number of individuals sampled per species. Second, we re-ran the model for the subset of species with at least 15 FID observations in each habitat. To test whether differences in FID across habitats were related to differences in brain size, we used information published in Sayol et al. (2016) on the residuals of a log-log PGLS of brain volume against body mass. Positive residuals mean that the brain of the species is larger than

expected by body size and negative residuals that is smaller than expected by body size.

4.3 Results

A Bayesian phylogenetic mixed model (BPMM) based on 11,852 observations of 317 bird species confirmed the existence of consistent among-species variation in FID (mode = 0.65, CI = 0.57– 0.77), much of which was shared among close relatives (Fig. 4.1, Table A.4.1). FID did not vary with sex (pMCMC = 0.920), age (pMCMC = 0.518), and flock size (pMCMC = 0.696). However, birds did tend to exhibit longer FID when located at certain height above the ground (mode = 0.026, CI = 0.013–0.038). Of the remaining residual variation, a significant fraction was accounted for differences among habitats. As shown in previous studies (reviewed in Møller and Erritzøe (2014)), FID was consistently shorter in urban than in rural habitats across all study regions (pMCMC <0.0001, Fig. 4.2, Table A.4.2). Variation in FID across species was also more consistent in rural than in urban habitats (Fig. 4.1).

The studied species exhibited substantial variation in their position along the fast-slow continuum, reflecting the existence of a fecundity-survival trade-off (Fig. 4.3). As expected, species at the slow extreme of the continuum tended to exhibit longer FID than those at the fast extreme (pMCMC <0.0001, Table A.4.3), consistent with the existence of a POLS. However, there was a negative interaction with habitat (Table 4.1), reflecting that FID and life history variation

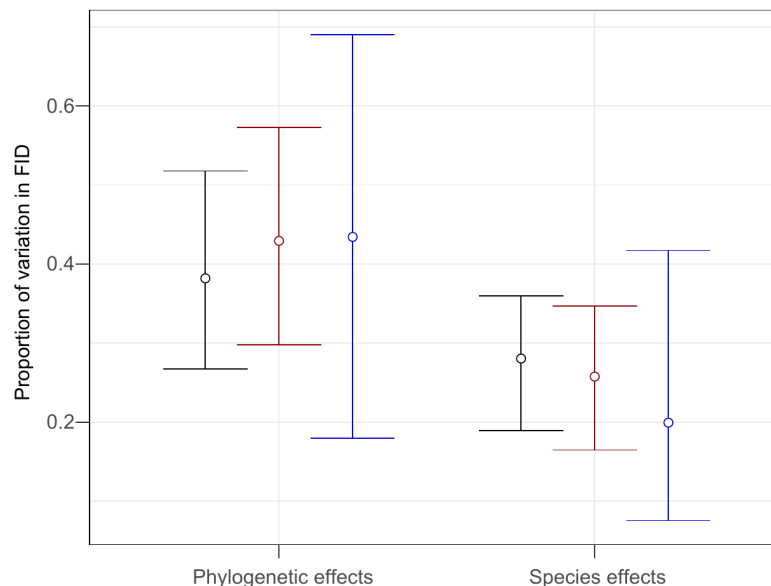


FIGURE 4.1: Proportion of variance in FID accounted for the phylogeny and within species variation when considering all observations (black), rural observations only (red) and urban observations only (blue). Values are the intra-class coefficients estimated by means of a BPMM with the constant as fixed effect and the phylogeny and species identity as random factors. Error bars are 95% credible intervals.

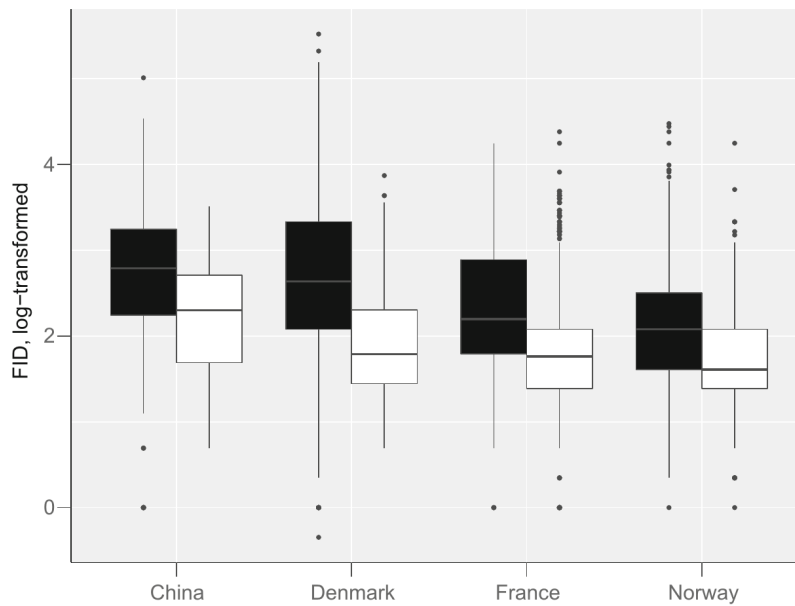


FIGURE 4.2: Differences in FID between urban (white) and rural (black) habitats across countries. The plot shows the median, interquartile range and 1st and 3rd quartiles.

became decoupled in urban environments (Fig. 4.4). This pattern was largely due to changes in FID across habitats by slow-lived species (Table 4.2, Fig. 4.4). In rural environments, where the POLS was detected, the best phylogenetic path models suggest that the FID-FS association was primarily caused by their common association with body size (Figs. 4.5, A.4.2). In urban environments, there is no direct effect of body size on FID, which might explain why the FID-FS association is no longer present (Figs. 4.5, A.4.3).

Because slow-lived species tend to have disproportionately larger brains than fast-lived species (Fig. 4.3), the reduction in FID observed in slow-lived species could reflect enhanced learning capacities. Species with larger brain residual exhibited longer FID in rural habitats than those with smaller brain residual ($p\text{MCMC} = 0.008$, Table S4), but they did not experience a more substantial change in FID between rural and urban habitats (Table A.4.5).

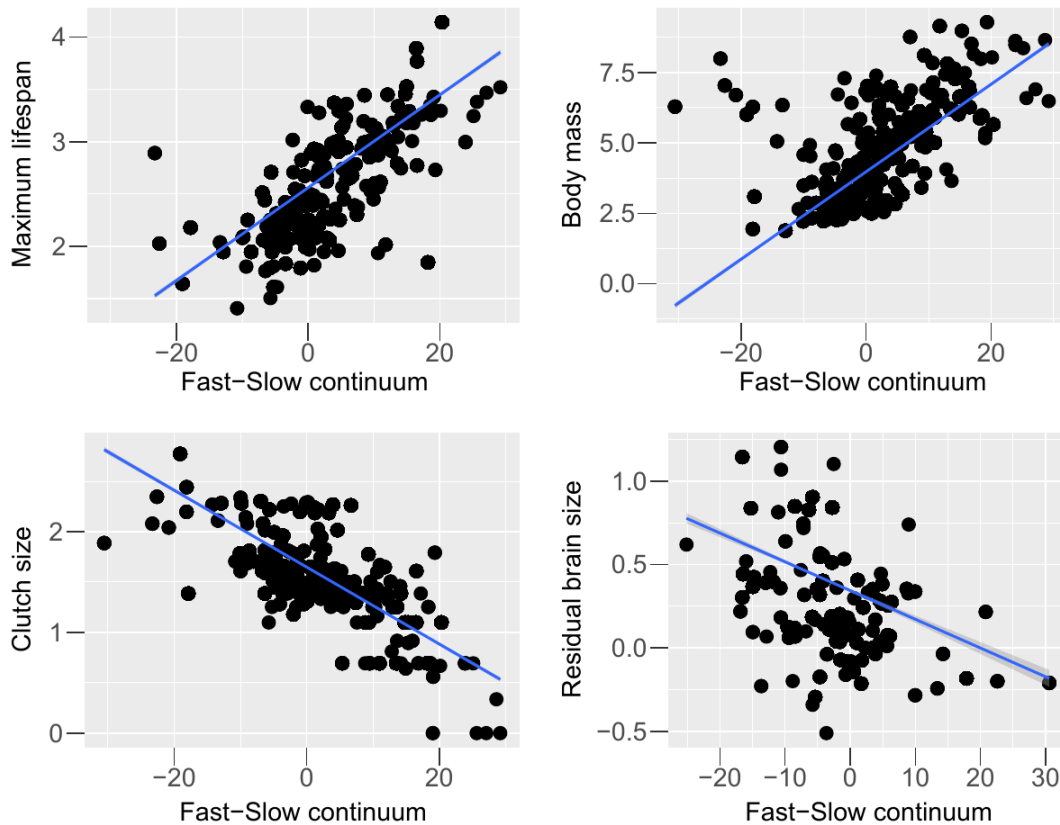


FIGURE 4.3: Relationship of the fast-slow continuum (FS) across species with maximum lifespan, clutch size, body mass, and residual brain size. The three first traits have been log transformed. Residual brain size represent the residuals of a log-log PGLS of brain volume against body mass (i.e., positive residuals mean that the brain of the species is larger than expected by body size and negative residuals that is smaller than expected by body size).

Table 4.1: BPMM accounting for variation in FID (response variable, log transformed) as a function of the interaction between habitat and the fast-slow continuum, based on information from all regions for which both urban and rural FID observations were available (Denmark, France, Norway, and China). The model was run with a Gaussian structure of the errors and a non-informative prior, the number of iterations being defined by nitt = 330,000, burnin = 30,000 and thin = 300.

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny					-
Species	0.143	0.095	0.199	1000	-
Country	0.168	0.011	0.477	1000	-
Residual	0.196	0.190	0.201	1000	-
Fixed effects					
Intercept	3.123	2.567	3.669	1000	<0.001
FS	0.024	0.0114	0.035	1000	<0.001
Habitat:urban	-0.321	-0.3444	-0.299	1000	<0.001
Height	0.014	0.0114	0.017	1000	<0.001
FS*Habitat:urban	-0.032	-0.035	-0.028	1000	<0.001

4.4 Discussion

Life history theory has mostly been developed under the view that organisms are passive subjects of selection, ignoring that behavior largely mediates how animals interact with their environment (Sol and Maspons, 2016). However, recent years have witnessed an increased appreciation that behavior can co-vary with the life history, an idea crystalized in the POLS concept (Ricklefs and Wikelski, 2002; Réale et al., 2010). Our results are in line with this new paradigm, confirming previous suggestions and evidence that FID can be part of a POLS.

Our finding that slow-lived species tend to be more risk-averse than fast-lived species in natural conditions fits well with life history theory. The fitness of slow-lived animals largely depends on ensuring a long reproductive life (Stearns, 2000*b*); hence, individuals should favor risk-avoidance strategies when the perception of risk is high (Martin et al., 2000; Wolf et al., 2007; Hau et al., 2010; Møller and Garamszegi, 2012; Møller and Liang, 2013). Under this view, behavior would be a consequence of life history. However, our analyses suggest that the relationship between FID and the fast-slow continuum is largely mediated by differences in body size among species. As body size is a major determinant of the fast-slow continuum, this does not deny the existence of a POLS. However, larger species may also decide to flee before than smaller species for reasons not directly induced by their life history, including a higher likelihood to be detected by predators, lower maneuverability to escape when attacked and higher energetic costs associated with flight (Blumstein, 2006).

An animal that is unable to tolerate human presence is likely to have problems to feed, communicate, or mate in densely populated urban environments. This may explain why FID is shorter in urban than in rural environments (Møller, 2010; Møller et al., 2015). While slow-lived species showed shorter or larger FID according to the perception of risk, fast-lived species did not accommodate their FID to the degree of human frequentation. The changes in FID observed in slow-lived species may reflect plastic adjustments, selection, and/or a non-random sorting of individuals by behaviors that affect invasion success. Our analyses do not allow us to distinguish between these alternatives, although plasticity is an obvious possibility. After detecting an approaching human, animals may decide to ignore the threat or to flee, and cognition may be involved in allowing informed decisions (Møller and Erritzøe, 2014). Some animals are, for instance, able to discriminate between people that pose a threat from people that do not (Levey et al., 2009; Lee et al., 2011). There is also evidence that fear of humans can diminish when individuals are exposed to human presence for long periods (e.g., Perals et al. (2017)). However, current evidence that FID may be modified by habituation in the wild remains inconclusive (Møller, 2015). Indeed, we did not find evidence that enlarged brains facilitate accommodating FID to the perception of risk, although this may simply indicate that habituation to humans does not require the type of advanced cognition associated with enlarged brains (Overington et al., 2009). Our insufficient understanding of how cognition and neural structures affect FID is also highlighted in the fact that we found that species with relatively larger brains exhibited longer FID, while a previous study found the opposite pattern (Møller and Erritzøe, 2014). As big-brained species

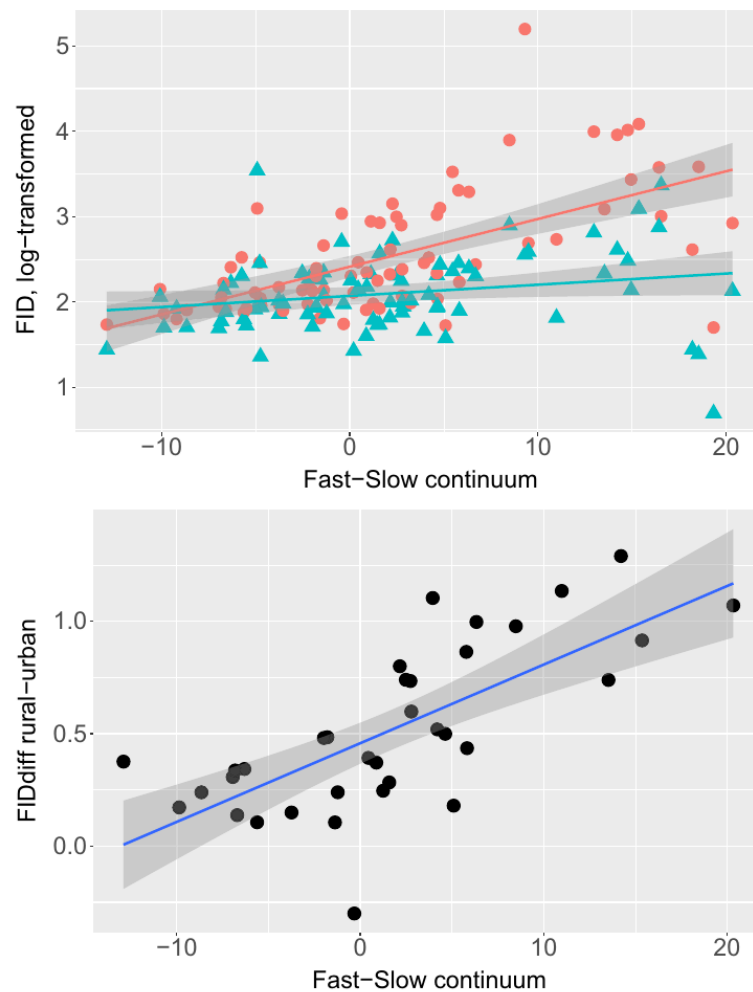


FIGURE 4.4: Above, relationship between FID and the fast-slow continuum for urban (blue triangles) and rural (red circles) habitats. Below, difference in FID between rural and urban habitats as a function of the fast-slow continuum.

tend to be at the slow extreme of the fast-slow continuum, the weak effect we found may be a mere by-product of the association between the FID and life history. Another possibility is that sense organs like eyes play a role in determining flight distance, with brain size only secondarily accounting for the response (Møller and Erritzøe, 2014).

The reasons why fast-lived species did not see their FID altered according to the perception of risk are also unclear. While it may be argued that these species already possess the appropriate behavior to persist in cities, it remains intriguing why they do not increase their FID in places where interactions with humans are rare enough to allow habituation. Elucidating whether this reflects constraints, perhaps associated with life history trade-offs, will represent an important avenue for future research. The existence of substantial phylogenetic heritability in FID, particularly when recorded in rural habitats, is consistent with the existence of such constraints (Blomberg et al., 2003). Further examples of possible constraints can be found in Møller et al. (2013), who reported that while FID of several

Table 4.2: BPMM accounting for the decline in FID per species from rural and urban habitats (response variable) a function of the fast-slow continuum, based on information from species for which both urban and rural FID observations were available. The decline of each species was estimated as the $\log(\text{meanFID}_{\text{rural}}) - \log(\text{meanFID}_{\text{urban}})$. The model was repeated again restricting the species to those with at least 15 FID observations in each habitat. The models were run with a Gaussian structure of the errors and non-informative priors. We weighted the observations by $1/(n-3)$, being “ n ” the number of FID observations of the species. The model was run with a Gaussian structure of the errors and a non-informative prior, the number of iterations being defined by $\text{nitt} = 440,000$, $\text{burni} = 40,000$ and $\text{thin} = 400$.

Model with all species					
	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.074	0.000	0.197	539	-
Residual	0.086	0.035	0.152	637	-
Fixed effects					
Intercepts	0.560	0.283	0.857	889.5	<0.001
FS	0.031	0.015	0.048	718.4	0.002
Model with species with at least 15 FID observations per habitat					
	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.095	0.019	0.192	794	-
Residual	0.018	0.000	0.043	703.6	-
Fixed effects					
Intercepts	0.711	0.358	1.010	1000	<0.001
FS	0.021	0.006	0.036	878.2	0.006

species of birds became shorter after a cold winter, this was only true in resident urban populations (frequently exposed to humans) but not in migratory or rural populations of the same species.

Much past theoretical and empirical work on life history has attempted to understand why organisms have diversified in a plethora of life history strategies (Stearns, 1992). The possibility that certain life histories offer advantages over others when it comes to adjustment to environmental changes has also been acknowledged (e.g., Sæther and Engen (2003)), but empirical support has been more difficult to assemble (but see Sol et al. (2012b, 2014)). Similarly, little effort has focused on considering behavior as a component of life history (e.g., Blumstein (2006); Møller and Garamszegi (2012), despite recent calls for the need to integrate behavior into life history theory to better understand how animals cope with environmental changes (reviewed in Sol and Maspons (2016); see also Estrada et al. (2016)). Our discovery of a POLS associated with risk-taking behavior contributes to fill these gaps, suggesting new ways by which behavior and life history interact to influence the response of animals to sudden changes in their environment.

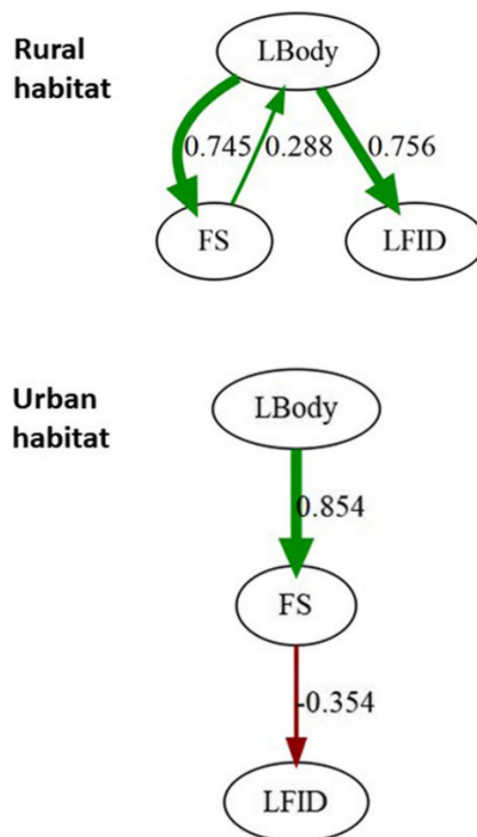


FIGURE 4.5: Phylogenetic path model averaged over all tested models (see Figs. S2 and S3, in the supplementary material) for rural and urban habitats, depicting the relationship between flight initiation distance (log transformed, LFID) and the fast-slow continuum (FS) according to differences in body mass (LBody) across species.

Life history theory seeks to explain how life history traits are selected in concert in the face of constraints, trade-offs. The theory has evolved from simple explanations based on single traits such as clutch size (Lack, 1946; Skutch, 1949) to broader explanations based on the allometric relations among life history traits and body size (Western, 1979), r-K selection where traits are selected according to the population density (Pianka, 1970), age-specific mortality (Gadgil and Bossert, 1970; Stearns, 1976; Charlesworth, 1980) and more recently, adding behaviour as a factor interacting with the evolution of the life history traits (Ricklefs and Wikelski, 2002; Réale et al., 2010; Sol and Maspons, 2016). Despite the progress made during all these years, there is a gap in the theory regarding the effects of the life history on the response of organisms to environmental changes. My thesis contributes to the advance of this field in two ways. First, by defining a demographically meaningful axes of life history variation in birds and confirming the existence of trade-offs among traits and restrictions for the existing combinations of life history traits (Chapter 2). Second, by understanding the mechanisms by which life history interacts with behaviour and clarifying how together they affect how species cope with new environmental conditions (Chapters 3 and 4).

The first objective of this thesis was to describe the diversity of life history in birds. Despite that it is not the first attempt to do so (Sæther, 1987; Gaillard et al., 1989; Sæther and Bakke, 2000; Jeschke and Kokko, 2009), my work in chapter 2 represents a significant improvement over previous works in three important ways. First, I used newly available statistical methods that control for the phylogenetic structure of the data by means of phylogenetic principal component analysis (Revell, 2009) and phylogenetic least square regressions (Ho and Ané, 2014). Second, the number of species in the compiled dataset is one order of magnitude larger than previous works. Finally, the availability of demographic data and the link with different combinations of life history traits allowed to objectively define the axes of life history variation that better describe demographic features of the species instead of using traits according to their availability. In addition of improving the quantification of the already known fast-slow continuum (Stearns, 1983; Sæther, 1987; Gaillard et al., 1989; Oli, 2004; Dobson and Oli, 2007; Jeschke and Kokko, 2009), my analyses also allowed to describe additional axes of life history variation such as the iteroparity axis (Gaillard et al., 1989), an axis related to the trade-off between offspring quantity and quality (Promislow and Harvey, 1990; Bielby et al., 2007; Dobson and Oli, 2007), and finally an axis that reflects the lifelong productivity of the species in terms of offspring number and egg mass produced relative to body size. The availability of a large data base of the species position in each life history axis opens new possibilities to understand

the implications of the life history in an evolutionary and ecological framework. Life history in birds is not as diverse as in other groups, perhaps due to the fly constraints (Gaillard et al., 1989; Healy et al., 2014). Future works could apply a similar methodology to other groups such as mammals for which traits and demographic data is already available (Myhrvold et al., 2015; Salguero-Gómez et al., 2016a).

A second objective of the thesis was to explore how life history affects the response of species to environmental changes. Previous attempts to elucidate the question showed contradictory patterns about the effects of the fast-slow axis on establishment success of introduced species (non significant for birds (Blackburn et al., 2009; Sol et al., 2012b) but significant for mammals and reptiles (Capellini et al., 2015; Allen et al., 2017)), or the ability to colonize urban habitats (non significant for birds (Sol et al., 2014) but significant for mammals (Santini et al., 2019)). As I argued in chapters 3 and 4, one possible explanation is the omission of an important factor that affects and is affected by the species position in the fast-slow axis: Behaviour.

As a first approach to the question, I explored mechanisms by which life history and behaviour can interact to influence demography in novel environments by means of a theoretical individual based model simulating the introduction of species with different life histories in a new environment (Chapter 3). The model shows that under maladaptive scenarios, where the match of the phenotype to the environment is insufficient, it pays off to have a slow life history that increases the value of adults over the value of offspring even at the cost of decreasing reproduction. This is in part owing to the demographic consequences of the life-history strategy itself and in part owing to the higher benefits of behavioural responses for slow species in comparison to fast species. The notion that slow animals exposed to novel environments generally gain greater benefits from behavioural responses has been suggested in previous studies (reviewed in Sol and Maspons (2016)). Animals at the 'slow' extreme of the fast-slow continuum are generally believed to explore more accurately the environment and exhibit better performance in learning than those at the 'fast' extreme. One reason for this difference being that they can develop disproportionately larger brains, which has been shown to enhance the capacity to innovate and learn (Lefebvre et al., 1997; Reader and Laland, 2002; Overington et al., 2009; Reader et al., 2011). The model in chapter 3 supports the idea that life history and behaviour are not independent and that studied together can help better understand the mechanisms by which they affect the responses to environmental changes, an issue of great relevance in the context of human induced rapid environmental changes where behavioural responses can be the key to adapt to novel conditions. Future studies can use similar approaches to look for demographic and ecological consequences of other relevant axes of life history variation such as iteroparity and offspring quality-quantity as described in Chapter 2. In particular, iteroparity seems a relevant axis to persist in novel environments as comparative studies have shown for invasive species (Sol et al., 2012b) an urban dwellers (Sol et al., 2014; Sayol et al., 2020).

A second approach to understand how life history and behaviour affect the response to environmental changes was developed in Chapter 4. In this chapter

we used a comparative analysis of flight initiation distances for birds in rural and urban habitats. The results show the existence of a peace-of-life syndrome (POLS) predicted by theory where slow-lived species tend to be more risk-averse than fast-lived species (Réale et al., 2010). Furthermore, the POLS structure vanishes in urbanized environments due to slow-lived species adjusting their flight distances based on the perception of risk. Even though there is no evidence in birds that slow species are better urban colonisers (Sol et al., 2014), the fact that slow species have a more plastic behaviour supports the idea that slow species can potentially better adapt to environmental changes. On the other hand, the pattern seems to revert in mammals, where species with traits related to the fast end of the fast-slow continuum are better urban dwellers in some groups (Santini et al., 2019). The contradictory results about whether fast or slow strategies are better to deal with environmental changes is still open. The fact that there is no clear pattern in birds could be because, even though there is a fast-slow continuum among species, the birds as a group are mostly in the slow end compared to mammals (Healy et al., 2014).

Human activities are altering natural environments through a wide range of processes, from land use changes to introduction of exotic species and climate change. Each type of changes can affect differently the resource availability and the age-specific mortality. Thus, the effects on the species and their responses should be different. Thus, there is no single life history strategy to deal with all changes. Rather, the nature of the changes will determine if the environment will become more or less predictable, including novel resource opportunities or qualitatively different threats such as new predators to which species are not adapted. In unpredictable environments, bet-hedging strategies can be a good strategy (Starrfelt and Kokko, 2012). Other less well-studied strategies for unpredictable environments include plastic life histories mediated by behaviour such as the ability to modulate the reproductive effort by skipping reproduction in bad years, the so called “storage effect” (Forcada et al., 2008). In environments with high pressure from new predators such as cats, juvenile mortality by predators can be compensated by increasing reproduction if enough resources are available (Yeh and Price, 2004) displacing the species towards the fast end of the fast-slow continuum. Also, the increase of the juvenile survival will have less impact for slow species which exhibit a life history buffer against the effects of demographic stochasticity and are less sensitive to changes in juvenile survival as I showed in Chapter 3. Species can respond to predictable changes through adjustments on the life history (Evans et al., 2005) or through behavioural plasticity mechanisms such as learning (Laundré et al., 2001; Evans et al., 2012). In the case of rapid changes for which there is not enough time for evolutive responses, behavioural plastic responses may be the only way to adapt to the new opportunities or threats (Sol, 2009a), and there is a growing number of evidences that behaviour affects and is affected by life history (Sol and Maspons, 2016). Thus, when we examine how life history affects the responses to environmental changes, we are considering not only life history mechanisms but also mechanisms related to behavioural responses.

Probably, the answer to the question of which life history strategies are better

to respond to environment changes is context-dependent, and only by carefully thinking about the relevant mechanisms, including behavioural responses, for each scenario of environmental change and the taxonomic group of study, we can refine the understanding of the effects of life history on the ability of the species to survive to environmental changes.

Conclusions

- **Chapter 2:**

- Not all combinations of life history traits exist in nature. The variation of life history traits is organized in different axes caused by trade-off and phylogenetic constraints.
- One of the main axes of traits' covariation is the fast-slow, described recurrently since 1983 by a varying set of traits more often justified by the traits data availability than for ecological reasons. This axis is related to the survival-fecundity trade-off. Defining the fast-slow axis in a demographically meaningful way (i.e. optimizing the correlation of the resulting axis with the elasticity to adult survival or generation time) allowed me to build an objective and more ecologically relevant characterisation of the axis.
- The remaining variation in life history traits once the fast-slow is ruled out is organized in three other axes of variation, sorted by variance explained:
 - * Iteroparity, describes the degree of concentration of the reproductive effort in few or many breeding attempts.
 - * Lifelong potential productivity, related to the lifelong investment in reproduction in terms of the number of offspring and the egg mass production relative to the body mass.
 - * Offspring quality-quantity trade-off, which sorts species along a continuum with species with a large relative egg mass and small clutch size in one end, and species with large clutch size and small relative egg size at the other end.

- **Chapter 3:**

- Theoretical models help to investigate the effects and mechanisms that affect the demography of species in novel or unfamiliar environments.
- Under maladaptive scenarios where the mismatch of phenotype to the environment is insufficient, simulations suggest that slow lived species, for which adults have more value than offspring, have more chances to be established.
- Behavioural responses interact with life history to influence the persistence of populations in novel and unknown environments. The benefits of learning behaviours are greater for slow strategies. Behaviours such as skipping a reproductive event, can improve the probabilities to be established for slow species while being detrimental for fast species. And finally, innate responses in a context of novel environments can be beneficial or impact negatively the probabilities to establish a population if preferences do not match habitat quality (ecological trap), being fast strategies more impacted by ecological traps on scenarios with higher offspring mortality and slow strategies more impacted on scenarios with higher adult mortality.

- **Chapter 4:**

- Slow-lived species tend to have a more risk-averse behaviour than fast-lived species.
- The relationship between flight initiation distance (FID) and the fast-slow continuum is largely mediated by differences in body size among species. Possible causes include a higher likelihood to be detected by predators, lower maneuverability to escape when attacked and higher energetic costs associated with flight.
- Flight initiation distance is shorter in urban than in rural environments. While slow-lived species showed shorter or larger FID according to the perception of risk, fast-lived species did not accommodate their FID to the degree of human frequentation. The changes in FID observed in slow-lived species may reflect plastic adjustments, selection, and/or a non-random sorting of individuals by behaviours that affect invasion success.

Appendix 2: Chapter 2 - Supplementary materials

Supplementary tables

Table A.2.1: Characteristics of the models used to select the PCs that better describe the generation time or elasticity to the fecundity. These models are used to define the fast-slow axes averaging and AIC weighting the PCs from the models predicting the elasticity to the fecundity (FSe) or generation time (FSgt) for each dataset and phylogeny. Columns describe the number of PCs included (n PCs), the variance explained by the PCs (PCvarExp), number of traits included in the PPCAs and the adjusted R^2 of the models predicting the elasticity to the fecundity or the generation time. Best AIC models include only the PCs with $\Delta AIC < 2$. The values with variability among PCs are reported as the mean \pm standard deviation. See the ESM for the complete data for all the models.

Axis	Phylogeny	Dataset	n PCs	PCvarExp	n traits	adjusted R^2
FSe	Ericson	maxN	7616	0.34 ± 0.08	7.29 ± 1.51	0.36 ± 0.11
		restricSet	7616	0.35 ± 0.07	7.29 ± 1.51	0.36 ± 0.11
	Hackett	maxN	7616	0.35 ± 0.07	7.29 ± 1.51	0.36 ± 0.11
		restricSet	7616	0.35 ± 0.07	7.29 ± 1.51	0.36 ± 0.11
FSe best AIC	Ericson	maxN	61	0.28 ± 0.05	6.02 ± 1.09	0.55 ± 0.01
		restricSet	59	0.28 ± 0.05	6 ± 1.11	0.55 ± 0.01
	Hackett	maxN	55	0.28 ± 0.05	5.98 ± 1.13	0.55 ± 0.01
		restricSet	103	0.3 ± 0.05	5.91 ± 1.2	0.55 ± 0.01
FSgt	Ericson	maxN	7616	0.34 ± 0.08	7.29 ± 1.51	0.39 ± 0.06
		restricSet	7616	0.35 ± 0.08	7.29 ± 1.51	0.39 ± 0.06
	Hackett	maxN	7616	0.35 ± 0.08	7.29 ± 1.51	0.39 ± 0.05
		restricSet	7616	0.35 ± 0.07	7.29 ± 1.51	0.39 ± 0.05
FSgt best AIC	Ericson	maxN	515	0.33 ± 0.07	6.27 ± 1.29	0.48 ± 0.01
		restricSet	499	0.33 ± 0.06	6.26 ± 1.28	0.48 ± 0.01
	Hackett	maxN	497	0.33 ± 0.07	6.23 ± 1.27	0.48 ± 0.01
		restricSet	468	0.34 ± 0.06	6.24 ± 1.28	0.48 ± 0.01

Table A.2.2: Mean \pm standard deviation AIC weighted loadings of the traits for the fast-slow axes based on models predicting generation time (FSgt) or elasticity to the fecundity (FSe) for all trait combination PCs o using only the PCs with AIC <2 (best AIC).

Phylogeny based on Ericson backbone								
	Restricted Set				Max N Set			
	FSe	FSe best AIC	FSgt	FSgt best AIC	FSe	FSe best AIC	FSgt	FSgt best AIC
CS	-0.44 \pm 0.3	-0.62 \pm 0.16	-0.4 \pm 0.32	-0.54 \pm 0.31	-0.43 \pm 0.31	-0.6 \pm 0.26	-0.39 \pm 0.33	-0.53 \pm 0.33
FEC	-0.3 \pm 0.32	-0.29 \pm 0.21	-0.39 \pm 0.33	-0.45 \pm 0.32	-0.29 \pm 0.32	-0.28 \pm 0.28	-0.39 \pm 0.33	-0.45 \pm 0.31
INC	0.18 \pm 0.42	0.01	0.33 \pm 0.42	0.36 \pm 0.39	0.18 \pm 0.42	0	0.33 \pm 0.42	0.36 \pm 0.39
DP	0.19 \pm 0.44	0.01	0.25 \pm 0.44	0.14 \pm 0.35	0.18 \pm 0.45	0.02 \pm 0.02	0.24 \pm 0.45	0.14 \pm 0.38
AFB	0.24 \pm 0.31	0.27 \pm 0.09	0.26 \pm 0.33	0.26 \pm 0.33	0.23 \pm 0.32	0.25 \pm 0.26	0.26 \pm 0.33	0.25 \pm 0.33
FLE	0.2 \pm 0.39	0.15 \pm 0.06	0.19 \pm 0.42	0.08 \pm 0.38	0.2 \pm 0.39	0.13 \pm 0.06	0.19 \pm 0.43	0.08 \pm 0.39
PRO	-0.12 \pm 0.36	-0.05 \pm 0.17	-0.12 \pm 0.39	0	-0.11 \pm 0.36	-0.05 \pm 0.18	-0.11 \pm 0.4	0
EMR	0.25 \pm 0.26	0.48 \pm 0.13	0.23 \pm 0.27	0.34 \pm 0.27	0.24 \pm 0.27	0.43 \pm 0.22	0.23 \pm 0.27	0.33 \pm 0.27
BM	0.04 \pm 0.53	0	0.05 \pm 0.54	0 \pm 0.03	0.04 \pm 0.53	0	0.05 \pm 0.54	0 \pm 0.01
OV	0 \pm 0.37	-0.02 \pm 0.21	0.07 \pm 0.38	0.11 \pm 0.33	0 \pm 0.36	-0.02 \pm 0.2	0.07 \pm 0.37	0.11 \pm 0.31
BV	-0.12 \pm 0.53	-0.35 \pm 0.23	-0.02 \pm 0.49	0.02 \pm 0.48	0.17 \pm 0.54	0.21 \pm 0.36	0.09 \pm 0.52	0.04 \pm 0.48
LFS	0.18 \pm 0.54	0.23 \pm 0.24	0.09 \pm 0.52	0.04 \pm 0.48	-0.11 \pm 0.53	-0.28 \pm 0.37	-0.01 \pm 0.48	0.04 \pm 0.46
RLS	0.17 \pm 0.52	0.2 \pm 0.25	0.09 \pm 0.5	0.06 \pm 0.46	0.16 \pm 0.52	0.17 \pm 0.38	0.08 \pm 0.5	0.03 \pm 0.45
PEP	0.05 \pm 0.38	0.18 \pm 0.22	-0.04 \pm 0.39	-0.03 \pm 0.24	0.05 \pm 0.38	0.16 \pm 0.22	-0.04 \pm 0.38	-0.02 \pm 0.24
Phylogeny based on Hackett backbone								
	Restricted Set				Max N Set			
	FSe	FSe best AIC	FSgt	FSgt best AIC	FSe	FSe best AIC	FSgt	FSgt best AIC
CS	-0.43 \pm 0.32	-0.6 \pm 0.23	-0.4 \pm 0.33	-0.54 \pm 0.33	-0.43 \pm 0.32	-0.6 \pm 0.24	-0.39 \pm 0.34	-0.53 \pm 0.34
FEC	-0.29 \pm 0.33	-0.26 \pm 0.27	-0.39 \pm 0.34	-0.45 \pm 0.33	-0.29 \pm 0.32	-0.28 \pm 0.26	-0.39 \pm 0.33	-0.44 \pm 0.33
INC	0.19 \pm 0.42	0.02 \pm 0.07	0.33 \pm 0.41	0.37 \pm 0.38	0.18 \pm 0.42	0	0.33 \pm 0.42	0.35 \pm 0.4
DP	0.19 \pm 0.45	0.06 \pm 0.06	0.25 \pm 0.44	0.14 \pm 0.37	0.18 \pm 0.45	0.01	0.25 \pm 0.45	0.13 \pm 0.41
AFB	0.24 \pm 0.32	0.25 \pm 0.09	0.26 \pm 0.34	0.26 \pm 0.34	0.23 \pm 0.32	0.27 \pm 0.2	0.26 \pm 0.35	0.25 \pm 0.37
FLE	0.2 \pm 0.39	0.16 \pm 0.19	0.19 \pm 0.42	0.07 \pm 0.38	0.2 \pm 0.39	0.11 \pm 0.33	0.2 \pm 0.41	0.08 \pm 0.38
PRO	-0.12 \pm 0.36	-0.04 \pm 0.16	-0.12 \pm 0.37	0	-0.11 \pm 0.36	-0.06 \pm 0.18	-0.12 \pm 0.39	0
EMR	0.25 \pm 0.28	0.45 \pm 0.18	0.23 \pm 0.28	0.34 \pm 0.29	0.24 \pm 0.27	0.45 \pm 0.2	0.23 \pm 0.28	0.33 \pm 0.29
BM	0.04 \pm 0.53	0	0.05 \pm 0.54	0 \pm 0.01	0.04 \pm 0.52	0	0.05 \pm 0.53	0 \pm 0
OV	0 \pm 0.38	-0.01 \pm 0.2	0.07 \pm 0.38	0.12 \pm 0.34	0.01 \pm 0.37	-0.01 \pm 0.21	0.08 \pm 0.36	0.12 \pm 0.29
BV	-0.11 \pm 0.55	-0.3 \pm 0.36	-0.01 \pm 0.5	0.02 \pm 0.49	0.17 \pm 0.55	0.2 \pm 0.37	0.1 \pm 0.52	0.05 \pm 0.48
LFS	0.17 \pm 0.56	0.2 \pm 0.39	0.09 \pm 0.53	0.04 \pm 0.51	-0.11 \pm 0.54	-0.29 \pm 0.36	-0.01 \pm 0.49	0.03 \pm 0.47
RLS	0.16 \pm 0.54	0.21 \pm 0.24	0.08 \pm 0.51	0.04 \pm 0.48	0.16 \pm 0.54	0.19 \pm 0.26	0.08 \pm 0.51	0.02 \pm 0.46
PEP	0.05 \pm 0.4	0.16 \pm 0.23	-0.05 \pm 0.39	-0.03 \pm 0.25	0.05 \pm 0.39	0.15 \pm 0.24	-0.04 \pm 0.39	-0.03 \pm 0.25

Table A.2.3: Relative weight of the life history traits in the fast-slow continuum. Values range from -1 to 1, where negative values means that the absolute value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait in the selected PPCAs (see main text for details). The loadings and frequencies come from selected PCs that better predict elasticities to the fecundity (FSe) or generation time (FSgt), weighted by the AIC based weight of the models taking all or only the models with $\Delta AIC < 2$ (best AIC).

Phylogeny based on Ericson backbone									
	Restricted Set				Max N Set				
	FSe	FSe best AIC	FSgt	FSgt best AIC	FSe	FSe best AIC	FSgt	FSgt best AIC	
CS	0.05	0.05	0.05	0.09	0.05	0.06	0.05	0.09	
FEC	0.03	-0.01	0.05	0.07	0.03	0.00	0.05	0.08	
INC	0.02	0.00	0.04	0.04	0.02	0.00	0.04	0.05	
DP	0.02	0.00	0.03	0.01	0.02	0.00	0.03	0.01	
AFB	0.01	0.01	0.02	0.01	0.01	0.01	0.02	0.01	
FLE	0.02	0.00	0.01	0.00	0.02	0.01	0.02	-0.01	
PRO	0.00	-0.01	0.01	0.00	0.00	-0.01	0.01	0.00	
EMR	0.01	0.03	0.00	0.01	0.00	0.02	0.00	0.01	
BM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
OV	-0.04	-0.03	-0.03	-0.01	-0.04	-0.03	-0.03	-0.01	
BV	-0.02	0.01	-0.05	-0.06	-0.01	0.01	-0.05	-0.08	
LFS	-0.01	0.01	-0.05	-0.08	-0.02	0.00	-0.05	-0.05	
RLS	-0.01	0.01	-0.05	-0.07	-0.01	0.00	-0.05	-0.08	
PEP	-0.06	-0.07	-0.04	-0.02	-0.06	-0.07	-0.04	-0.03	
Phylogeny based on Hackett backbone									
	Restricted Set				Max N Set				
	FSe	FSe best AIC	FSgt	FSgt best AIC	FSe	FSe best AIC	FSgt	FSgt best AIC	
CS	0.05	0.05	0.05	0.09	0.05	0.06	0.05	0.09	
FEC	0.03	0.00	0.05	0.07	0.03	0.00	0.05	0.08	
INC	0.02	0.00	0.04	0.05	0.02	0.00	0.04	0.04	
DP	0.02	0.00	0.03	0.01	0.02	0.00	0.03	0.01	
AFB	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01	
FLE	0.02	0.00	0.02	-0.01	0.02	-0.01	0.02	0.00	
PRO	0.00	-0.01	0.02	0.00	0.00	-0.01	0.01	0.00	
EMR	0.01	0.03	-0.01	0.01	0.00	0.03	-0.01	0.01	
BM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
OV	-0.04	-0.03	-0.03	-0.01	-0.04	-0.03	-0.03	-0.01	
BV	-0.02	0.01	-0.05	-0.05	-0.01	0.01	-0.05	-0.07	
LFS	-0.01	0.00	-0.05	-0.08	-0.02	0.00	-0.05	-0.05	
RLS	-0.02	0.01	-0.05	-0.08	-0.02	0.01	-0.05	-0.09	
PEP	-0.06	-0.07	-0.04	-0.02	-0.06	-0.08	-0.04	-0.02	

Table A.2.4: Characteristics of the PCs in each cluster defining other axes than the fast-slow for the life history variation. Columns describe the variance explained by the PCs (PCvarExp), number of traits included in the PPCAs (nTraits), the number of PCs (nPCs) and the main trait. The values with variability among PCs are reported as the mean \pm standard deviation.

Group	Axis	PCvarExp	nTraits	nPCs
Ericson-maxN				
Iteroparity	grCor0.7_11	0.36 \pm 0.09	7.41 \pm 1.4	780
	grCor0.7_30	0.37 \pm 0.1	7.53 \pm 1.49	521
	grCor0.75_1	0.4 \pm 0.1	7.42 \pm 1.38	577
	grCor0.8_63	0.41 \pm 0.09	7.71 \pm 1.51	591
Offspring Q-Q	grCor0.7_21	0.14 \pm 0.02	8.1 \pm 1.23	828
	grCor0.8_23	0.15 \pm 0.03	7.81 \pm 1.36	756
	grCor0.8_31	0.14 \pm 0.02	8.27 \pm 1.22	623
Lifelong prod.	grCor0.75_7	0.4 \pm 0.06	7.33 \pm 1.37	529
Ericson-Restricted Set				
Iteroparity	grCor0.7_1	0.38 \pm 0.1	7.47 \pm 1.44	649
	grCor0.7_13	0.36 \pm 0.09	7.53 \pm 1.36	793
	grCor0.75_1	0.38 \pm 0.1	7.63 \pm 1.39	546
	grCor0.8_60	0.41 \pm 0.09	7.77 \pm 1.47	623
Offspring Q-Q	grCor0.7_17	0.15 \pm 0.03	7.65 \pm 1.27	736
	grCor0.7_19	0.15 \pm 0.03	7.72 \pm 1.4	487
	grCor0.8_22	0.15 \pm 0.03	7.7 \pm 1.32	601
Lifelong prod.	grCor0.8_5	0.39 \pm 0.06	7.47 \pm 1.41	674
Hackett-maxN				
Iteroparity	grCor0.7_11	0.36 \pm 0.08	7.39 \pm 1.4	855
	grCor0.75_1	0.37 \pm 0.11	7.53 \pm 1.53	477
	grCor0.75_11	0.4 \pm 0.07	7.38 \pm 1.39	545
Offspring Q-Q	grCor0.8_25	0.15 \pm 0.03	7.89 \pm 1.31	645
	grCor0.85_31	0.15 \pm 0.03	7.88 \pm 1.35	533
Lifelong prod.	grCor0.75_5	0.38 \pm 0.06	7.5 \pm 1.43	691
Hackett-Restricted Set				
Iteroparity	grCor0.7_43	0.4 \pm 0.09	7.77 \pm 1.49	672
	grCor0.75_18	0.37 \pm 0.09	7.47 \pm 1.38	487
	grCor0.75_29	0.33 \pm 0.08	7.84 \pm 1.43	586
Offspring Q-Q	grCor0.7_17	0.15 \pm 0.03	7.9 \pm 1.29	831
	grCor0.75_19	0.15 \pm 0.03	8.01 \pm 1.3	710
	grCor0.8_24	0.15 \pm 0.03	7.82 \pm 1.43	514
Lifelong prod.	grCor0.8_5	0.4 \pm 0.05	7.41 \pm 1.33	522

Table A.2.5: Mean \pm standard deviation of the loadings of the traits for clusters of similar significant PCs (Eigenvalue >1) not selected for the fast-slow axes. Each group contains PCs with scores correlation greater than the correlation specified in the group name (e.g. gr0.8 means correlation >0.8). The main trait of the axes appear among brackets, following the conventions in the table 2.1.

Phylogeny based on Ericson backbone and max N dataset								
	Iteroparity				Offspring Q-Q			Lifelong prod.
	gr0.7_11	gr0.7_30	gr0.75_1	gr0.8_63	gr0.7_21	gr0.8_23	gr0.8_31	gr0.75_7
BV	-0.45 \pm 0.01	-0.55 \pm 0.04	-0.6 \pm 0.07	-0.58 \pm 0.01	-0.02 \pm 0.08	0.01 \pm 0.1	-0.01 \pm 0.02	0.22 \pm 0.13
OV	-0.46 \pm 0.03	-0.29 \pm 0.02	-0.41 \pm 0.09	-0.56 \pm 0.01	0.02 \pm 0.08	0.02 \pm 0.11	0.02 \pm 0.01	0.45 \pm 0.06
LFS	0.45 \pm 0.04	0.73 \pm 0.08	0.69 \pm 0.12	0.56 \pm 0.03	0.02 \pm 0.12	-0.05 \pm 0.11	0.01 \pm 0.03	-0.27 \pm 0.15
RLS	0.47 \pm 0.03	0.73 \pm 0.08	0.66 \pm 0.12	0.59 \pm 0.02	0.02 \pm 0.12	-0.06 \pm 0.11	0.01 \pm 0.03	-0.3 \pm 0.15
EMR	-0.04 \pm 0.07	0.04 \pm 0.09	0.01 \pm 0.05	0 \pm 0.06	0.86 \pm 0.04	0.91 \pm 0.05	0.87 \pm 0.05	0.05 \pm 0.08
BM	-0.02 \pm 0.09	0.11 \pm 0.08	0.06 \pm 0.09	0.03 \pm 0.06	-0.21 \pm 0.08	-0.01 \pm 0.08	-0.15 \pm 0.05	0.04 \pm 0.09
PRO	0.24 \pm 0.11	0.04 \pm 0.1	0.06 \pm 0.09	0.14 \pm 0.06	0.1 \pm 0.09	0.4 \pm 0.07	0.13 \pm 0.06	-0.5 \pm 0.11
PEP	0.52 \pm 0.03	0.46 \pm 0.02	0.63 \pm 0.08	0.77 \pm 0.02	0.13 \pm 0.08	0.07 \pm 0.14	0.13 \pm 0.02	-0.74 \pm 0.06
AFB	-0.09 \pm 0.07	0.06 \pm 0.05	0.01 \pm 0.14	-0.03 \pm 0.04	0.03 \pm 0.11	0.09 \pm 0.09	0.06 \pm 0.04	0.18 \pm 0.07
CS	0.26 \pm 0.08	0.09 \pm 0.12	0.1 \pm 0.09	0.15 \pm 0.06	-0.23 \pm 0.09	-0.1 \pm 0.09	-0.21 \pm 0.06	-0.48 \pm 0.08
FEC	0.43 \pm 0.08	0.15 \pm 0.09	0.25 \pm 0.1	0.38 \pm 0.05	-0.14 \pm 0.1	0.01 \pm 0.12	-0.15 \pm 0.05	-0.55 \pm 0.08
DP	-0.09 \pm 0.05	0.11 \pm 0.06	0.05 \pm 0.07	-0.01 \pm 0.04	-0.1 \pm 0.07	0.02 \pm 0.1	-0.12 \pm 0.04	0.12 \pm 0.08
FLE	-0.06 \pm 0.05	0.12 \pm 0.06	0.06 \pm 0.07	0.01 \pm 0.04	-0.19 \pm 0.07	-0.03 \pm 0.11	-0.21 \pm 0.04	0.1 \pm 0.07
INC	-0.12 \pm 0.04	0.06 \pm 0.05	0.01 \pm 0.07	-0.04 \pm 0.03	0.02 \pm 0.04	0.12 \pm 0.09	0.04 \pm 0.03	0.17 \pm 0.09
Phylogeny based on Ericson backbone and restricted dataset								
	Iteroparity				Offspring Q-Q			Lifelong prod.
	gr0.7_1	gr0.7_13	gr0.75_1	gr0.8_60	gr0.7_17	gr0.7_19	gr0.8_22	gr0.8_5
BV	-0.49 \pm 0.01	-0.42 \pm 0.12	-0.47 \pm 0.1	-0.58 \pm 0.02	0 \pm 0.05	0 \pm 0.01	0 \pm 0.13	-0.28 \pm 0.15
OV	-0.55 \pm 0.01	-0.41 \pm 0.07	-0.54 \pm 0.11	-0.58 \pm 0.01	0.02 \pm 0.03	0.02 \pm 0.01	0.02 \pm 0.1	-0.36 \pm 0.14
LFS	0.69 \pm 0.03	0.45 \pm 0.16	0.71 \pm 0.13	0.56 \pm 0.04	-0.03 \pm 0.09	-0.04 \pm 0.03	-0.03 \pm 0.14	0.21 \pm 0.14
RLS	0.65 \pm 0.03	0.48 \pm 0.16	0.66 \pm 0.14	0.58 \pm 0.03	-0.03 \pm 0.09	-0.05 \pm 0.17	-0.03 \pm 0.14	0.24 \pm 0.14
EMR	-0.01 \pm 0.08	-0.05 \pm 0.06	-0.01 \pm 0.03	-0.01 \pm 0.04	0.89 \pm 0.07	0.89 \pm 0.08	0.9 \pm 0.04	-0.06 \pm 0.09
BM	0.07 \pm 0.06	-0.03 \pm 0.12	0.08 \pm 0.06	0.03 \pm 0.05	-0.13 \pm 0.08	0 \pm 0.07	-0.13 \pm 0.06	-0.07 \pm 0.06
PRO	0.08 \pm 0.05	0.3 \pm 0.09	0.08 \pm 0.08	0.15 \pm 0.07	0.26 \pm 0.12	0.38 \pm 0.07	0.3 \pm 0.08	0.57 \pm 0.08
PEP	0.45 \pm 0.02	0.57 \pm 0.07	0.53 \pm 0.12	0.77 \pm 0.02	0.1 \pm 0.02	0.09 \pm 0.02	0.1 \pm 0.12	0.74 \pm 0.19
AFB	0.01 \pm 0.03	-0.1 \pm 0.08	0.01 \pm 0.08	-0.03 \pm 0.04	0.01 \pm 0.06	0.12 \pm 0.04	0.02 \pm 0.09	-0.22 \pm 0.09
CS	0.16 \pm 0.09	0.3 \pm 0.08	0.17 \pm 0.09	0.16 \pm 0.06	-0.16 \pm 0.11	-0.03 \pm 0.09	-0.18 \pm 0.09	0.37 \pm 0.11
FEC	0.25 \pm 0.06	0.39 \pm 0.08	0.26 \pm 0.12	0.37 \pm 0.05	-0.09 \pm 0.09	0.02 \pm 0.09	-0.07 \pm 0.12	0.59 \pm 0.13
DP	0.05 \pm 0.04	-0.1 \pm 0.1	0.05 \pm 0.05	-0.01 \pm 0.05	-0.04 \pm 0.07	0.04 \pm 0.05	-0.04 \pm 0.07	-0.19 \pm 0.09
FLE	0.06 \pm 0.04	-0.07 \pm 0.1	0.06 \pm 0.05	0 \pm 0.04	-0.11 \pm 0.06	-0.01 \pm 0.05	-0.08 \pm 0.09	-0.15 \pm 0.11
INC	0.01 \pm 0.03	-0.13 \pm 0.09	0 \pm 0.06	-0.05 \pm 0.04	0.03 \pm 0.06	0.13 \pm 0.04	0.04 \pm 0.08	-0.22 \pm 0.07

Phylogeny based on Hackett backbone and max N dataset

	Iteroparity			Offspring Q-Q		Lifelong prod.
	gr0.7_11	gr0.75_1	gr0.75_11	gr0.8_25	gr0.85_31	gr0.75_5
BV	-0.37 ± 0.11	-0.57 ± 0.13	-0.44 ± 0.11	0.01 ± 0.04	0.01 ± 0.02	-0.29 ± 0.04
OV	-0.5 ± 0.1	-0.6 ± 0.08	-0.59 ± 0.1	0.03 ± 0.02	0.02 ± 0.01	-0.25 ± 0.02
LFS	0.45 ± 0.12	0.56 ± 0.17	0.39 ± 0.11	-0.04 ± 0.08	-0.06 ± 0.03	0.21 ± 0.07
RLS	0.48 ± 0.13	0.57 ± 0.17	0.43 ± 0.11	-0.04 ± 0.08	-0.07 ± 0.03	0.23 ± 0.07
EMR	-0.06 ± 0.03	-0.02 ± 0.07	-0.03 ± 0.05	0.9 ± 0.1	0.9 ± 0.08	-0.06 ± 0.07
BM	-0.02 ± 0.06	0.06 ± 0.13	-0.03 ± 0.04	-0.12 ± 0.1	0 ± 0.06	-0.14 ± 0.06
PRO	0.23 ± 0.07	0.11 ± 0.1	0.29 ± 0.08	0.26 ± 0.1	0.42 ± 0.05	0.59 ± 0.07
PEP	0.52 ± 0.11	0.4 ± 0.07	0.73 ± 0.12	0.12 ± 0.02	0.06 ± 0.02	0.71 ± 0.02
AFB	-0.09 ± 0.1	0 ± 0.08	-0.1 ± 0.08	0.04 ± 0.06	0.1 ± 0.04	-0.23 ± 0.05
CS	0.28 ± 0.07	0.14 ± 0.09	0.24 ± 0.07	-0.18 ± 0.09	-0.05 ± 0.09	0.35 ± 0.09
FEC	0.46 ± 0.11	0.37 ± 0.08	0.53 ± 0.12	-0.08 ± 0.08	0.03 ± 0.06	0.48 ± 0.06
DP	-0.09 ± 0.06	0.03 ± 0.1	-0.08 ± 0.09	-0.04 ± 0.07	0.03 ± 0.04	-0.23 ± 0.07
FLE	-0.07 ± 0.07	0.05 ± 0.1	-0.07 ± 0.09	-0.13 ± 0.07	-0.02 ± 0.04	-0.19 ± 0.06
INC	-0.12 ± 0.07	-0.02 ± 0.09	-0.11 ± 0.08	0.04 ± 0.05	0.14 ± 0.03	-0.27 ± 0.06

Phylogeny based on Hacket backbone and restricted dataset

	Iteroparity			Offspring Q-Q			Lifelong prod.
	gr0.7_43	gr0.75_18	gr0.75_29	gr0.7_17	gr0.75_19	gr0.8_24	gr0.8_5
BV	-0.55 ± 0.12	-0.57 ± 0.01	-0.32 ± 0.14	0.01 ± 0.01	0 ± 0.04	0.01 ± 0.12	-0.25 ± 0.08
OV	-0.48 ± 0.1	-0.45 ± 0.02	-0.39 ± 0.08	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.1	-0.33 ± 0.09
LFS	0.65 ± 0.12	0.43 ± 0.04	0.64 ± 0.16	-0.03 ± 0.04	-0.02 ± 0.06	-0.06 ± 0.12	0.16 ± 0.1
RLS	0.62 ± 0.11	0.48 ± 0.04	0.61 ± 0.16	-0.03 ± 0.04	-0.02 ± 0.07	-0.07 ± 0.13	0.19 ± 0.1
EMR	0 ± 0.06	-0.03 ± 0.06	0.02 ± 0.06	0.89 ± 0.05	0.9 ± 0.05	0.9 ± 0.03	-0.06 ± 0.03
BM	0.03 ± 0.06	-0.01 ± 0.08	0.12 ± 0.13	-0.12 ± 0.05	-0.14 ± 0.07	0 ± 0.07	-0.1 ± 0.07
PRO	0.12 ± 0.08	0.29 ± 0.08	0.06 ± 0.08	0.28 ± 0.06	0.27 ± 0.1	0.41 ± 0.09	0.68 ± 0.1
PEP	0.82 ± 0.13	0.6 ± 0.04	0.59 ± 0.07	0.11 ± 0.02	0.12 ± 0.02	0.07 ± 0.11	0.78 ± 0.09
AFB	-0.01 ± 0.07	-0.07 ± 0.05	0.05 ± 0.08	0.04 ± 0.04	0.05 ± 0.04	0.11 ± 0.1	-0.22 ± 0.09
CS	0.15 ± 0.08	0.17 ± 0.08	0.14 ± 0.07	-0.21 ± 0.08	-0.22 ± 0.08	-0.03 ± 0.11	0.42 ± 0.11
FEC	0.32 ± 0.13	0.4 ± 0.09	0.21 ± 0.06	-0.06 ± 0.06	-0.06 ± 0.07	0.03 ± 0.11	0.52 ± 0.12
DP	0 ± 0.08	-0.07 ± 0.07	0.13 ± 0.1	-0.05 ± 0.05	-0.05 ± 0.05	0.04 ± 0.07	-0.18 ± 0.06
FLE	0.02 ± 0.09	-0.05 ± 0.06	0.14 ± 0.1	-0.13 ± 0.05	-0.12 ± 0.05	-0.02 ± 0.08	-0.16 ± 0.06
INC	-0.03 ± 0.07	-0.1 ± 0.06	0.06 ± 0.1	0.04 ± 0.05	0.04 ± 0.04	0.14 ± 0.07	-0.22 ± 0.05

Table A.2.6: Relative weights of the life history traits for each axes described in the table A.2.4. Values range from -1 to 1, where negative values means that the absolute value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait in the selected PPCAs (see main text for details).

Phylogeny based on Ericson backbone and max N dataset								
	Iteroparity				Offspring Q-Q			Lifelong prod.
	gr0.7_11	gr0.7_30	gr0.75_1	gr0.8_63	gr0.7_21	gr0.8_23	gr0.8_31	gr0.75_7
BV	0.05	0.08	0.08	0.07	-0.05	-0.05	-0.05	0.01
OV	0.06	0.04	0.06	0.07	-0.04	-0.05	-0.04	0.04
LFS	0.04	0.10	0.09	0.06	-0.06	-0.05	-0.06	-0.01
RLS	0.04	0.10	0.09	0.06	-0.06	-0.05	-0.06	0.00
EMR	-0.05	-0.06	-0.07	-0.06	0.29	0.35	0.29	-0.06
BM	-0.05	-0.02	-0.03	-0.05	0.02	0.00	0.00	-0.01
PRO	0.00	-0.04	-0.02	-0.02	0.01	0.09	0.01	0.02
PEP	0.07	0.06	0.08	0.09	-0.02	-0.02	-0.03	0.06
AFB	-0.04	-0.05	-0.06	-0.05	-0.06	-0.03	-0.04	-0.03
CS	0.00	-0.06	-0.03	-0.01	0.04	-0.02	0.04	0.01
FEC	0.02	-0.04	-0.02	0.00	0.00	-0.09	0.00	0.04
DP	-0.04	-0.03	-0.05	-0.06	-0.02	-0.05	-0.03	-0.02
FLE	-0.05	-0.03	-0.05	-0.06	0.01	-0.04	0.01	-0.03
INC	-0.04	-0.05	-0.07	-0.05	-0.05	-0.01	-0.04	-0.02
Phylogeny based on Ericson backbone and restricted dataset								
	Iteroparity				Offspring Q-Q			Lifelong prod.
	gr0.7_1	gr0.7_13	gr0.75_1	gr0.8_60	gr0.7_17	gr0.7_19	gr0.8_22	gr0.8_5
BV	0.07	0.05	0.07	0.07	-0.05	-0.06	-0.05	0.01
OV	0.08	0.05	0.08	0.07	-0.04	-0.05	-0.04	0.03
LFS	0.09	0.03	0.09	0.06	-0.06	-0.05	-0.06	-0.02
RLS	0.09	0.04	0.09	0.06	-0.06	-0.04	-0.06	-0.01
EMR	-0.06	-0.05	-0.06	-0.06	0.33	0.36	0.33	-0.05
BM	-0.03	-0.04	-0.03	-0.05	0.02	0.00	0.01	-0.01
PRO	-0.03	0.00	-0.03	-0.02	0.05	0.09	0.06	0.03
PEP	0.06	0.07	0.07	0.09	-0.02	-0.01	-0.02	0.06
AFB	-0.06	-0.04	-0.06	-0.05	-0.07	-0.01	-0.07	-0.03
CS	-0.02	0.00	-0.02	-0.01	0.01	-0.03	0.01	0.01
FEC	-0.02	0.02	-0.02	0.00	-0.03	-0.10	-0.03	0.04
DP	-0.05	-0.04	-0.05	-0.06	-0.03	-0.04	-0.04	-0.02
FLE	-0.05	-0.05	-0.05	-0.06	0.00	-0.05	-0.01	-0.02
INC	-0.07	-0.03	-0.07	-0.05	-0.05	0.00	-0.04	-0.01

Phylogeny based on Hackett backbone and max N dataset

	Iteroparity			Offspring Q-Q		Lifelong prod.
	gr0.7_11	gr0.75_1	gr0.75_11	gr0.8_25	gr0.85_31	gr0.75_5
BV	0.04	0.08	0.04	-0.05	-0.05	0.00
OV	0.06	0.09	0.06	-0.04	-0.05	0.02
LFS	0.03	0.07	0.02	-0.05	-0.05	-0.02
RLS	0.04	0.08	0.02	-0.05	-0.04	-0.02
EMR	-0.05	-0.06	-0.05	0.32	0.35	-0.05
BM	-0.05	-0.03	-0.03	0.01	0.00	-0.01
PRO	0.00	-0.02	0.00	0.04	0.09	0.04
PEP	0.06	0.06	0.08	-0.03	-0.02	0.06
AFB	-0.04	-0.07	-0.04	-0.06	-0.02	-0.02
CS	0.00	-0.01	0.00	0.01	-0.02	0.01
FEC	0.02	0.00	0.02	-0.03	-0.09	0.03
DP	-0.04	-0.06	-0.03	-0.03	-0.04	-0.01
FLE	-0.05	-0.06	-0.04	0.00	-0.04	-0.02
INC	-0.04	-0.06	-0.03	-0.04	-0.01	-0.01

Phylogeny based on Hackett backbone and restricted dataset

	Iteroparity			Offspring Q-Q			Lifelong prod.
	gr0.7_43	gr0.75_18	gr0.75_29	gr0.7_17	gr0.75_19	gr0.8_24	gr0.8_5
BV	0.07	0.07	0.05	-0.05	-0.05	-0.05	0.00
OV	0.06	0.06	0.06	-0.04	-0.05	-0.05	0.02
LFS	0.07	0.04	0.09	-0.06	-0.07	-0.05	-0.03
RLS	0.07	0.05	0.09	-0.06	-0.07	-0.04	-0.02
EMR	-0.06	-0.06	-0.05	0.32	0.32	0.34	-0.05
BM	-0.04	-0.04	-0.03	0.01	0.01	0.00	-0.01
PRO	-0.02	-0.01	-0.03	0.05	0.05	0.09	0.04
PEP	0.10	0.08	0.08	-0.02	-0.01	-0.02	0.06
AFB	-0.05	-0.04	-0.06	-0.06	-0.05	-0.01	-0.02
CS	-0.02	-0.01	-0.04	0.02	0.02	-0.02	0.01
FEC	-0.01	0.02	-0.02	-0.03	-0.03	-0.10	0.04
DP	-0.06	-0.05	-0.05	-0.03	-0.04	-0.04	-0.01
FLE	-0.06	-0.05	-0.04	0.00	0.00	-0.04	-0.02
INC	-0.05	-0.04	-0.06	-0.04	-0.04	-0.01	-0.01

Table A.2.7: Phylogenetic signal of the life history traits and the averaged life history axes from the PPCAs. All Pagel's λ and Blomberg's K are significant with p-value <0.001.

Group	Trait/Axis	K Ericson	K Hackett	λ Ericson	λ Hackett
Traits	AFB	0.34	0.33	0.92	0.91
	BM	2.62	2.67	0.99	0.99
	BV	0.09	0.09	0.62	0.62
	CS	0.63	0.71	0.97	0.97
	DP	1.10	1.16	0.95	0.95
	EMR	1.04	1.11	0.93	0.93
	FEC	0.51	0.56	0.94	0.94
	FLE	0.60	0.62	0.93	0.93
	INC	2.42	2.59	0.98	0.98
	LFS	0.11	0.11	0.71	0.70
	OV	0.14	0.15	0.71	0.71
	PEP	0.12	0.13	0.73	0.73
	PRO	0.48	0.50	0.95	0.95
	RLS	0.11	0.12	0.71	0.71
FSe	FSe best AIC-Ericson-maxN	0.70		0.96	
	FSe best AIC-Ericson-restricSet	0.88		0.96	
	FSe best AIC-Hackett-maxN		0.67		0.95
	FSe best AIC-Hackett-restricSet		0.97		0.96
	FSe-Ericson-maxN	0.62		0.95	
	FSe-Ericson-restricSet	1.34		0.97	
	FSe-Hackett-maxN		0.63		0.94
FSe-Hackett-restricSet		1.34		0.97	
FSgt	FSgt best AIC-Ericson-maxN	0.97		0.97	
	FSgt best AIC-Ericson-restricSet	1.59		0.98	
	FSgt best AIC-Hackett-maxN		1.05		0.97
	FSgt best AIC-Hackett-restricSet		1.78		0.98
	FSgt-Ericson-maxN	0.81		0.96	
	FSgt-Ericson-restricSet	1.79		0.98	
	FSgt-Hackett-maxN		0.86		0.96
FSgt-Hackett-restricSet		1.89		0.98	
Iteroparity	gr0.7_11-Ericson-maxN	0.15		0.75	
	gr0.7_30-Ericson-maxN	0.12		0.62	
	gr0.75_1-Ericson-maxN	0.10		0.56	
	gr0.8_63-Ericson-maxN	0.10		0.60	
	gr0.7_1-Ericson-restricSet	0.10		0.58	
	gr0.7_13-Ericson-restricSet	0.16		0.74	
	gr0.75_1-Ericson-restricSet	0.10		0.58	
	gr0.8_60-Ericson-restricSet	0.10		0.57	
	gr0.7_11-Hackett-maxN		0.17		0.76
	gr0.75_1-Hackett-maxN		0.12		0.61
	gr0.75_11-Hackett-maxN		0.17		0.77
	gr0.7_43-Hackett-restricSet		0.10		0.53
	gr0.75_18-Hackett-restricSet		0.14		0.66
	gr0.75_29-Hackett-restricSet		0.14		0.64

Group	Axis	K Ericson	K Hackett	λ Ericson	λ Hackett
Offspring Q-Q	gr0.7_21-Ericson-maxN	0.44		0.92	
	gr0.8_23-Ericson-maxN	0.70		0.92	
	gr0.8_31-Ericson-maxN	0.49		0.92	
	gr0.7_17-Ericson-restricSet	0.61		0.92	
	gr0.7_19-Ericson-restricSet	0.95		0.92	
	gr0.8_22-Ericson-restricSet	0.64		0.92	
	gr0.8_25-Hackett-maxN		0.61		0.92
	gr0.85_31-Hackett-maxN		0.86		0.92
	gr0.7_17-Hackett-restricSet		0.71		0.92
	gr0.75_19-Hackett-restricSet		0.71		0.92
	gr0.8_24-Hackett-restricSet		1.06		0.92
Lifelong prod.	gr0.75_7-Ericson-maxN	0.29		0.88	
	gr0.8_5-Ericson-restricSet	0.38		0.89	
	gr0.75_5-Hackett-maxN		0.35		0.88
	gr0.8_5-Hackett-restricSet		0.48		0.91

Table A.2.8: Phylogenetic corrected correlation among life history traits and the averaged life history axes from PPCAs. All axes in the columns are for the restricted data set and Hackett phylogeny.

Group	Trait/Axis	FSe best AIC	FSe	FSgt best AIC	FSgt
Traits	CS	-0.66	-0.58	-0.81	-0.73
	F / AFB	-0.60	-0.65	-0.84	-0.84
	FEC	-0.51	-0.53	-0.80	-0.77
	AFB	0.42	0.48	0.49	0.52
	FLE	0.39	0.57	0.42	0.58
	DP	0.46	0.66	0.56	0.71
	INC	0.41	0.58	0.64	0.69
	EMR	0.53	0.38	0.51	0.38
	LFS	0.66	0.67	0.09	0.22
	RLS	0.64	0.63	0.05	0.18
	BV	-0.55	-0.50	0.10	0.00
	PRO	-0.38	-0.54	-0.63	-0.72
	BM	0.34	0.51	0.34	0.49
	OV	-0.24	-0.23	0.41	0.28
	PEP	0.22	0.11	-0.41	-0.37
FSe	FSe best AIC-Ericson-maxN	1.00	0.94	0.76	0.77
	FSe best AIC-Ericson-restricSet	1.00	0.94	0.74	0.75
	FSe best AIC-Hackett-maxN	1.00	0.94	0.75	0.76
	FSe best AIC-Hackett-restricSet	1.00	0.95	0.75	0.77
	FSe-Ericson-maxN	0.95	1.00	0.79	0.87
	FSe-Ericson-restricSet	0.95	1.00	0.79	0.87
	FSe-Hackett-maxN	0.95	1.00	0.78	0.86
	FSe-Hackett-restricSet	0.95	1.00	0.77	0.86
FSgt	FSgt best AIC-Ericson-maxN	0.76	0.79	1.00	0.97
	FSgt best AIC-Ericson-restricSet	0.75	0.78	1.00	0.97
	FSgt best AIC-Hackett-maxN	0.75	0.78	1.00	0.97
	FSgt best AIC-Hackett-restricSet	0.75	0.77	1.00	0.97
	FSgt-Ericson-maxN	0.77	0.87	0.97	1.00
	FSgt-Ericson-restricSet	0.77	0.86	0.97	1.00

Group	Axis	FSe best AIC	FSe	FSgt best AIC	FSgt
FSgt	FSgt-Hackett-maxN	0.77	0.87	0.97	1.00
	FSgt-Hackett-restricSet	0.77	0.86	0.97	1.00
Iteroparity	gr0.7_11-Ericson-maxN	0.15	0.09	-0.51	-0.42
	gr0.8_63-Ericson-maxN	0.32	0.28	-0.35	-0.24
	gr0.7_30-Ericson-maxN	0.55	0.54	-0.09	0.05
	gr0.75_1-Ericson-maxN	0.45	0.42	-0.21	-0.09
	gr0.7_1-Ericson-restricSet	0.42	0.41	-0.24	-0.11
	gr0.75_1-Ericson-restricSet	0.41	0.39	-0.25	-0.12
	gr0.7_13-Ericson-restricSet	0.13	0.07	-0.53	-0.44
	gr0.8_60-Ericson-restricSet	0.32	0.27	-0.35	-0.25
	gr0.7_11-Hackett-maxN	0.13	0.08	-0.53	-0.44
	gr0.75_11-Hackett-maxN	0.12	0.05	-0.53	-0.45
	gr0.75_1-Hackett-maxN	0.36	0.34	-0.30	-0.18
	gr0.7_43-Hackett-restricSet	0.36	0.32	-0.30	-0.20
	gr0.75_29-Hackett-restricSet	0.48	0.47	-0.16	-0.03
	gr0.75_18-Hackett-restricSet	0.21	0.15	-0.46	-0.37
	Offspring Q-Q	gr0.7_21-Ericson-maxN	0.48	0.25	0.40
gr0.8_31-Ericson-maxN		0.48	0.25	0.41	0.22
gr0.8_23-Ericson-maxN		0.37	0.19	0.32	0.17
gr0.7_17-Ericson-restricSet		0.38	0.16	0.33	0.15
gr0.7_19-Ericson-restricSet		0.38	0.22	0.31	0.18
gr0.8_22-Ericson-restricSet		0.39	0.18	0.34	0.16
gr0.8_25-Hackett-maxN		0.39	0.17	0.34	0.16
gr0.85_31-Hackett-maxN		0.33	0.17	0.31	0.16
gr0.7_17-Hackett-restricSet		0.39	0.17	0.33	0.15
gr0.75_19-Hackett-restricSet		0.42	0.20	0.34	0.16
gr0.8_24-Hackett-restricSet	0.33	0.17	0.30	0.16	
Lifelong prod.	gr0.75_7-Ericson-maxN	0.12	0.20	0.70	0.65
	gr0.8_5-Ericson-restricSet	-0.17	-0.27	-0.74	-0.71
	gr0.75_5-Hackett-maxN	-0.19	-0.31	-0.75	-0.74
	gr0.8_5-Hackett-restricSet	-0.21	-0.32	-0.76	-0.74

Group	Trait/Axis	Iteroparity			Offspring Q-Q			Lifelong prod. gr0.8_5
		gr0.7_43	gr0.75_29	gr0.75_18	gr0.7_17	gr0.75_19	gr0.8_24	
Traits	CS	0.30	0.22	0.41	-0.28	-0.29	-0.12	0.64
	F / AFB	0.31	0.17	0.46	-0.08	-0.09	-0.03	0.76
	FEC	0.44	0.32	0.58	-0.09	-0.09	0.06	0.82
	AFB	-0.03	0.09	-0.13	0.04	0.05	0.14	-0.35
	FLE	0.03	0.20	-0.10	-0.22	-0.20	-0.04	-0.36
	DP	0.01	0.19	-0.14	-0.14	-0.13	0.05	-0.44
	INC	-0.06	0.08	-0.19	0.03	0.04	0.17	-0.43
	EMR	0.00	0.04	-0.05	0.93	0.93	0.93	-0.09
	LFS	0.85	0.91	0.75	-0.06	-0.03	-0.08	0.35
	RLS	0.86	0.92	0.76	-0.07	-0.03	-0.10	0.38
	BV	-0.94	-0.94	-0.89	-0.01	-0.04	0.00	-0.59
	PRO	0.30	0.14	0.46	0.42	0.41	0.48	0.79
	BM	0.08	0.22	-0.04	-0.30	-0.29	-0.16	-0.35
	OV	-0.98	-0.95	-0.97	0.13	0.09	0.06	-0.79
PEP	0.91	0.84	0.95	0.23	0.25	0.24	0.89	
FSe	FSe best AIC-Ericson-maxN	0.33	0.45	0.18	0.40	0.43	0.33	-0.23
	FSe best AIC-Ericson-restricSet	0.37	0.48	0.22	0.41	0.44	0.35	-0.19
	FSe best AIC-Hackett-maxN	0.35	0.46	0.20	0.41	0.44	0.34	-0.22
	FSe best AIC-Hackett-restricSet	0.36	0.48	0.21	0.39	0.42	0.33	-0.21
	FSe-Ericson-maxN	0.30	0.45	0.12	0.17	0.20	0.17	-0.34
	FSe-Ericson-restricSet	0.30	0.46	0.13	0.17	0.20	0.17	-0.34
	FSe-Hackett-maxN	0.32	0.47	0.14	0.17	0.20	0.17	-0.33
	FSe-Hackett-restricSet	0.32	0.47	0.15	0.17	0.20	0.17	-0.32
FSgt	FSgt best AIC-Ericson-maxN	-0.28	-0.13	-0.43	0.32	0.33	0.30	-0.74
	FSgt best AIC-Ericson-restricSet	-0.29	-0.15	-0.45	0.33	0.34	0.30	-0.75
	FSgt best AIC-Hackett-maxN	-0.29	-0.15	-0.44	0.33	0.34	0.30	-0.75
	FSgt best AIC-Hackett-restricSet	-0.30	-0.16	-0.46	0.33	0.34	0.30	-0.76
	FSgt-Ericson-maxN	-0.19	-0.02	-0.36	0.15	0.16	0.16	-0.73
	FSgt-Ericson-restricSet	-0.20	-0.03	-0.37	0.15	0.16	0.16	-0.73
	FSgt-Hackett-maxN	-0.19	-0.02	-0.36	0.15	0.16	0.16	-0.73
	FSgt-Hackett-restricSet	-0.20	-0.03	-0.37	0.15	0.16	0.16	-0.74

Group	Axis	Iteroparity			Offspring Q-Q			Lifelong prod.
		gr0.7_43	gr0.75_29	gr0.75_18	gr0.7_17	gr0.75_19	gr0.8_24	gr0.8_5
Iteroparity	gr0.7_11-Ericson-maxN	0.97	0.91	1.00	-0.03	-0.01	-0.01	0.89
	gr0.8_63-Ericson-maxN	1.00	0.97	0.99	-0.01	0.02	0.02	0.80
	gr0.7_30-Ericson-maxN	0.97	0.99	0.90	-0.03	0.01	0.01	0.58
	gr0.75_1-Ericson-maxN	0.99	0.99	0.95	-0.02	0.01	0.01	0.69
	gr0.7_1-Ericson-restricSet	0.99	0.99	0.95	-0.06	-0.03	-0.02	0.69
	gr0.75_1-Ericson-restricSet	0.99	0.99	0.96	-0.06	-0.02	-0.01	0.70
	gr0.7_13-Ericson-restricSet	0.97	0.90	1.00	-0.02	0.01	0.00	0.91
	gr0.8_60-Ericson-restricSet	1.00	0.97	0.99	-0.01	0.02	0.02	0.80
	gr0.7_11-Hackett-maxN	0.97	0.91	1.00	-0.05	-0.02	-0.02	0.90
	gr0.75_11-Hackett-maxN	0.96	0.89	0.99	0.00	0.02	0.03	0.92
	gr0.75_1-Hackett-maxN	1.00	0.99	0.97	-0.07	-0.04	-0.02	0.74
	gr0.7_43-Hackett-restricSet	1.00	0.98	0.98	-0.01	0.03	0.02	0.77
	gr0.75_29-Hackett-restricSet	0.98	1.00	0.93	-0.04	0.00	0.02	0.64
	gr0.75_18-Hackett-restricSet	0.98	0.93	1.00	0.00	0.03	0.02	0.87
Offspring Q-Q	gr0.7_21-Ericson-maxN	0.00	-0.02	-0.01	0.98	0.98	0.86	0.03
	gr0.8_31-Ericson-maxN	0.00	-0.02	-0.01	0.98	0.98	0.87	0.02
	gr0.8_23-Ericson-maxN	0.03	0.03	0.03	0.96	0.96	1.00	0.10
	gr0.7_17-Ericson-restricSet	-0.01	-0.04	-0.01	1.00	1.00	0.94	0.08
	gr0.7_19-Ericson-restricSet	0.08	0.08	0.07	0.94	0.94	1.00	0.13
	gr0.8_22-Ericson-restricSet	0.00	-0.03	0.00	1.00	1.00	0.95	0.08
	gr0.8_25-Hackett-maxN	-0.03	-0.05	-0.02	1.00	1.00	0.95	0.06
	gr0.85_31-Hackett-maxN	0.02	0.01	0.02	0.95	0.95	1.00	0.10
	gr0.7_17-Hackett-restricSet	-0.01	-0.04	0.00	1.00	1.00	0.94	0.08
	gr0.75_19-Hackett-restricSet	0.03	0.00	0.03	1.00	1.00	0.94	0.10
gr0.8_24-Hackett-restricSet	0.02	0.02	0.02	0.94	0.94	1.00	0.10	
Lifelong prod.	gr0.75_7-Ericson-maxN	-0.85	-0.75	-0.93	-0.02	-0.04	-0.06	-0.99
	gr0.8_5-Ericson-restricSet	0.81	0.69	0.90	0.06	0.07	0.08	1.00
	gr0.75_5-Hackett-maxN	0.78	0.65	0.88	0.08	0.10	0.09	1.00
	gr0.8_5-Hackett-restricSet	0.77	0.64	0.87	0.08	0.10	0.10	1.00

Supplementary figures

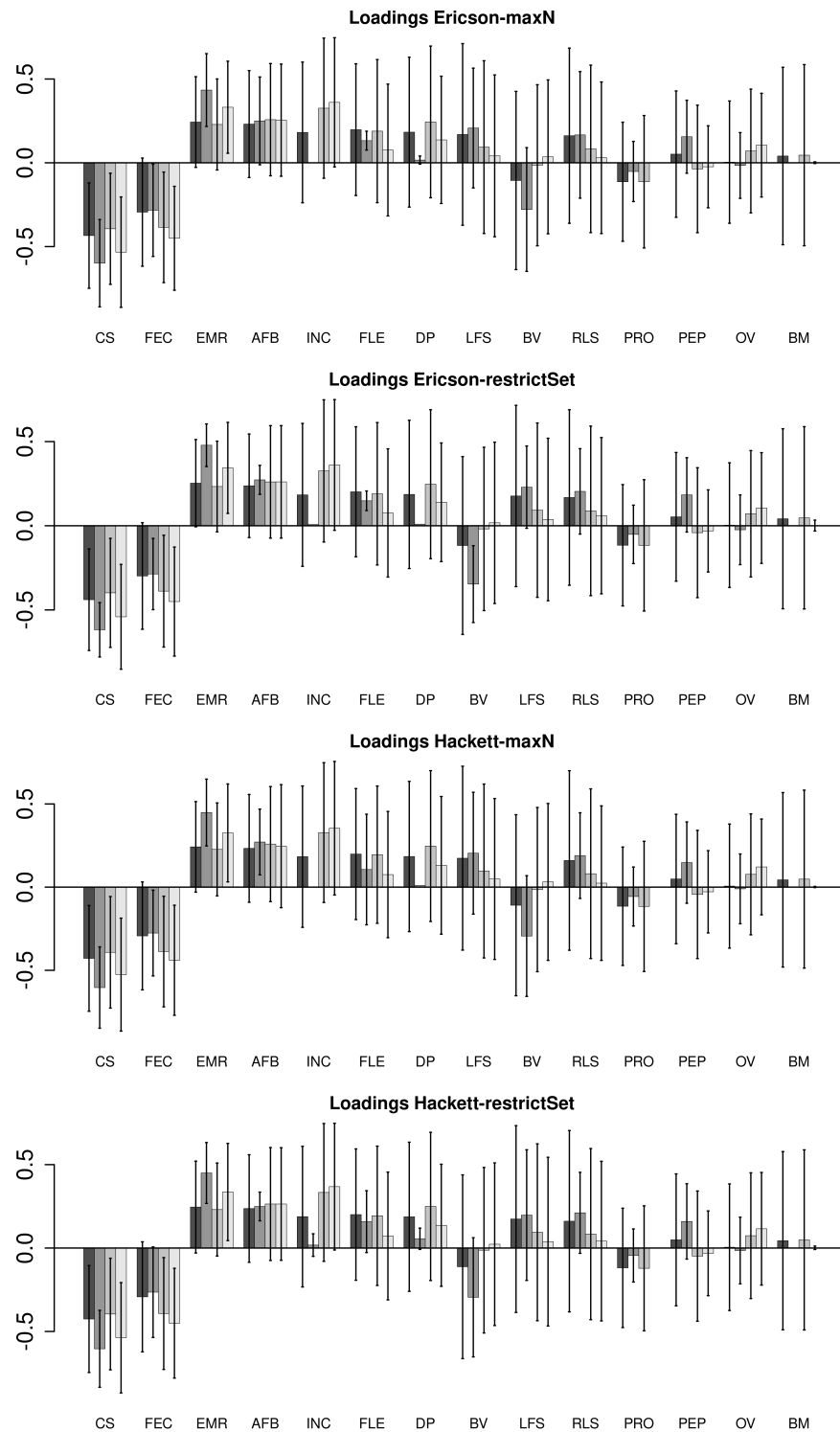


FIGURE A.2.1: Mean \pm standard deviation AIC weighted loadings of the traits for the fast-slow axes based on models predicting generation time or elasticity to fecundity for all trait combination PCs o using only the PCs with AIC <2 (best AIC). From darker to lighter color: FSe, FSe best AIC, FSgt and FSgt best AIC.

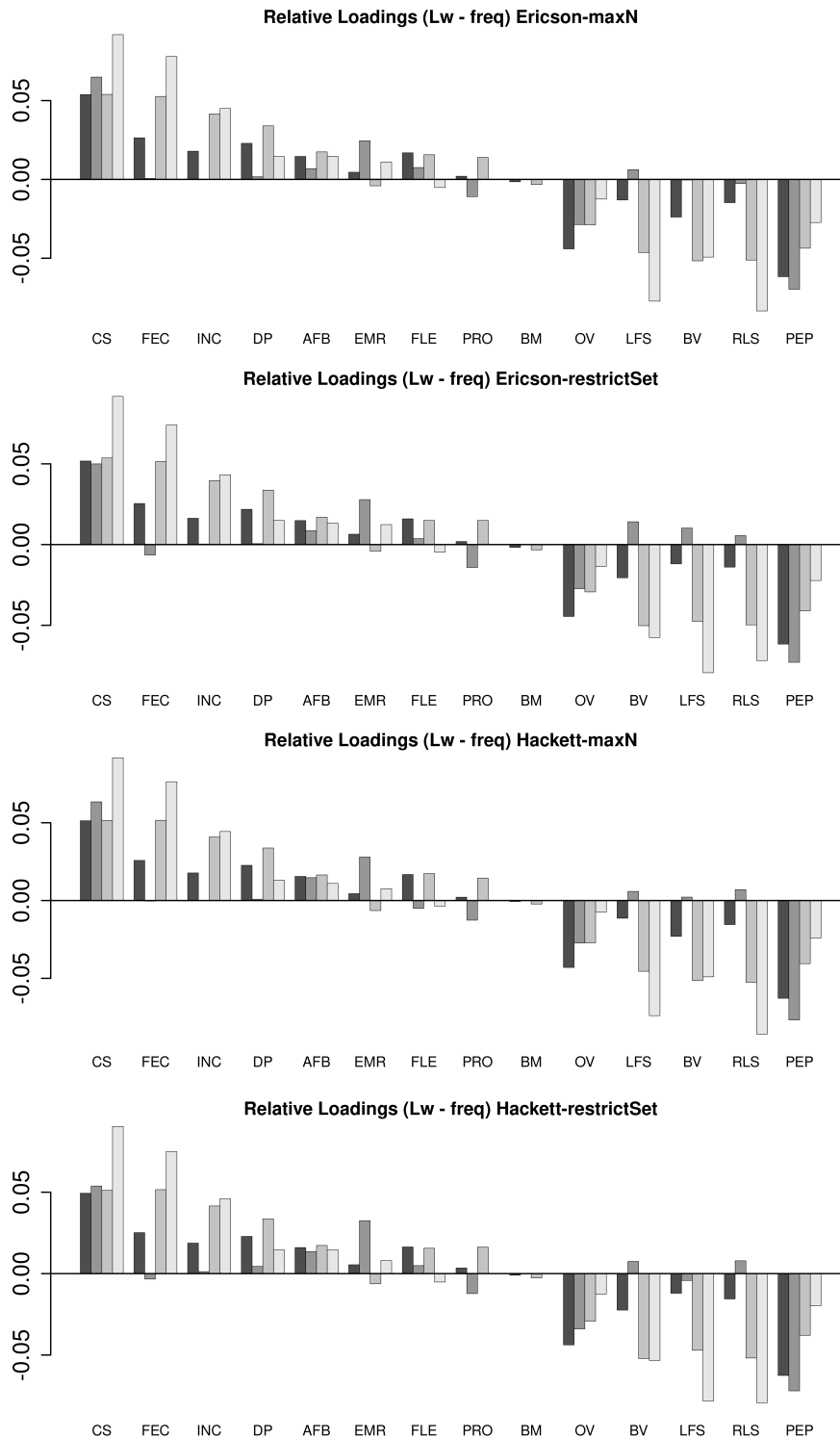


FIGURE A.2.2: Relative weight of the life history traits in the fast-slow continuum. Values range from -1 to 1, where negative values means that the absolute value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait in the selected PPCAs (see main text for details). The loadings and frequencies come from selected PCs that better predict elasticities to the fecundity (FSe) or generation time (FSgt), weighted by the AIC based weight of the models taking all or only the models with $\Delta AIC < 2$ (best AIC). From darker to lighter color: FSe, FSe best AIC, FSgt and FSgt best AIC.

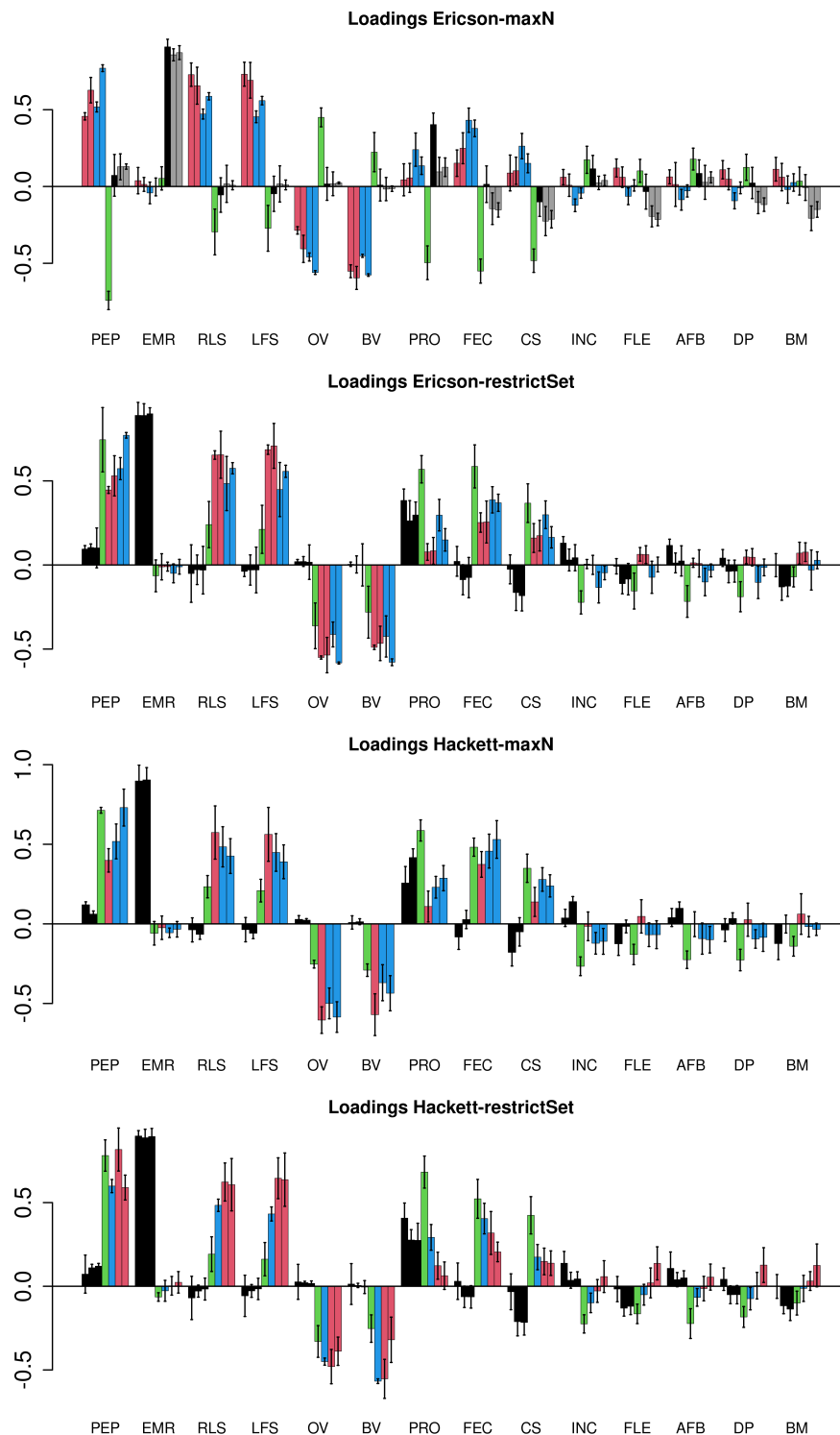


FIGURE A.2.3: Mean \pm standard deviation of the loadings of the traits for clusters of similar significant PCs (Eigenvalue >1) not selected for the fast-slow axes. Groups follow the same order and colors than figure A.2.5.

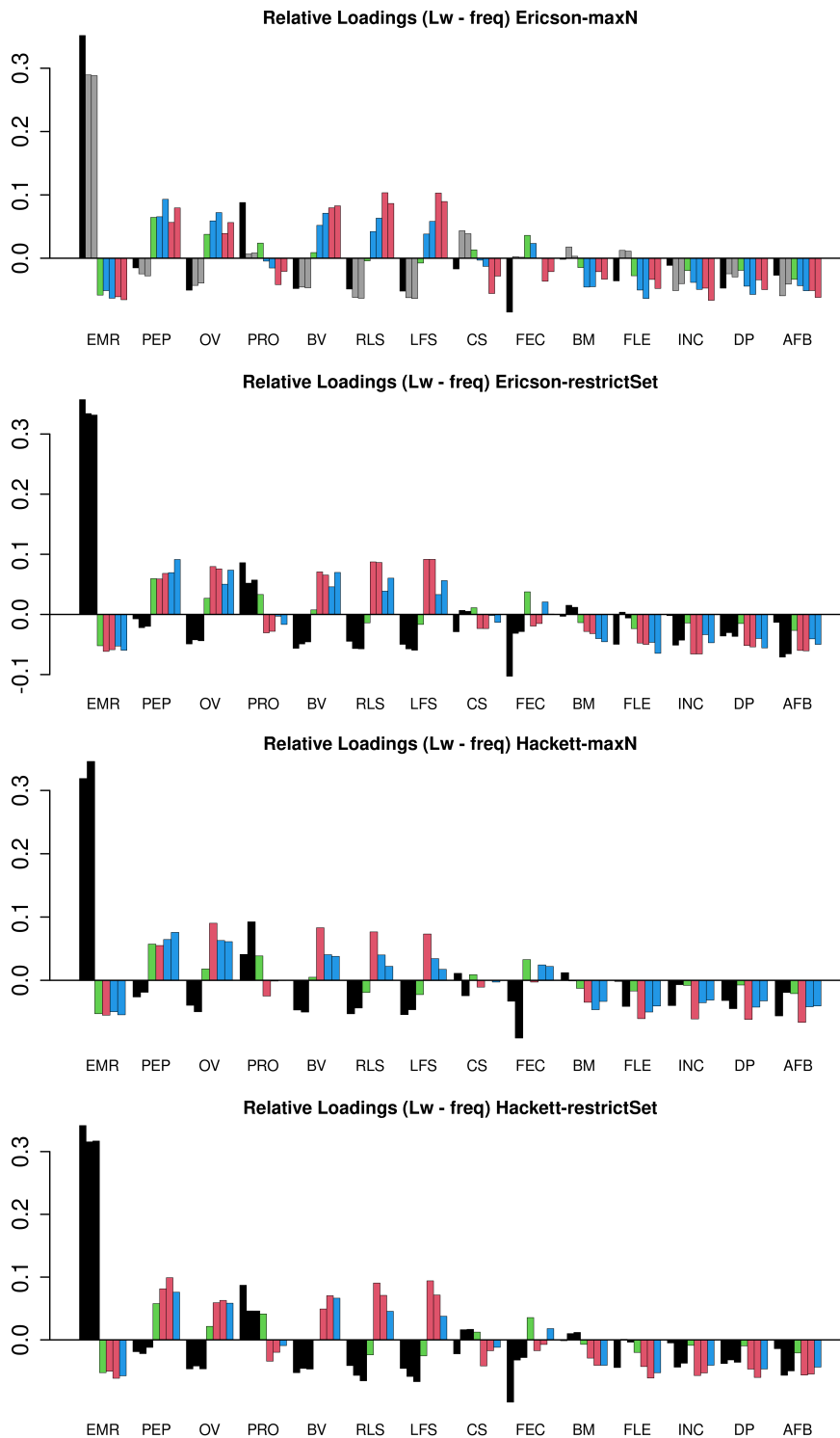


FIGURE A.2.4: Relative weights of the life history traits for each axes described in the table A.2.4. Values range from -1 to 1, where negative values means that the absolute value of the trait loadings are lower than expected by the frequency of the trait and positive values for traits with higher loadings than expected by the frequency of the trait in the selected PPCAs (see main text for details). Groups follow the same order and colors as figure A.2.5.

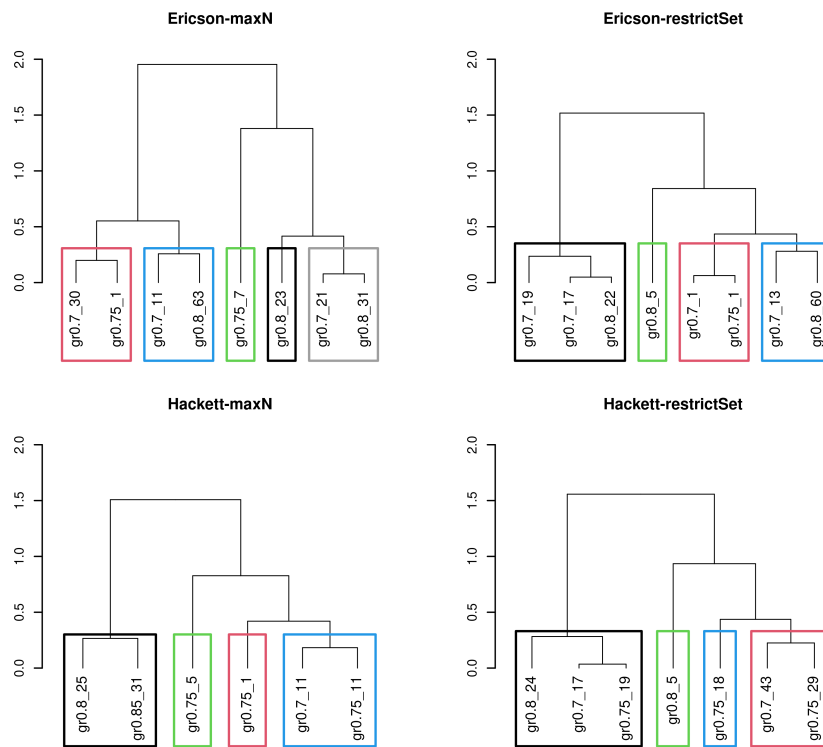


FIGURE A.2.5: Dendrogram of the distance among clusters of similar significant PCs (Eigenvalue >1) not selected for the fast-slow axes. Each group contains PCs with scores correlation greater than the correlation specified in the group name (e.g. gr0.8 means correlation >0.8). Boxes include clusters with a correlation among averaged loadings >0.95 and can be conceptualized as a offspring quality-quantity trade-off in black and grey, lifelong productivity in green and iteroparity in blue and red.

Appendix 3.1: Chapter 3 - Model description and parameterization

Description of the stochastic population model

At any temporal point in a given simulation run the population is described by a cohort of juveniles, sub-adults at all stages, non-breeding adults (i.e. those that skip breeding) and failed and successful adult breeders. Those individuals may belong to one of the two habitats that typify our simulated scenario. Growth from one stage to the next one, shift between habitats and the birth and establishment of new individuals are all computed by stochastically drawing from corresponding binomial distributions. See Figure A.3.2.1 for a graphic overview of all possible state transitions and Table A.3.1.1 for parameters definition.

1. The first calculation, for a given temporal step t and for each habitat, is to calculate how many full adults will become non-breeders and how many will be (successful or failed) breeders:

$$A_{h,t}^b = \text{Bin}(A_{h,t}, p_h^b)$$

2. Then, we enter the breeding algorithm, which runs recursively m times within a loop. Within this loop only juvenile recruitment and survival, as well as habitat shift for successful and failed adult breeders are evaluated.

- a) Within the loop, at the beginning of a given brooding event i , the number of adults that breed successfully is decided for each habitat by randomly drawing from a binomial distribution:

$$A_{h,t}^{b_s} = \text{Bin}(A_{h,t}^b, 1 - p_h^{b_f})$$

- b) That, in turn, allows us to calculate the number of adults that fail to breed:

$$A_{h,t}^{b_f} = A_{h,t}^b - A_{h,t}^{b_s}$$

- c) Then, the number of juveniles that are bred and survive until the next year are updated at each loop step as:

$$J_{h,t} = J_{h,t} + \text{Bin}(A_{h,t}^{b_s} \cdot q, p_{h,S_j})$$

- d) Next, after hatching has taken place, part of the successful or failed adult population may move between habitats. We model those actions by stochastically drawing from a binomial distribution the number of adults that change habitat:

$$\Delta_{1 \rightarrow 2}^x = \text{Bin}(A_{1,t}^x, p_{1 \rightarrow 2}^x)$$

$$\Delta_{2 \rightarrow 1}^x = \text{Bin}(A_{2,t}^x, p_{2 \rightarrow 1}^x)$$

Where, in this case, $x \in \{b_s, b_f\}$.

- e) Then, the number of successful and failed breeders will be updated:

$$A_{1,t}^x = A_{1,t}^x - \Delta_{1 \rightarrow 2}^x + \Delta_{2 \rightarrow 1}^x$$

$$A_{2,t}^x = A_{2,t}^x - \Delta_{2 \rightarrow 1}^x + \Delta_{1 \rightarrow 2}^x$$

And thus, with the new calculation:

$$A_{1,t}^b = A_{1,t}^{b_s} + A_{1,t}^{b_f}$$

$$A_{2,t}^b = A_{2,t}^{b_s} + A_{2,t}^{b_f}$$

Then the algorithm goes back to point a) above m times, after which it jumps from e) above to point 3 just below.

3. When the simulation includes sub-adults (i.e. age of first reproduction > 1), we must account for the fact that they may also move between habitats:

$$\Delta_{1 \rightarrow 2}^r = \text{Bin}(S_{1,t}^r, p_{1 \rightarrow 2}^r)$$

$$\Delta_{2 \rightarrow 1}^r = \text{Bin}(S_{2,t}^r, p_{2 \rightarrow 1}^r)$$

4. Moreover, sub-adults are also affected by survival, which is modeled by stochastically drawing from a binomial distribution:

$$S_{1,t+1}^r = \text{Bin}(S_{1,t+1}^r - \Delta_{1 \rightarrow 2}^r + \Delta_{2 \rightarrow 1}^r, p_{1, S_{sa}}^r)$$

$$S_{2,t+1}^r = \text{Bin}(S_{2,t+1}^r - \Delta_{2 \rightarrow 1}^r + \Delta_{1 \rightarrow 2}^r, p_{2, S_{sa}}^r)$$

5. Then, we also allow non-breeders to change habitats by stochastically drawing from a binomial distribution:

$$\Delta_{1 \rightarrow 2, t}^{nb} = \text{Bin}(A_{1,t}^{nb}, p_{1 \rightarrow 2}^{nb})$$

$$\Delta_{2 \rightarrow 1, t}^{nb} = \text{Bin}(A_{2,t}^{nb}, p_{2 \rightarrow 1}^{nb})$$

6. Consequently, the population at $t + 1$ of those non-breeding adults must be updated as follows:

$$A_{1,t+1}^{nb} = A_{1,t}^{nb} - \Delta_{1 \rightarrow 2}^{nb} + \Delta_{2 \rightarrow 1}^{nb}$$

$$A_{2,t+1}^{nb} = A_{2,t}^{nb} - \Delta_{2 \rightarrow 1}^{nb} + \Delta_{1 \rightarrow 2}^{nb}$$

7. Next, we account for survival probability of all types of adults:

$$A_{h,t+1}^x = \text{Bin}(A_{h,t+1}^x, p_{h,S_x})$$

where, in this case, $x \in \{b_s, b_f, nb\}$. Values $A_{h,t+1}^x$ inside the binomial correspond to those at the end of the breeding loop when $x = b_s$ or $x = b_f$.

8. Total adult population is then:

$$A_{h,t+1} = \sum_{x \in \{b_s, b_f, nb\}} A_{h,t+1}^x$$

9. Finally, populations are updated simply by moving up one stage and juveniles become adults or sub-adults according to the age of first reproduction.

Exploration of the parameter space

The range of demographic parameters comes from empirical data from birds. With the chosen parameters we estimated juvenile survival $p_{1,s}$ for a given deterministic growth rate λ corresponding to the Leslie matrix model by solving the Euler-Lotka equation:

$$p_{1,S_j} = \frac{p_{1,S_{sa}}^{1-AFR} (\lambda^{1+AFR} - p_{1,S_b} \cdot \lambda^{AFR})}{q \cdot \lambda}$$

where AFR is the age at first reproduction and other notation follows Table A.3.1.1. Once demographic parameters in habitat 1 are defined we modify the habitat 2 parameters according to the different scenarios. In Scenario 1, the parameters in habitat 2 are the same than in habitat 1. In Scenario 2 we increase adult and subadult mortality n times (1.5 in Scenario 2.1 and 2 in Scenario 2.2). To increase p probabilities n times we apply p^n and therefore, adult survival in habitat 2 is:

$$p_{2,S_b} = 1 - (1 - p_{1,S_b})^{1/n}$$

For Scenario 3 we apply the increase in breeding fail as follows:

$$p_2^{b_f} = 1 - (1 - p_1^{b_f})^{1/n}$$

Table A.3.1.1: Notation followed to describe the stochastic population model.

Symbol	Definition
q	Number of offsprings per brood in habitat h
m	Number of broods per year
n_{Sa}	Number of sub-adult stages
x	Labels x may take the values j, sa, b, nb, b_s, b_f , where these values refer to juveniles, subadults, adults (i.e. sum of all types), non-breeding adults, successful breeders and failed breeders, respectively
h	Index for habitat type, $h = \{1, 2\}$
r	Label for subadult stage, $r \in \{r_1 \dots r_{n_{Sa}}\}$
t	Subindex for time steps, measured in years, $t = \{1 \dots 50\}$
p_h^b	Probability for an individual to become a breeder (successful or not) in habitat h
$p_h^{b_f}$	Probability for a possible breeder individual to be a failed breeder in habitat h
p_{h,S_x}	Probability of survival in habitat h for individuals x
$p_{1 \rightarrow 2}^x$ $p_{2 \rightarrow 1}^x$	Probability for an adult to move from habitat type 1 to 2, or vice versa
$p_{1 \rightarrow 2}^r$ $p_{2 \rightarrow 1}^r$	Probability for a stage- r subadult to move from habitat type 1 to 2, or vice versa
$J_{h,t}$	Number of juveniles that have born in habitat h at time step t
$S_{h,t}^r$	Number of stage- r subadults in habitat h in year t
$A_{h,t}$	Total number of adults in habitat h at time t
$A_{h,t}^x$	Number of adults of type x in habitat h at time step t
$\Delta_{1 \rightarrow 2}^x$ $\Delta_{2 \rightarrow 1}^x$	Number of adults that will move from habitat type 1 to habitat 2, or viceversa
$\Delta_{1 \rightarrow 2}^r$ $\Delta_{2 \rightarrow 1}^r$	Number of sub-adults that will move from habitat type 1 to habitat 2, or viceversa

Appendix 3.2: Chapter 3 - Supplementary figures

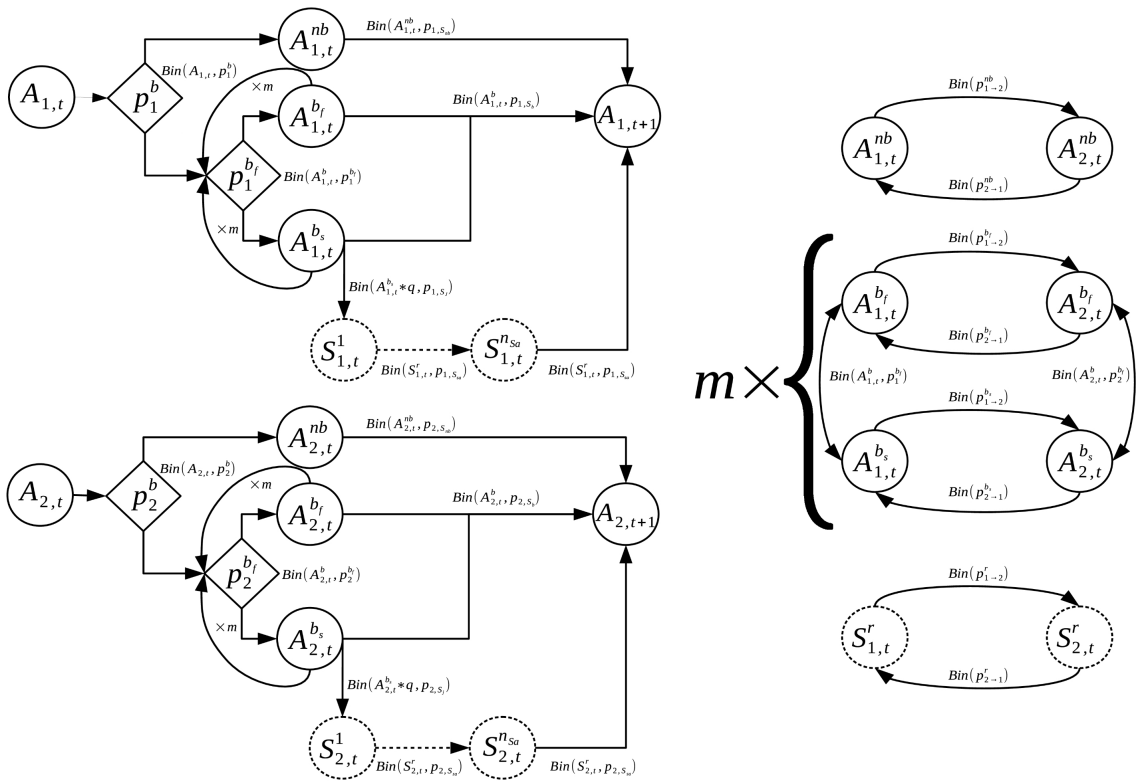


FIGURE A.3.2.1: Flowchart of the stochastic simulation model. Notation is the same as in Table A.3.1.1 above.

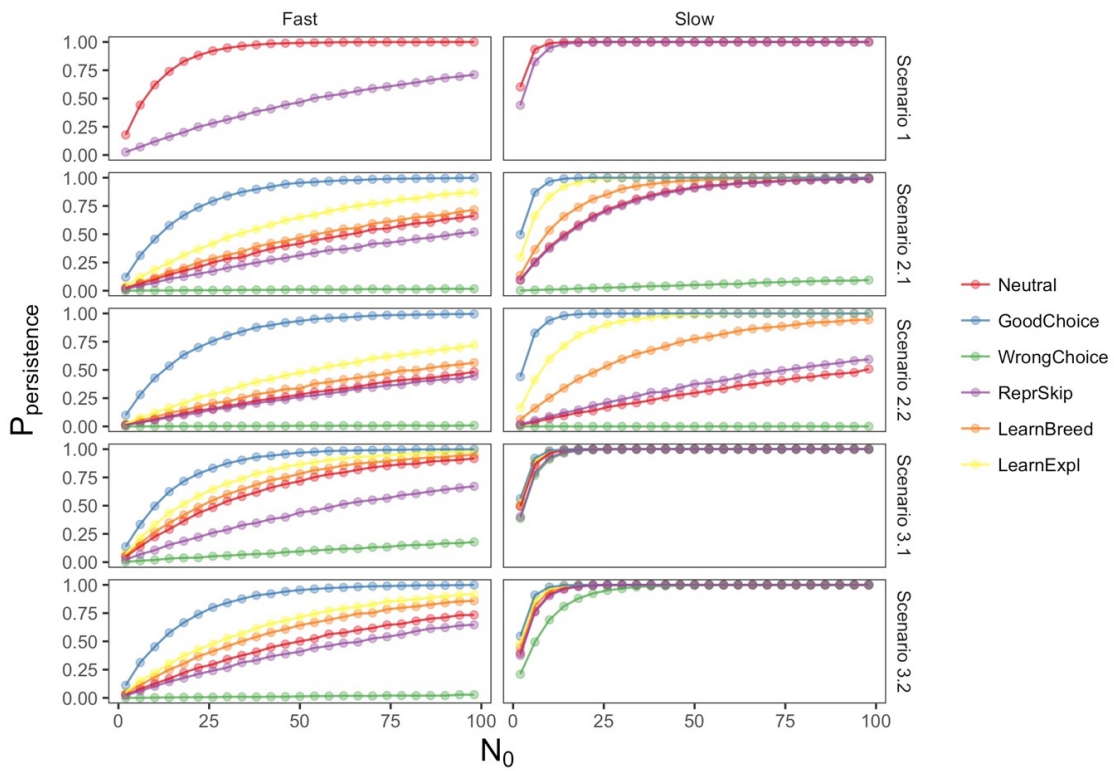


FIGURE A.3.2.2: Simulations of probability of population persistence as a function of behavioural responses for different initial population sizes according to different life histories (fast and slow). See figure 3.1 for details. In this case we shown the results for simulations with strong behavioural responses.

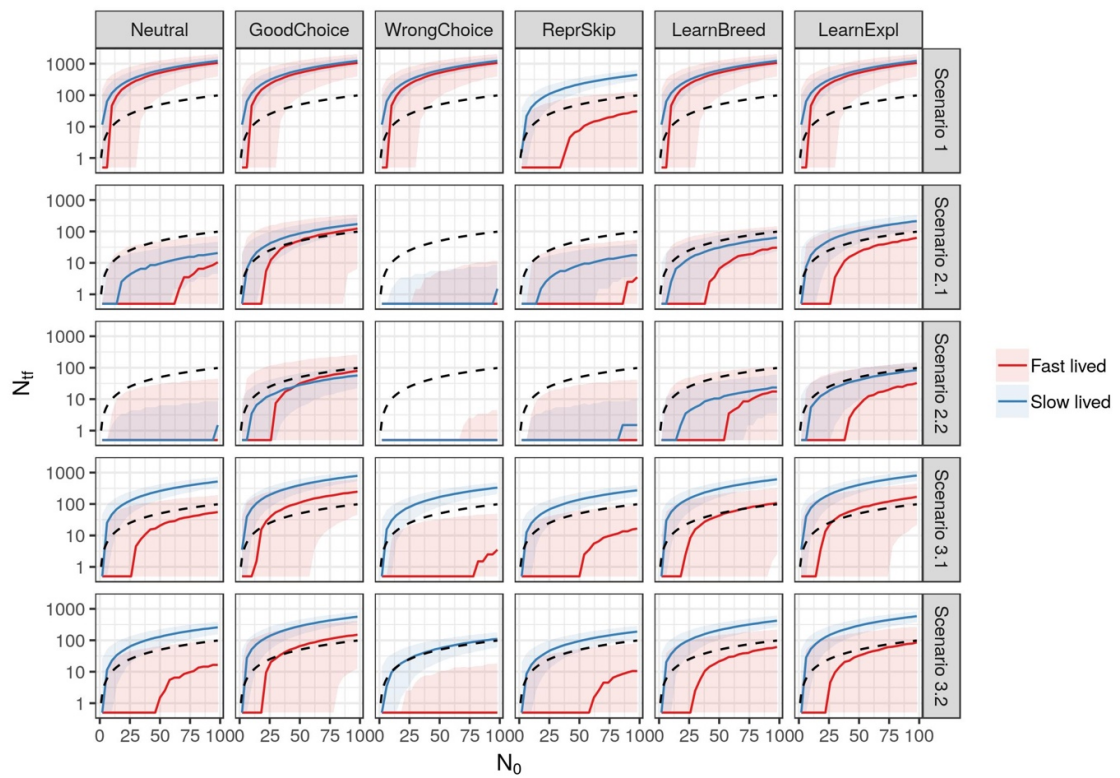


FIGURE A.3.2.3: Final population size (N_{tr} , median and 95% confidence interval of the 10000 replicates) of the simulations shown in figure 3.1. Black dashed lines show the initial population size.

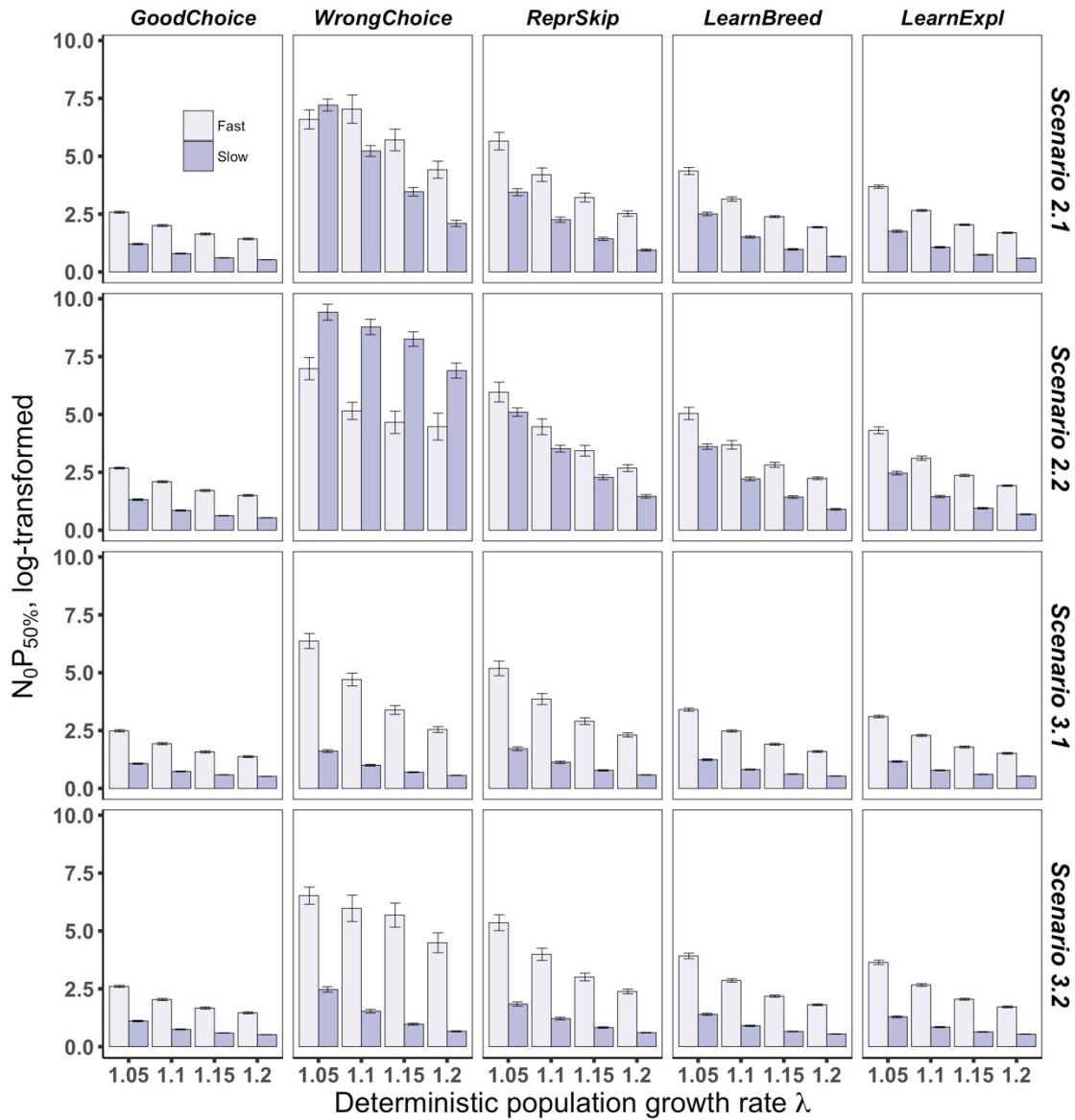


FIGURE A.3.2.4: Effects of behavioural responses on population persistence in novel environments as a function of the position of the animal along the fast-slow continuum. Population persistence is estimated as $N_0P_{50\%}$ and behavioural responses are strong. The position of the animal along the fast-slow continuum is assessed as the relative sensitivity (i.e. elasticity) of population growth to changes in fecundity, with slow-lived strategies exhibiting low elasticities and fast-lived strategies exhibiting high elasticities. For details on abbreviation, see figure 3.1.

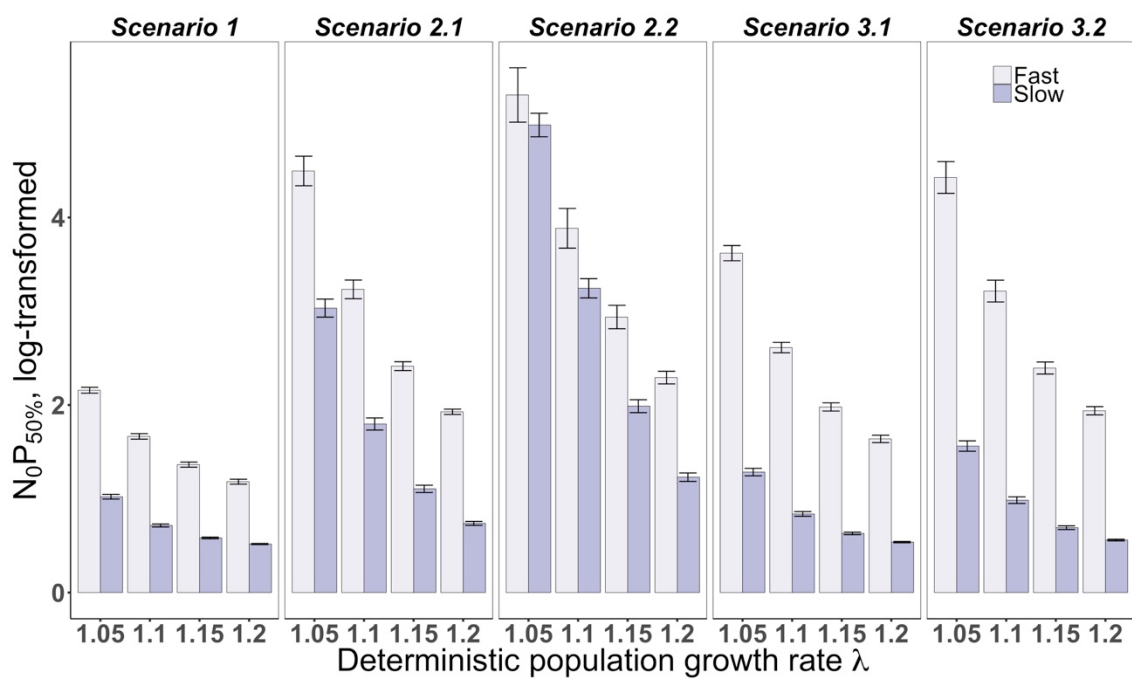


FIGURE A.3.2.5: Population persistence in novel environments as a function of the position of the animal along the fast-slow continuum for different scenarios and neutral behaviour. Population persistence is estimated as $N_0P_{50\%}$.

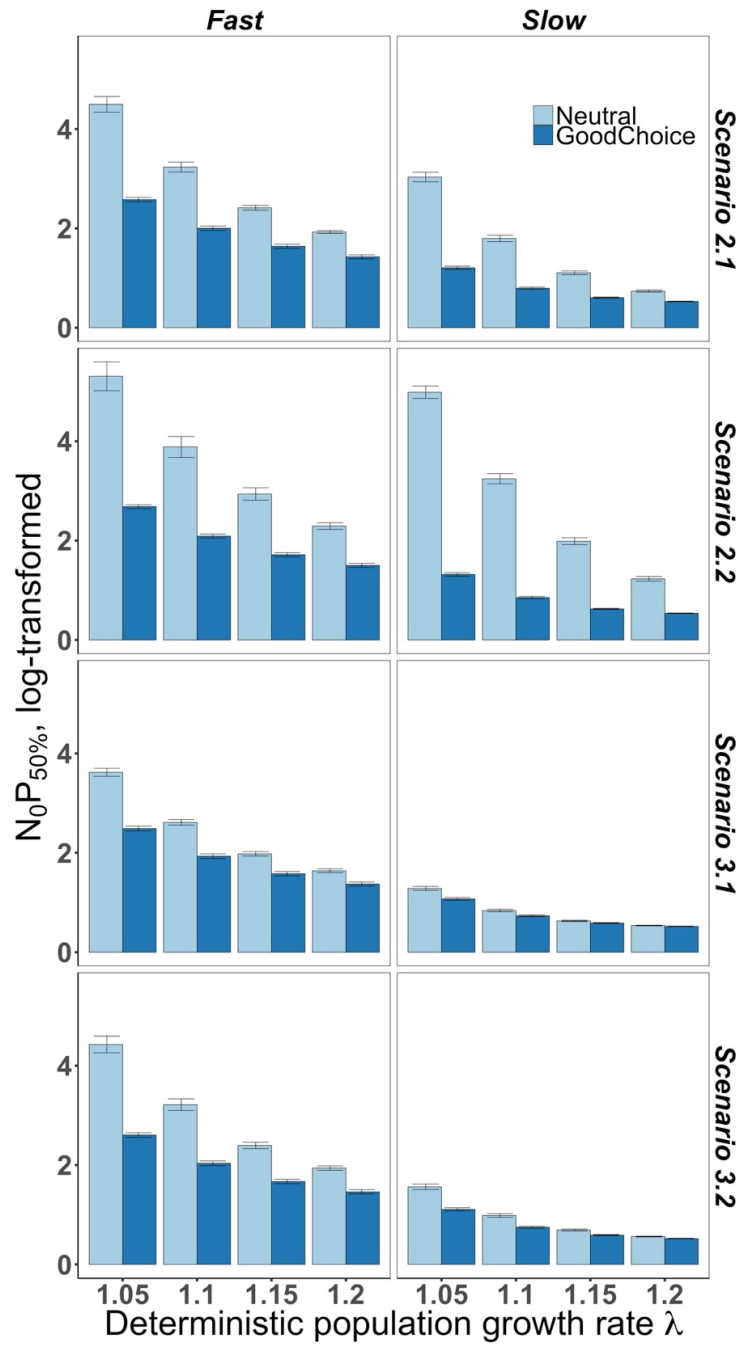


FIGURE A.3.2.6: Influence of habitat matching choice on population persistence in novel environments as a function of the position of the species along the fast-slow continuum. Benefits and costs of the behaviour under different environmental scenarios are reflected in differences in $N_0P_{50\%}$ between simulations where individuals' behaviour is either considered neutral or to reflect an innate preference for the high-quality habitat.

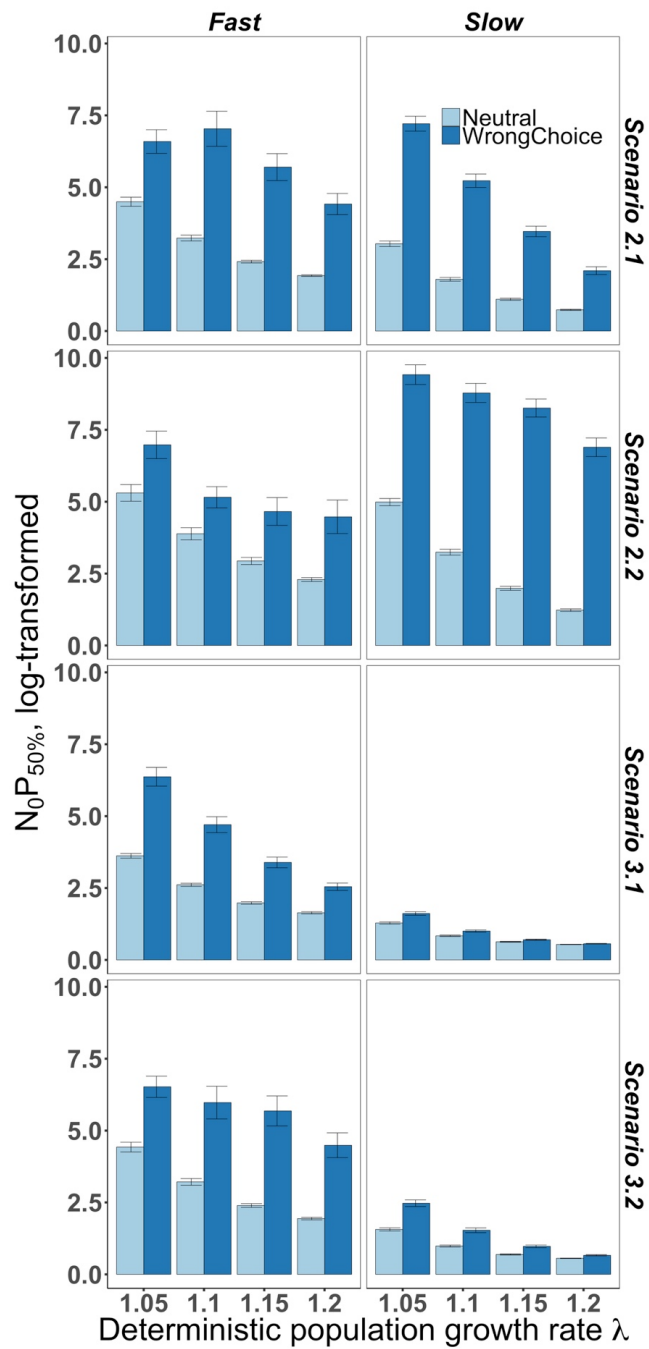


FIGURE A.3.2.7: Influence of an inappropriate habitat matching choice on population persistence in novel environments as a function of the position of the species along the fast-slow continuum. Benefits and costs of the behaviour under different environmental scenarios are reflected in differences in $N_0P_{50\%}$ between simulations where individuals' behaviour is either considered neutral or to reflect an innate preference for the low-quality habitat.

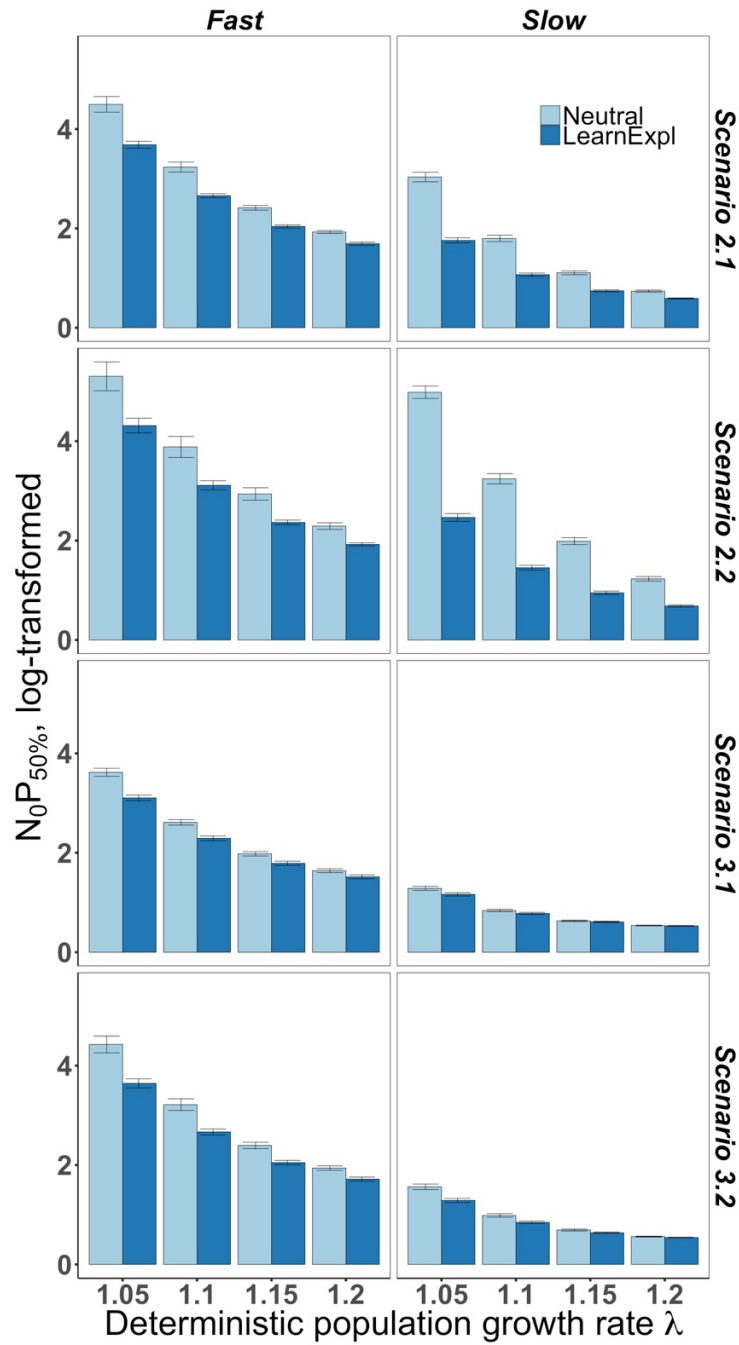


FIGURE A.3.2.8: Influence of learning through exploration on population persistence in novel environments as a function of the position of the species along the fast-slow continuum. Benefits and costs of the behaviour under different environmental scenarios are reflected in differences in $N_0P_{50\%}$ between simulations where individuals show (*LearnExpl*) or do not show (*Neutral*) a decreased preference for the low-quality habitat after exploring any of the two habitats.

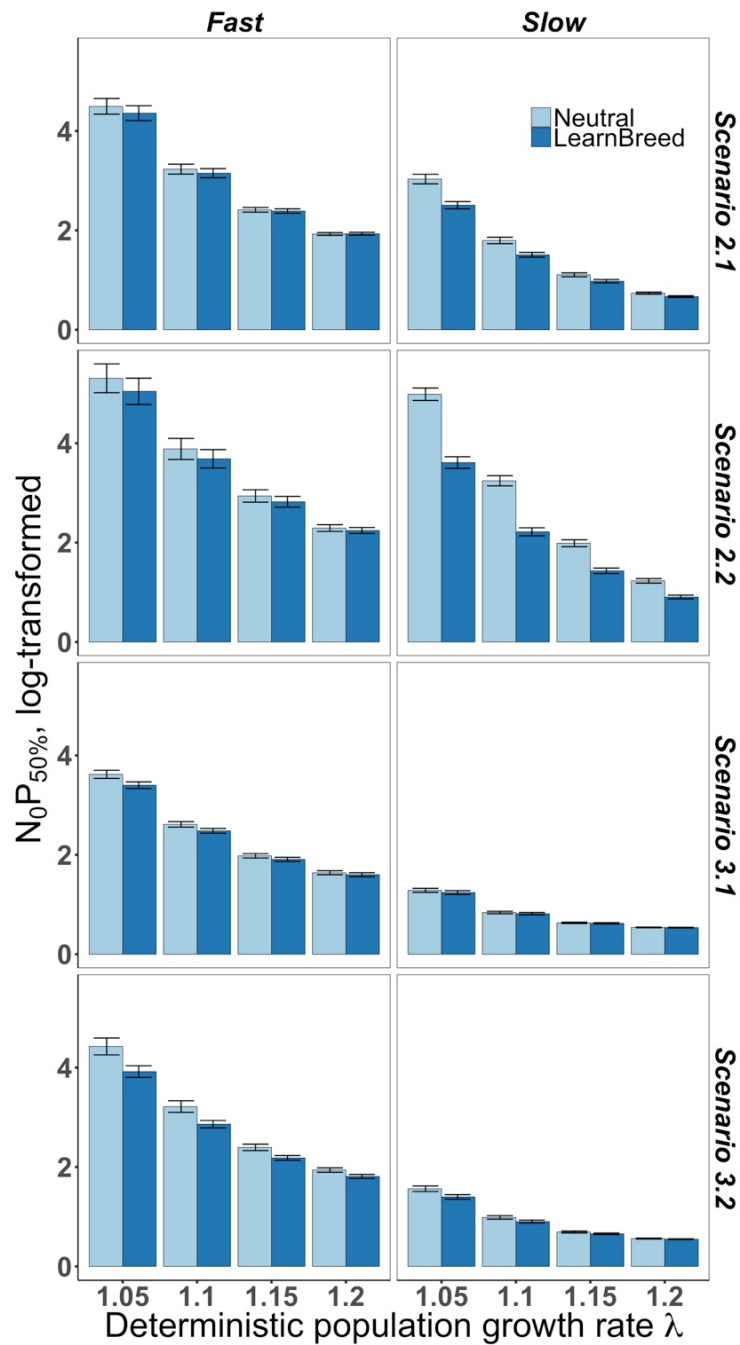


FIGURE A.3.2.9: Influence of learning from a breeding experience on population persistence in novel environments as a function of the position of the species along the fast-slow continuum. Benefits and costs of the behaviour under different environmental scenarios are reflected in differences in $N_0P_{50\%}$ between simulations where individuals' decision about changing habitat depends (*LearnBreed*) or not (*Neutral*) on the success of the past breeding attempt.

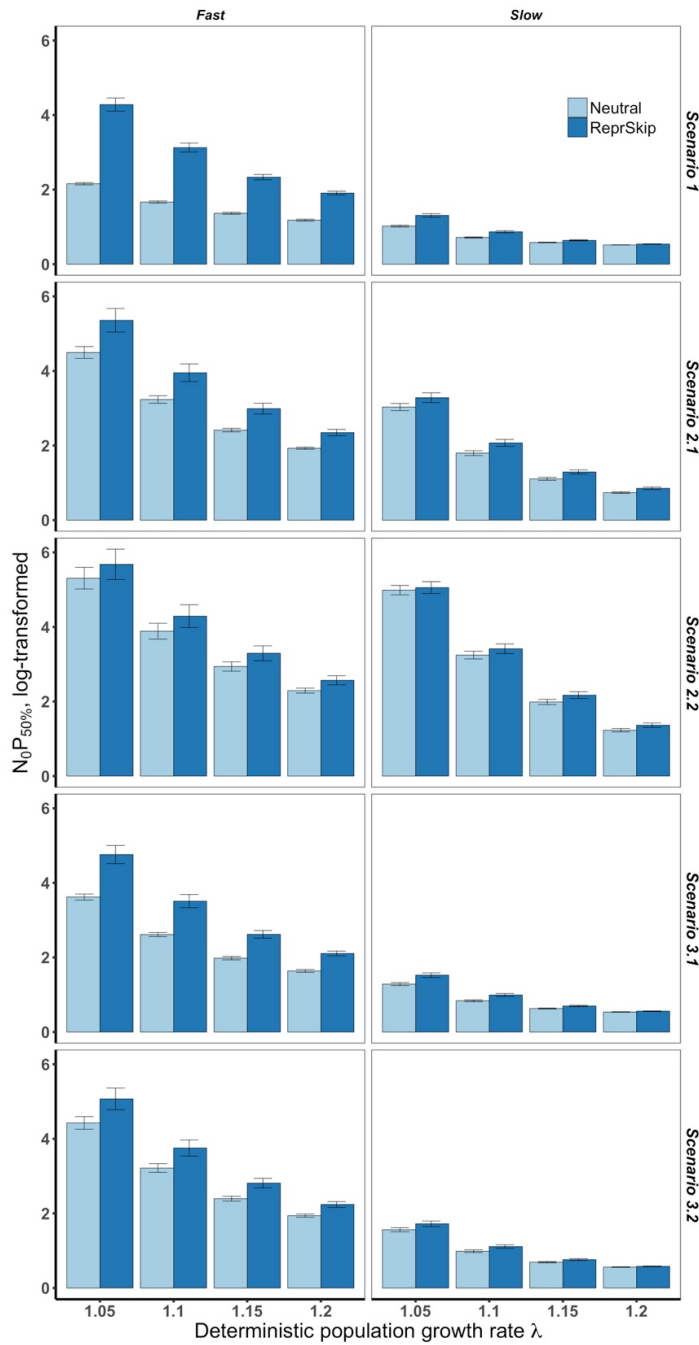


FIGURE A.3.2.10: Influence of a reproductive skip on population persistence in novel environments as a function of the position of the species along the fast-slow continuum. Benefits and costs of the behaviour under different environmental scenarios are reflected in differences in $N_0P_{50\%}$ between simulations where individuals either have the option (*ReprSkip*) or not (*emphNeutral*) to skip a reproductive event.

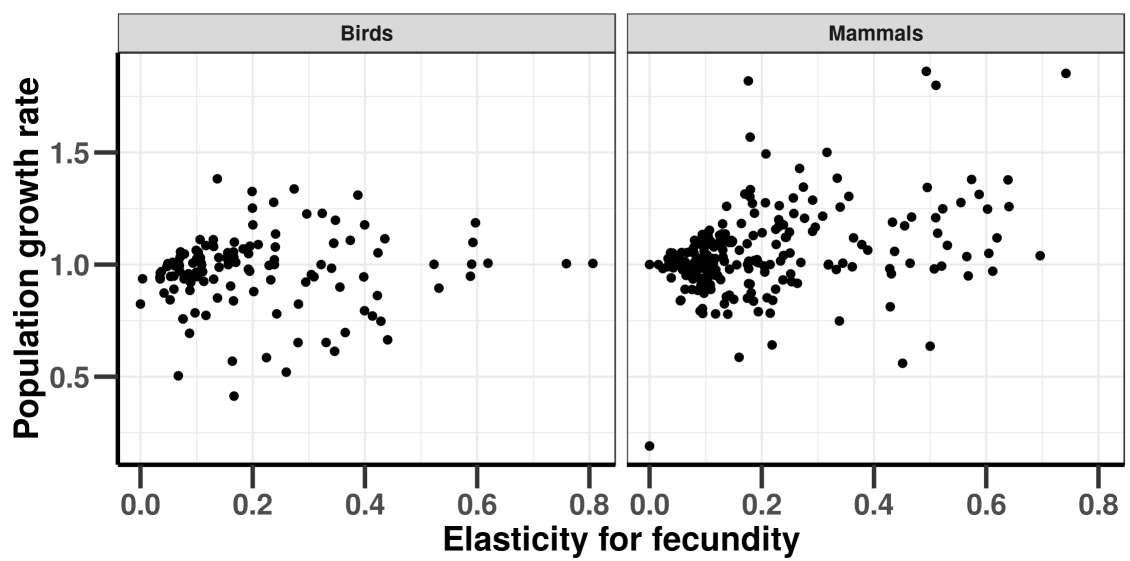


FIGURE A.3.2.11: Relationship between the fast-slow continuum and population growth rate (λ) in wild populations of birds and mammals suggesting that population growth rate is not higher for fast-lived strategies than for slow-lived strategies. Data come from COMADRE (Salguero-Gómez et al., 2016a). The fast-slow continuum is defined as the elasticity of population growth to changes in net fecundity, based on demographic analysis using the popbio R-package Stubben and Milligan (2007).

Appendix 4: Chapter 4 - Supplementary materials

Supplementary tables

Table A.4.1: Gaussian BPMs used to estimate intra-class correlation coefficients for variation in FID (log-transformed).

Model for all observations (n = 11,852 observations of 317 species)					
	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.299	0.172	0.451	1000	-
Species	0.222	0.163	0.274	890.6	-
Residual	0.263	0.256	0.269	1151	-
Fixed effects					
Intercept	3.238	2.780	3.675	1000	<0.001
Model for rural observations (n = 7,373 observations of 303 species)					
	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.316	0.178	0.465	1000	-
Species	0.187	0.135	0.247	1585	-
Residual	0.230	0.223	0.238	638.2	-
Fixed effects					
Intercept	3.348	2.924	3.801	1201	<0.001
Model for urban observations (n = 4479 observations of 108 species)					
	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.249	0.065	0.477	1000	-
Species	0.127	0.055	0.215	1000	-
Residual	0.173	0.166	0.180	1000	-
Fixed effects					
Intercept	2.491	2.050	2.955	1000	<0.001

Table A.4.2: Gaussian BPMMs accounting for variation in FID (log-transformed) as a function of habitat, based on information from regions for which both urban and rural FID observations were available (Denmark, France, Norway and China). The model below includes only species for which FIDs were recorded for both urban and rural habitats.

Model for all observations (n = 11,852 observations of 317 species)

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.424	0.205	0.656	871	-
Species	0.132	0.064	0.192	1000	-
Country	0.133	0.011	0.459	1000	-
Residual	0.204	0.198	0.209	1000	-
Fixed effects					
Intercept	3.069	2.519	3.719	1000	<0.001
Habitat:urban	-0.397	-0.417	-0.377	1222	<0.001
Height	0.017	0.014	0.020	1000	<0.001

Model for species present in both urban and rural habitats (9266 observations of 246 species)

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.204	0.080	0.346	1000	-
Species	0.098	0.050	0.151	1000	-
Country	0.174	0.010	0.513	596	-
Residual	0.204	0.198	0.209	1093	-
Fixed effects					
Intercept	2.854	2.343	3.415	1182	<0.001
Habitat:urban	-0.400	-0.423	-0.380	906	<0.001
Height	0.016	0.013	0.020	1000	<0.001

Table A.4.3: Gaussian BPMM accounting for variation in FID (log-transformed) as a function of the fast-slow continuum, based on information from all regions (11,392 observations belonging to 246 species).

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Animal	0.238	0.118	0.358	1791	-
Species	0.153	0.103	0.202	1000	-
Country	0.113	0.020	0.307	1118	-
Residual	0.209	0.204	0.214	1000	-
Fixed effects					
Intercept	3.192	2.694	3.655	1000	<0.001
FS	0.019	0.008	0.030	1074	<0.001
Habitat:urban	-0.403	-0.424	-0.382	1000	<0.001
Height	0.014	0.011	0.017	1000	<0.001

Table A.4.4: Gaussian BPMM accounting for variation in FID (log-transformed) in rural habitats as a function of residual brain size, based on information from all regions (3297 observations of 105 species). We restricted the analysis to rural habitats as previous work suggests that large-brained birds are over-represented in urbanised environments.

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.290	0.136	0.480	1000	-
Species	0.112	0.051	0.174	1000	-
Residual	0.242	0.231	0.253	1000	-
Fixed effects					
Intercept	3.135	2.701	3.635	827.9	<0.001
Brain residual	0.667	0.260	1.132	1020.6	0.008
Height	0.010	0.003	0.017	1000	0.014

Table A.4.5: Gaussian BPMM accounting for across species differences in FID from rural and urban habitats (response variable) as a function of residual brain size, based on information from species for which both urban and rural FID observations were available. The decline of each species was estimated as the $\log(\text{mean FID}_{\text{rural}}) - \log(\text{mean FID}_{\text{urban}})$. The model was repeated again restricting the species to those with at least 15 FID observations in each habitat. The models were run with a Gaussian structure of the errors and non-informative priors. We weighted the observations by $1/(n-3)$, being “n” the number of FID observations of the species.

Model for all observation (71 species)

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.228	0.085	0.390	975	-
Residual	0.040	0.007	0.082	975	-
Fixed effects					
Intercept	0.837	0.429	1.300	975	0.002
Brain residual	0.160	-0.296	0.694	975	0.545

Model with species with at least 15 FID observations per hábitat (34 species)

	post mean	L-95% CI	U-95%	eff.samp	pMCMC
Random effects					
Phylogeny	0.154	0.059	0.258	975	-
Residual	0.010	0.000	0.027	975	-
Fixed effects					
Intercept	0.867	0.471	1.281	975	<0.001
Brain residual	0.162	-0.315	0.690	975	0.539

Supplementary figures

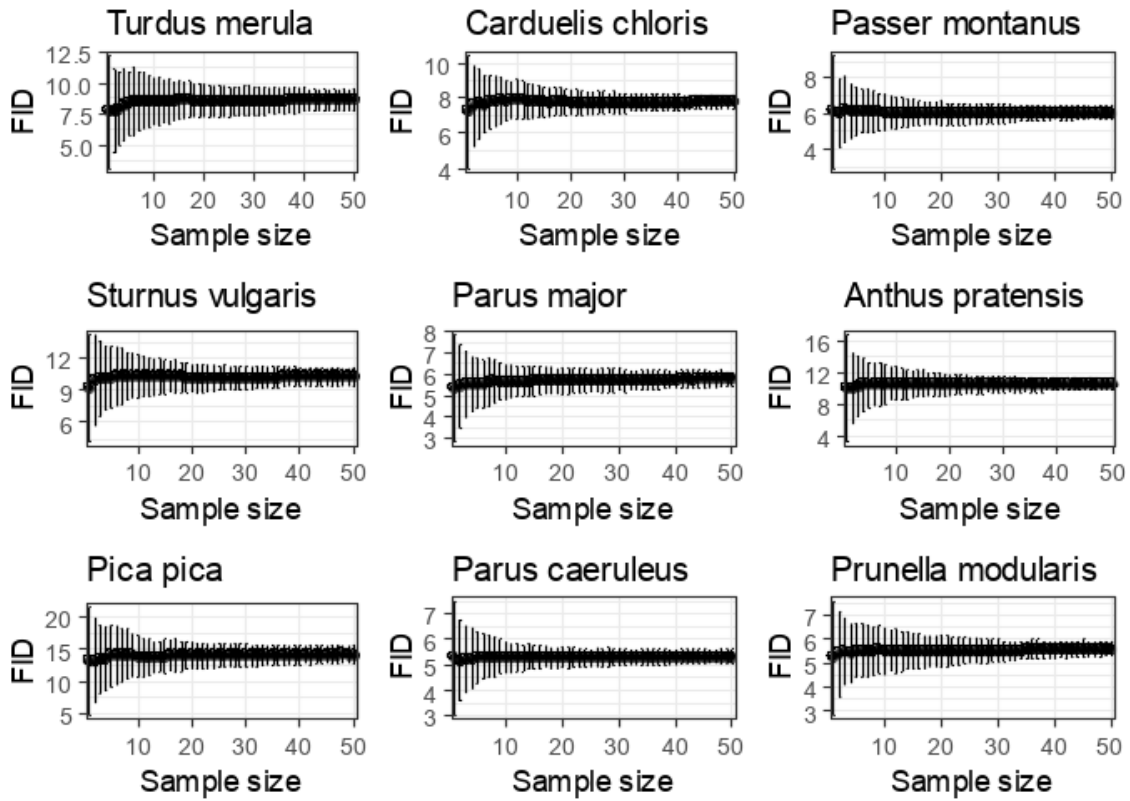


FIGURE A.4.1: Simulations to estimate the minimum sample size needed to accurately estimate FID. See main text for details.

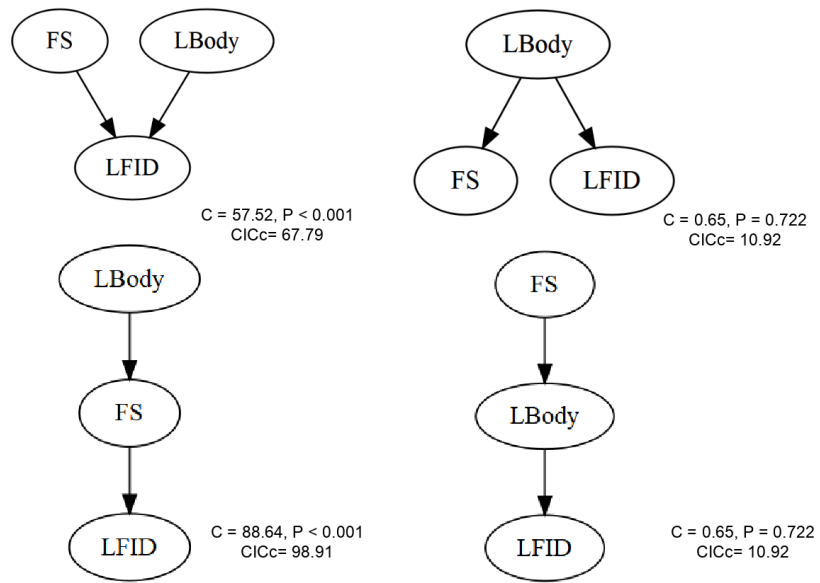


FIGURE A.4.2: Path diagrams of the causal scenarios analysed to study how body size affects the relationship between flight initiation distance (FID) and the fast-slow continuum (FS) in rural habitats. The letter “L” before body and FID denotes log-transformation.

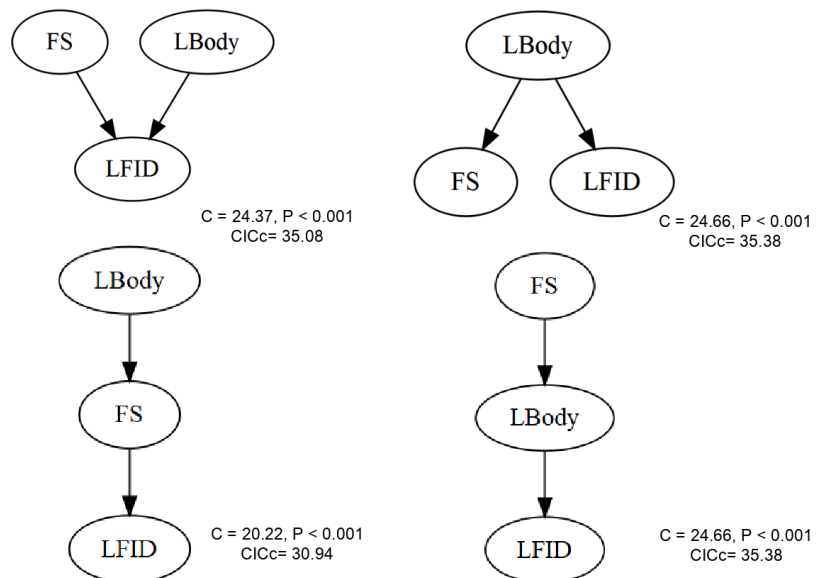


FIGURE A.4.3: Path diagrams of the causal scenarios analysed to study how body size affects the FID-FS association in urban habitats. The letter “L” before body and FID denotes log-transformation.

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```
N1j<- N2j<- numeric(nRep) # Juveniles
saAges<- grep("sa", colnames(N), value=TRUE)
if (length(saAges) / 2 < params$AFR - 1){
saAges<- paste0("sa", 1:(params$AFR - 1))
saAges<- c(paste0("N1", saAges), paste0("N2", saAges))
Nsa<- matrix(0, nrow=nRep, ncol=length(saAges), dimnames=list(rep(1:nRep, 2), saAges))
N<- cbind(N, Nsa)
rm(Nsa)
}

saAges1<- grep("N1", saAges, value=TRUE)
saAges2<- grep("N2", saAges, value=TRUE)

## BREEDING
adultN1<- rowSums(N[,c("N1b", "N1bF", "N1s"), drop=FALSE])
adultN2<- rowSums(N[,c("N2b", "N2bF", "N2s"), drop=FALSE])

## Breeders
breedingN1<- with(params, rbinom(nRep, size=adultN1, prob=Pb1))
breedingN2<- with(params, rbinom(nRep, size=adultN2, prob=Pb2))

# Skip reproduction
N[,"N1s"]<- adultN1 - breedingN1
N[,"N2s"]<- adultN2 - breedingN2

for (i in 1:params$broods){
## Breeding success
N[,"N1b"]<- with(params, rbinom(nRep, size=breedingN1, prob=(1 - PbF1)))
N[,"N2b"]<- with(params, rbinom(nRep, size=breedingN2, prob=(1 - PbF2)))
# Breeding Fail
N[,"N1bF"]<- breedingN1 - N[,"N1b"]
N[,"N2bF"]<- breedingN2 - N[,"N2b"]

Juvenile recruitment and mortality
N1j<- N1j + with(params, rbinom(nRep, size=N[,"N1b"] * b1, prob=j1))
N2j<- N2j + with(params, rbinom(nRep, size=N[,"N2b"] * b2, prob=j2))

MOVEMENTS (habOLD_NEW)
hab2_1Nb<- with(params, rbinom(nRep, size=N[,"N2b"], prob=c2 * P1b))
hab2_2Nb<- with(params, rbinom(nRep, size=N[,"N1b"], prob=c1 * (1 - P1b)))
hab2_1NbF<- with(params, rbinom(nRep, size=N[,"N2bF"], prob=cF * P1b))
hab2_2NbF<- with(params, rbinom(nRep, size=N[,"N1bF"], prob=cF * (1 - P1b)))

only movements
hab2_1b"]<- N[,"N1b"] + hab2_1Nb - hab1_2Nb
hab2_2b"]<- N[,"N2b"] + hab1_2Nb - hab2_1Nb
hab2_1bF"]<- N[,"N1bF"] + hab2_1NbF - hab1_2NbF
hab2_2bF"]<- N[,"N2bF"] + hab1_2NbF - hab2_1NbF

N1<- N[,"N1b"] + N[,"N1bF"]
N2<- N[,"N2b"] + N[,"N2bF"]

MOVEMENTS (not based on breeding experience, only once per year)
hab2_1Ns"]<- N[,"N1s"] + hab2_1Ns - hab1_2Ns
hab2_2Ns"]<- N[,"N2s"] + hab1_2Ns - hab2_1Ns

R > 1){
apply(N[, saAges2, drop=FALSE], 2, function(x) with
apply(N[, saAges1, drop=FALSE], 2, function(x) with
```

```
ab1=.1,sa1=.25,ab2=.1,sa2=.25,j2=.1,AFR=1,Pb1=1,Pb2=1,
N[,"N1s"]<- with(params, rbinom(nRep, size=N[,"N2s"] *
N[,"N2s"]<- with(params, rbinom(nRep, size=N[,"N1s"] *
## Subadults
if (params$AFR > 1){
N1sa<- apply(N[, saAges1, drop=FALSE], 2, function(x)
N2sa<- apply(N[, saAges2, drop=FALSE], 2, function(x)
} else {
N1sa<- as.matrix(t(N1sa))
N2sa<- as.matrix(t(N2sa))
}
}

## GROWTH
if (params$AFR > 1){
N[, saAges1[-1]]<- N1sa[, -ncol(N1sa)] # subadult
N[, saAges2[-1]]<- N2sa[, -ncol(N2sa)] # subadult
N[, "N1b"]<- N[, "N1b"] + N1sa[, ncol(N1sa)] # sub
N[, "N2b"]<- N[, "N2b"] + N2sa[, ncol(N2sa)] # sub
N[, saAges1[1]]<- N1j # juvenil -> subadult
N[, saAges2[1]]<- N2j # juvenil -> subadult
} else { # Juveniles grow to N*b
N[, "N1b"]<- N[, "N1b"] + N1j
N[, "N2b"]<- N[, "N2b"] + N2j
}

return(N)
}

findF_EulerLotka<- function(lambda, a, s=a, AFR
F<- -(a * lambda^AFR - lambda^(AFR+1)) / (s^(AFR+1))
F[F < 0]<- NA
return (F)
}

eigen.analisys2df<- function(x){
tmpRes<- popbio::eigen.analysis(x)

## Elasticities of survival for reproductive
selReproClass<- which(x[1, ] != 0)
selSurvReproClass<- which(x[-1, selReproClass])
elasSurvRepro<- sum(tmpRes$elasticities[-1, selSurvReproClass])

## Elasticities of survival for non reproductive
selNonReproClass<- which(x[1, ] == 0)
selSurvNonReproClass<- which(x[-1, selNonReproClass])
elasSurvNonRepro<- sum(tmpRes$elasticities[-1, selSurvNonReproClass])

## Elasticities of net fecundity (for pre-reproductive)
elasFecundity<- sum(tmpRes$elasticities[1, selReproClass])

tmp<- popbio::fundamental.matrix(x)
if (is.list(tmp)){
# Life expectancy for the first reproductive
matureLifeExpectancy<- as.numeric(tmp$maturity)
} else {
matureLifeExpectancy<- NA
}

generation.time<- popbio::generation.time(x)
net.life.expectancy<- popbio::net.life.expectancy(x)
elasSurvRepro<- sum(tmpRes$elasticities[-1, selSurvReproClass])
reproductive.rate<- sum(tmpRes$elasticities[1, selReproClass])
damping.ratio<- t
```

