DE L'ECOLOGIA DEL COMPORTAMENT A LA DEMOGRAFIA: LLIÇONS PER A LA CONSERVACIÓ DEL SISÓ COMÚ (*TETRAX TETRAX*)

From Behavioral Ecology to Demography: lessons for the Little Bustard (*Tetrax tetrax*) conservation

Francesc Cuscó Martínez

Barcelona, Setembre 2018

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Memòria presentada per

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Diu que ha anat fent al seu aire,
que ha fet vida a mil ciutats,
que ha dormit en llocs que feien feredat
i que tu, mare, mai haguessis aprovat.
Que està content, que tot va bé.
Diu que està content, que tot va bé.

fragment de Louisiana o els camps de cotó. Els amics de les arts

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INTRODUCCIÓ GENERAL

Les activitats antropogèniques són la principal causa de transformació i degradació dels ecosistemes (Vitousek et al. 1997). La transformació dels paisatges naturals per a la producció d'aliments, l'obtenció d'energia i minerals o la urbanització i construcció d'infraestructures són, entre altres, grans elements transformadors dels entorns naturals. En l'actualitat, les terres de cultiu i les pastures s'han convertit en un dels biomes més extensos del planeta ocupant una extensió del 40% de la superfície terrestre del planeta (Foley et al. 2005). L'incessant creixement de la població humana incrementa la demanda sobre la producció d'aliments convertint-la en una activitat cada vegada més intensificada (Tilman et al. 2002).

La intensificació dels sistemes de producció d'aliments, en definitiva dels sistemes agropastorals, ha estat identificada com un dels principals factors causants de la pèrdua de biodiversitat d'aquests sistemes (Benton et al. 2003). La intensificació agrícola té un gran impacte sobre diferents taxons, afectant les poblacions d'espècies de plantes, artròpodes i vertebrats (Robinson i Sutherland 2002). Aquest procés d'intensificació actua des d'un complex multifactorial dirigit a maximitzar la producció i a minimitzar els costos econòmics. La mecanització dels sistemes de producció, l'increment en l'ús de fertilitzants sintètics, l'ús d'herbicides i pesticides, la irrigació de les terres de secà, la substitució de cultius o la concentració parcel·laria són alguns clars exemples d'aquesta intensificació (Suárez et al. 1997, Robinson i Sutherland 2002).

Sota aquest context, les espècies que habiten els sistemes agrícoles s'han d'adaptar, en un sentit ampli de la paraula, als canvis ràpids i constants que aquests medis pateixen. No obstant això, no totes les espècies ho aconsegueixen i com a resultat es produeixen dràstiques davallades poblacionals (Donald et al. 2001) i fins i tot una pèrdua de la biodiversitat (Benton et al. 2003). Dins d'aquestes espècies, els ocells esteparis són un dels grups d'espècies que han vist minvar més les seves poblacions i a dia d'avui són considerats un dels grups més amenaçats a escala europea (BirdLife International 2004, Burfield 2005). Les característiques d'aquest heterogeni grup d'espècies des d'un punt de vista filogenètic, però amb condicions de vida i adaptacions al medi similars (De Juana 2005), fa que molts dels reptes que se'ns plantegen des d'un punt de vista de la seva conservació a nivell específic siguin compartits per una gran majoria d'elles.

Per tal de revertir les negatives i abruptes tendències poblacionals d'algunes d'aquestes espècies i la pèrdua de biodiversitat d'aquests espais calen doncs mesures correctores que facin compatible l'activitat agrícola amb l'existència d'una biodiversitat rica en espècies, tal i com han estat tradicionalment els sistemes agrícoles (Benton et al. 2003, Kleijn et al. 2006).

Demografia i estratègies de vida en un entorn canviant

A nivell demogràfic, les poblacions d'ocells presenten fluctuacions en la seva mida poblacional de manera natural. La densitat poblacional està afectada principalment per tres paràmetres demogràfics: la natalitat, la mortalitat i la dispersió (Perrins and Birkhead 1983). En poblacions sedentàries i relativament tancades, la dispersió juga un paper secundari en les dinàmiques poblacionals. Així, el creixement poblacional d'una determinada població depèn principalment del balanç entre el reclutament amb dels nounats i els individus morts. Una població amb una mortalitat més elevada que el reclutament (creixement negatiu) i sostinguda en el temps pot acabar desapareixent. Mentre que una població on el reclutament és més alt que la mortalitat (creixement positiu), si és suficientment elevat, pot assolir un límit màxim de mida poblacional, conegut com a capacitat de càrrega (Begon et al. 2005). La capacitat de càrrega d'un ambient està relacionada amb la disponibilitat de recursos. I el nombre d'individus que una població pot sostenir està regulada per la limitació en algun d'aquests recursos. Per a moltes espècies, la disponibilitat d'aliment és el factor més limitant i defineix el nombre d'individus que un sistema pot suportar, mentre que per altres ho pot ser la disponibilitat d'àrees de cria (Perrins and Birkhead 1983), entre altres factors. Les alteracions antropogèniques modifiquen els recursos disponibles per a les espècies i alteren el nombre d'individus que un sistema pot suportar. Les estratègies de vida de les espècies i les respostes dels seus individus als canvis de l'entorn són aspectes fonamentals que determinaran les dinàmiques poblacionals.

Els diferents individus d'una població poden mostrar estratègies diferents en la manera en la que exploten l'hàbitat disponible o l'espai (Cardador et al. 2012a, Roever et al. 2013, Brown and Crone 2016). De fet, les diferències individuals en la conducta, la morfologia, la fisiologia, la personalitat i els trets de la història de vida són freqüents entre els tàxons, la qual cosa pot conduir a diferències interindividuals en els balanços de cost-benefici de les diferents estratègies (Réale et al. 2007, Wilson and McLaughlin 2007, Boon et al. 2008). Un dels principals paradigmes en l'ecologia del comportament és que la variació individual existeix i aquesta variació pot afectar a l'èxit reproductor i a la probabilitat de supervivència dels diferents individus (Sæther et al. 1996). Sæther et al. 1996, analitzant la relació entre la mida de posta i la supervivència adulta de més de 100 espècies d'ocells, va identificar tres estratègies de vida diferents. Moltes espècies presentaven elevades taxes de supervivència i mides de posta petita, mentre que altres mostraven una baixa taxa de supervivència i mides de posta gran. Un tercer grup, més reduït en nombre d'espècies, exhibia taxes de supervivència relativament altes i mides de posta també elevades. En el mateix estudi, utilitzant un conjunt de dades més reduït, es descriuen diferències en el moment del cicle vital de major importància en la regulació de la dinàmica poblacional entre espècies precocials i altricials. Per a la majoria d'espècies precocials, les fluctuacions poblacionals es correlacionaven amb l'època de cria, mentre que per a la majoria de les espècies altricials les fluctuacions poblacionals s'explicaven millor per les pèrdues durant el període no reproductor.

En ambients canviants per l'acció de l'home, els individus han d'ajustar el seu comportament a aquestes condicions (Wong i Candolin 2015). La modificació del comportament es genera com a primera resposta a aquests canvis. El comportament es considerat com un element plàstic que permet als individus respondre davant de noves situacions. Així, la plasticitat comportamental juga un paper clau en explicar perquè algunes espècies són capaces de sobreviure en ambients alterats per l'home i altres no (Van Buskirk 2012). Per algunes espècies les alteracions antropogèniques es confronten directament amb les seves estratègies de vida (Kriska et al. 2006, Bretagnolle et al. 2018). A més, sovint aquestes alteracions es produeixen d'una manera tant ràpida i accentuada que moltes espècies no tenen suficient capacitat de resposta (Van Buskirk 2012, Sih 2013). Per altra banda, les alteracions creades per l'home poden minar la fiabilitat de les senyals utilitzades per els animals a l'hora d'avaluar la qualitat de l'hàbitat. Aquestes modificacions poden resultar en l'elecció d'un hàbitat subòptim i aquest fet pot tenir conseqüències sobre la supervivència (Battin 2004) i l'èxit reproductor (Kokko i Sutherland 2001, Hale i Swearer 2016, Lameris et al. 2016, Bretagnolle et al. 2018).

Efectes de la intensificació agrícola sobre l'avifauna

La conservació de les espècies requereix entendre els factors que influencien la selecció d'hàbitat, la supervivència i la productivitat de les seves poblacions. Els principals factors d'intensificació agrícola són elements transformadors dels paisatges i dels ecosistemes agraris i tenen una gran influència sobre les espècies vinculades a aquests ambients. La intensificació dels sistemes de producció agrícola ha estat identificada com la principal responsable de la reducció de les poblacions d'ocells a Europa vinculades als medis agrícoles (Donald et al. 2001) i de la pèrdua de biodiversitat (Benton et al. 2003). I com ja hem mencionat, els ocells esteparis es consideren actualment un dels grups d'ocells més amenaçats a nivell europeu (BirdLife International 2004, Burfield 2005).

La irrigació de les terres de secà produeix una reducció de les àrees de distribució de les espècies esteparies. A més a més, tenint en compte que moltes d'aquestes espècies nidifiquen a terra, les fa especialment sensibles a les pràctiques agrícoles, com són el reg per inundació, la sega dels cultius o les activitats d'aplicació dels tractaments fitosanitaris. Aquestes espècies també es veuen afectades, tant per l'abandonament de les activitats ramaderes en algunes zones, ocasionant la pèrdua d'hàbitats, com per la seva intensificació a causa de les pèrdues de nius al pas dels ramats. A més a més, tant la sega com la sobrepastura redueixen dràsticament l'alçada i cobertura de la vegetació, exposant als ocells a l'acció depredadors (Onrubia and Andrés 2005, Santos and Suárez 2005).

D'altra banda, la implantació del regadiu provoca canvis en les espècies cultivades, provocant de vegades la proliferació de cultius llenyosos. Aquest punt és especialment rellevant per als ocells esteparis ja que són espècies d'espais oberts i que poden no tolerar una configuració del paisatge excessivament tancada provocada per cultius llenyosos (Cardador et al. 2015) o altres cultius, com el blat de moro, que assoleixen una gran alçada.

Els canvis en els usos del sòl, com per exemple el provocat per l'abandonament de zones agrícoles, també té conseqüències sobre les comunitats d'ocells. L'abandonament d'aquestes zones afavoriria les espècies forestals i de matollar, en detriment de les espècies d'ambients agrícoles (EBCC 2015). Concretament, a l'oest de la conca del Mediterrani les espècies que es veurien més afectades per aquest abandonament serien les espècies d'ambients agrícoles (Sirami et al. 2008).

Per altra banda, els canvis de sòl agrícola per a usos urbans o d'infraestructures suposen una pèrdua directe de l'hàbitat per a aquestes espècies que veuen reduïda així les zones d'hàbitat disponible i conseqüentment la seva distribució. Addicionalment, aquests canvis fomenten la fragmentació de l'hàbitat que pot tenir conseqüències negatives per algunes espècies (Fahrig 2003, Liu et al. 2016, Xu et al. 2018).

La biodiversitat dels ambients agrícoles s'ha vinculat directament a la heterogeneïtat del paisatge (Benton et al. 2003, Katayama et al. 2014, Fahrig et al. 2015). En concret, la biodiversitat estaria més relacionada amb l'heterogeneïtat configuracional del paisatge, és a dir com els diferents usos del sòl es distribueixen en l'espai, que amb l'heterogeneïtat composicional, el percentatge dels diferents usos del sòl (Fahrig et al. 2011). Per altra banda els ambients més homogenis formats per parcel·les de mida gran presenten una menor diversitat dels diferents taxons (Fahrig et al. 2015).

L'ús de fertilitzants sintètics promou l'eliminació dels guarets, que suposa la destrucció de zones de nidificació, aprovisionament d'aliment i àrees de refugi per als ocells esteparis (Lapiedra et al. 2011, Morales et al. 2013).

Finalment, l'ús excessiu de herbicides, insecticides i fungicides afecta a tot l'ecosistema. La disminució d'espècies de plantes arvenses es dóna tant en abundància com en nombre d'espècies (Romero et al. 2008, Geiger et al. 2010). Aquesta reducció en el nivell basal de la cadena tròfica provoca una afectació en tots els nivells del sistema (Abrams et al. 1996)

Estat de conservació dels piocs a escala global

El desenvolupament de l'agricultura ha tingut lloc, principalment, en sòls fèrtils i relativament plans. Que a la mateixa vegada, han sigut els entorns escollits per a situar els assentaments humans, incloses les grans metròpolis. El creixement d'una agricultura cada vegada més intensificada i l'expansió de les poblacions humanes han anat guanyant terreny a les àrees de distribució de les espècies que habitaven aquests paisatges en el passat.

La família dels piocs o otídids són un clar exemple d'espècies lligades a zones planes o terrenys ondulants i que, a més a més, habiten espais oberts amb vegetació arbòria escassa i dispersa (Cramp and Simmons 1980, Figura 1 del Requadre 2). El sol·lapament de les àrees de distribució d'aquestes espècies amb les zones d'interès humà i alterades per l'home, ha produït la pèrdua forçosa de part de l'hàbitat ocupat per aquestes espècies en un passat recent, posant en risc la existència d'algunes d'elles. De les 26 espècies que conformen la família *Otididae*, el 58% d'elles es troben catalogades en l'actualitat dins d'alguna de les categories amb grau d'amenaça de la Unió Internacional per a la Conservació de la Natura. D'aquestes, 2 espècies es troben en perill crític d'extinció, altres 2 en perill d'extinció, 4 d'elles són vulnerables i 7 espècies es troben pròximes a l'amenaça (veure Requadre 1).

A continuació, sense pretendre fer una revisió exhaustiva sobre la matèria, es descriuen les principals amenaces i estat de conservació de les espècies de la família *Otididae*, basant-nos en la informació procedent de les fitxes específiques de la IUCN (www.iucnredlist.org). Les principals amenaces per a les espècies d'aquesta familia són la intensificació agrícola, la caça, les col·lisions amb infraestructures i el canvi climàtic (Fig. 1 del requadre 1). Les activitats antropogèniques relacionades amb la agricultura i la cria de bestiar, amenacen actualment a un total de 14 espècies de piocs distribuïdes en 3 continents (Àfrica, Àsia i Europa). D'aquestes, a més a més, 11 espècies són objecte de caça, essent un total de 12 espècies de piocs les que pateixen els efectes de la pressió cinegètica. A més, per a una altre espècie (*Ardeotis australis*), originària d’Oceania, tant la intensificació dels sistemes agropastorals com la caça eren factors d’amença de la espècie en el passat. Per altra banda, 8 espècies (*Ardeotis kori*, *A. Nigriceps*, *Chlamydotis macqueenii*, *C. undulata*, *Neotis denhami*, *N. Ludwigii*, *Otis tarda* i *Tetrax tetrax*) es veuen afectades per les vies de serveis, com són les línies elèctriques i una novena (*Houbaropsis bengalensis*) se’n podria veure afectada en un futur. En addició, les carreteres i les vies ferroviàries suposen una amenaça per a les 4 espècies que es distribueixen en el Paleàrtic (*Chlamydotis macqueenii*, *C. undulata*, *Otis tarda* i *Tetrax tetrax*) i una cinquena que habita el subconti-nent indi (*Ardeotis nigriceps*). Cal destacar però, l’impacte present o possible en un futur de les víes de transport i línies de serveis sobre *A. nigriceps* i *H. bengalensis*, donat que ambdues espècies es troben en perill crític d’extinció. El canvi climàtic i les condicions de clima sever, com són les sequeres, les temperatures extremes, les tempestes o les inundacions, afecten a les poblacions d’hubares i de pioc salvatge. Per altra banda, s’ha descrit que en un futur el canvi climàtic podria agreujar l’estat de conservació d’almenys 8 espècies de piocs (*Afrotis afra*, *Chlamydotis macqueenii*, *Eupodotis caerulescens*, *Heterotetrax humilis*, *H. vigorsii*, *Neotis denhami*, *Sypheotides indicus*, *Tetrax tetrax*). Altres factors d’amenaça rellevants són les activitats humanes i molèsties generades per les activitats recreatives, guerres i activitats militars, entre altres. També la producció d’energia i la mineria.

A nivell continental, les poblacions asiàtiques són les que presenten un pitjor estat de conservació, on de les 6 espècies que hi habiten 1 es troba pròxima a la amenaça a nivell mundial (*T. tetrax*), 2 són vulnerables (*C. macqueenii* i *O. tarda*), 1 està en perill (*S. indicus*) i 2 en perill crític (*A. nigriceps* i *H. bengalensis*). Del conjunt d’amenaces que hem descrit per als piocs, hi hauríem d’afegir l’efecte dels gossos, sobretot salvatges, sobre les poblacions asiàtiques de pioc salvatge i que afectaria també a altres espècies (*A. nigriceps*, *H. bengalensis*, *S. indicus, T. tetrax*) (Collar et al. 2017). Al continent africà, hi trobem la major diversitat d’espècies amb un total de 22 espècies. En general, les espècies africanes presenten un millor estat de conservació que les espècies asiàtiques. Excloent les 3 espècies que presenten una distribució marginal a Àfrica (*C. macqueenii*, *O. tarda* i *T. tetrax*) (Fig. 2 del requa re 1), 10 espècies presenten un estat de conservació de preocupació menor, 6 es troben properes a l’amenaça, 2 són vulnerables i 1 es troba en perill. No obstant, s’hauria d’estar atent i monitoritzar les tendències poblacionals a través de censos específics.

A Europa tan sols hi trobem 2 espècies (*O. tarda* i *T. tetrax*) que a nivell regional es troben catalogades com a “Vulnerables” (BirdLife International 2015). No obstant, a la península Ibèrica, on trobem les poblacions europees més importants per ambdues espècies, les poblacions de pioc salvatge s’han recuperat en les últimes dècades, mentre que en el cas del sisó comú s’ha produït l’efecte contrari (veure Casas et al. 2018). Dins dels límits administratius d’Espanya també s’hi troba una subespècie de l’hubara africana (*C. undulata fuertaventurae*) que habita les illes orientals de l’arxipèlag canari i que compta amb uns pocs centenars d’efectius poblacionals (Martin et al. 1997, Carrascal et al. 2006).

Requadre 1 Estat de conservació, principals amenaces i hàbitats de les espècies de pioc. Catalogació del nivell d’amenaça designada per la Unió Internacional per a la Conservació de la Natura (UICN, 2018) de les 26 espècies representants de la familia *Otididae*. També es descriuen les principals amenaces per a les diferents espècies, així com també la seva distribució.

	Nom (anglès)	Espècie	Estatus	
1.-	Asian houbara	*Chlamydotis macqueenii*	VU	🟧
2.-	African houbara	*Chlamydotis undulata*	VU	🟧
3.-	Little bustard	*Tetrax tetrax*	NT	🟨
4.-	Great bustard	*Otis tarda*	VU	🟧
5.-	Australian bustard	*Ardeotis australis*	LC	🟩
6.-	Great Indian bustard	*Ardeotis nigriceps*	CR	🟥
7.-	Arabian bustard	*Ardeotis arabs*	NT	🟨
8.-	Kori bustard	*Ardeotis kori*	NT	🟨
9.-	Nubian bustard	*Neotis nuba*	NT	🟨
10.-	Denham's bustard	*Neotis denhami*	NT	🟨
11.-	Heuglin's bustard	*Neotis heuglinii*	LC	🟩
12.-	Ludwig's bustard	*Neotis ludwigii*	EN	🟧
13.-	Black-bellied bustard	*Lissotis melanogaster*	LC	🟩
14.-	Hartlaub's bustard	*Lissotis hartlaubii*	LC	🟩
15.-	White-bellied bustard	*Eupodotis senegalensis*	LC	🟩
16.-	Blue bustard	*Eupodotis caerulescens*	NT	🟨
17.-	Little brown bustard	*Heterotetrax humilis*	NT	🟨
18.-	Black-throated bustard	*Heterotetrax vigorsii*	LC	🟩
19.-	Ruppell's bustard	*Heterotetrax rueppelii*	LC	🟩
20.-	Southern black bustard	*Afrotis afra*	VU	🟧
21.-	Northern black bustard	*Afrotis afraoides*	LC	🟩
22.-	Bengal florican	*Houbaropsis bengalensis*	CR	🟥
23.-	Lesser florican	*Sypheotides indicus*	EN	🟧
24.-	Buff-crested bustard	*Lophotis gindiana*	LC	🟩
25.-	Red-crested bustard	*Lophotis ruficrista*	LC	🟩
26.-	Savile's bustard	*Lophotis savilei*	LC	🟩

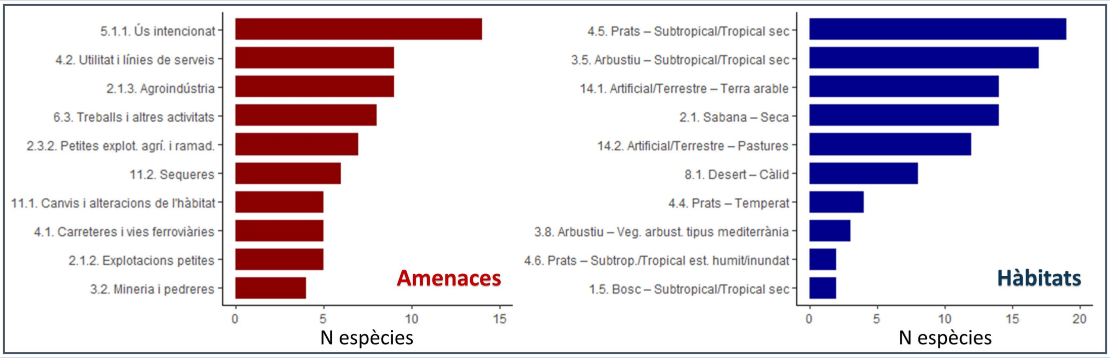


Figura 1 Principals amenaces i hàbitats de les 26 espècies de la familia Otididae segons la UICN. Dades adaptades.

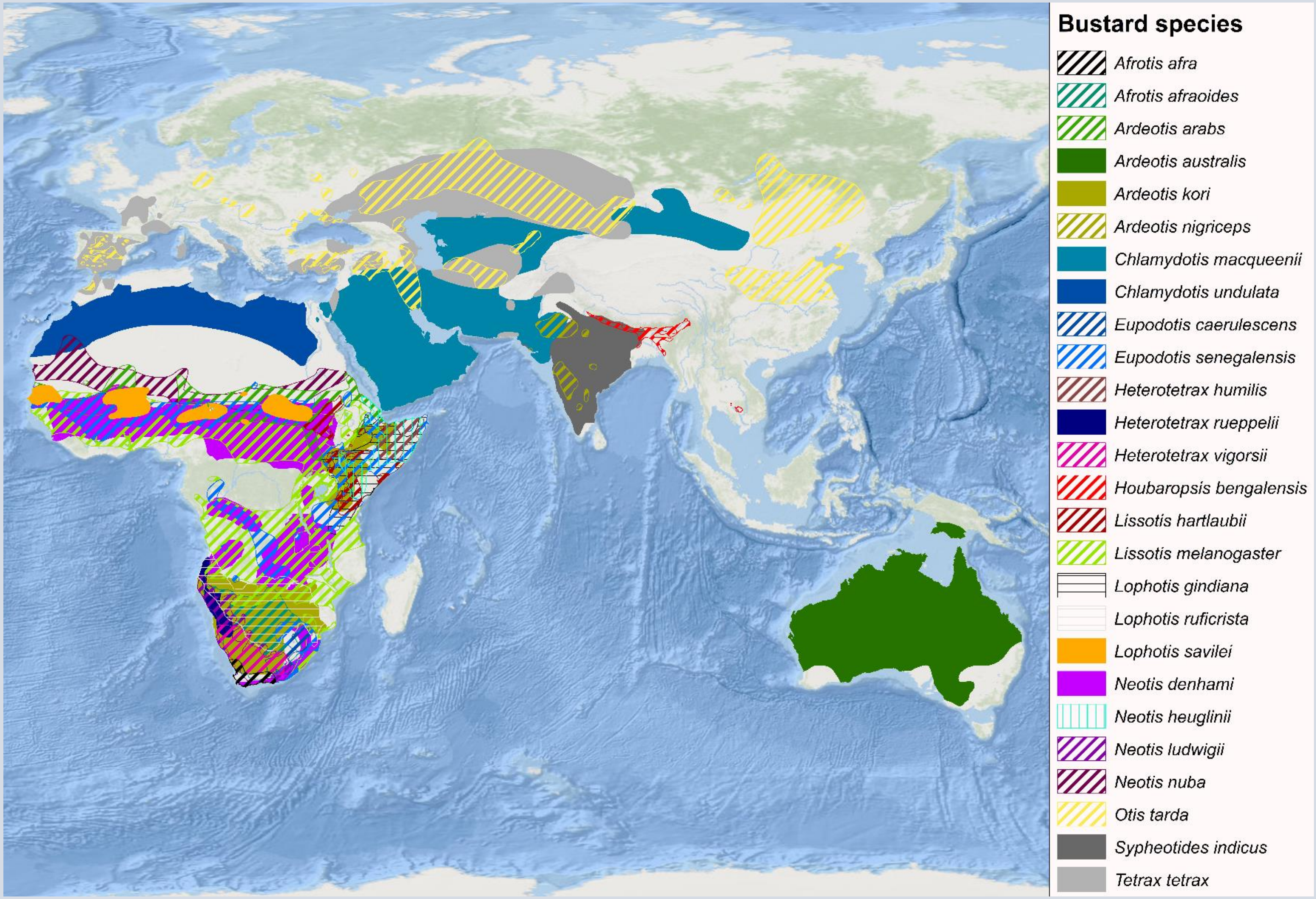


Figura 2 Distribució de les 26 espècies de la familia Otididae. Mapa derivat de les dades procedents de la Unió Internacional per a la Conservació de la Natura (IUCN; https://www.iucnredlist.org). Mapa de confecció pròpia.

El sisó comú

1. Biologia de l'espècie

El sisó comú (*Tetrax* tetrax) és un ocell estepari que es distribueix al llarg de la regió Paleàrtica. El seu rang de distribució comprèn des de la península Ibèrica i el nord d'Àfrica fins al nord-oest de la Xina (del Hoyo et al. 2014, BirdLife International 2017) (Fig. 1). Originàriament, l'espècie ocupava les estepes naturals d'Euràsia, però a mesura que la transformació dels usos del sòl cap a medis agrícoles avançava al llarg de la història de la humanitat, el sisó comú va anar colonitzant de manera secundària les àrees cultivades. En latituds superiors als 46º N l'espècie és migradora i tan sols hi és present durant el període reproductor. Una vegada finalitzada la reproducció i cria dels polls, aquestes poblacions comencen la migració postnupcial cap a latituds més baixes on quedaran a resguard de les temperatures rigorosament baixes de les latituds més septentrionals. D'altra banda, en latituds entre els 33–46º N podem trobar importants poblacions de sisons considerades com a sedentàries o migradores parcials (Cramp and Simmons 1980, García de la Morena et al. 2015). A la Península Ibèrica hi trobem la població més important d'individus sedentaris de l'espècie i una de les poblacions més importants de

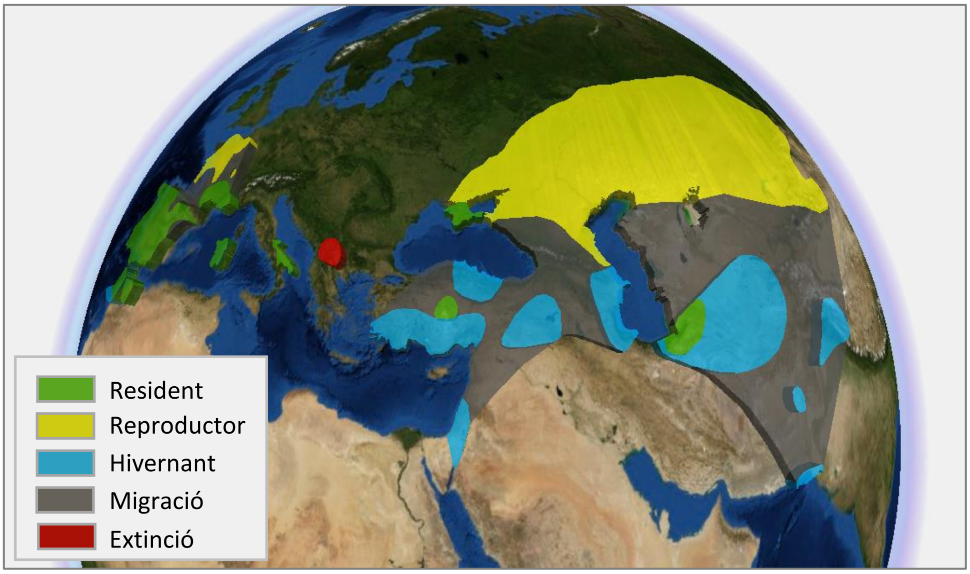


Figura 1 Distribució del sisó comú (*Tetrax* tetrax). Mapa de distribució de l'espècie segons BirdLife International i el Handbook of the Birds of the World (2016). Tetrax tetrax. Llista Vermella de les espècies amenaçades IUCN. Versió 2017-2. Mapa de confecció pròpia.

l’espècie a nivell mundial (García de la Morena et al. 2006, 2015).

Des d’un punt de vista reproductiu, el sisó comú és una espècie poligínica que presenta un sistema d’aparellament basat en lek dispers (Jiguet and Bretagnolle 2001). Els mascles es distribueixen en arenes formades per agregacions de mascles on efectuen un característic comportament de display per tal d’atreure femelles amb les que copular. Les femelles, per la seva banda, acudeixen als territoris dels mascles exclusivament a la recerca de mascles de bona qualitat per aparellar-s’hi. No obs-tant això, les femelles poden nidifi-car dins dels territoris defensats per mascles (Jiguet et al. 2002, Morales et al. 2013) o visitar els territoris dels mascles en busca de recursos tròfics quan aquests són escassos. De ben segur que la dis-ponibilitat d’un hàbitat adequat per a la nidificació i aspectes rela-cionats amb la densitat de mascles hi estan involucrats (Jiguet et al. 2002, Morales et al. 2014, Devoucoux et al. 2018).

Durant la incubació dels ous i la cria de les pollicades, el mascle no contribueix en l’atenció parental (Jiguet et al. 2000). Així que tota la responsabilitat de la cura parental recau en la femella. El niu és una simple depressió al terra guarnida amb herba (Boutinot 1957) localitzat entre vegetació herbàcia baixa, sovint en guarets o camps de cultiu. La posta, generalment formada per 3–4 ous (Shlyakhtin et al. 2004), té lloc principalment a la primavera, encara que al Marroc s’han descrit nius des del febrer al mes de juny. A la península Ibèrica el mes de maig és el període on ocorren la majoria de postes (Johnsgard 1991). Probablement, la femella comença a covar abans que l’últim dels ous sigui post i la incubació es perllonga durant 20–22 dies. Encara que després del fracàs del niu les femelles són capaces de pondre postes de reposició, aquestes s’han descrit com a infreqüents (Lapiedra et al. 2011, Bretagnolle et al. 2018). Els polls són precocials i atesos exclusivament per la femella (Cramp and Simmons 1980).

Estat de conservació

En les últimes dècades, l’espècie ha patit una forta regressió poblacional deguda, principalment, a la intensificació agrícola. Els efectes negatius de la caça i de les col·lisions amb infraestructures i transports s’han descrit, també, com a factors d’amenaça per a les seves poblacions. Actualment, l’espècie està catalogada com a Vulnerable (VU) a nivell europeu (Staneva and Bur-field 2017) i Propera a l’Amenaça (NT, de les seves sigles de l’anglès) a nivell mundial (BirdLife International 2016). Tot i que els resultats obtinguts en els últims censos efectuats a Europa (García de la Morena et al. 2017, Silva et al. 2018) posen de manifest la urgència d’una actualització del seu estat de conservació.

Els processos específics vinculats a la intensificació agrícola i a la davallada poblacional del sisó comú són de ben segur complexes i multifactorials. Investigacions dutes a terme a l’oest de França (Bretagnolle et al. 2011) i al nord-est de la península Ibèrica (Lapiedra et al. 2011) indiquen que l’èxit reproductor d’aquestes poblacions està per sota del que es considera el llindar de viabilitat demogràfica (Inchausti and Bretagnolle 2005, Morales et al. 2005a) en ambdues poblacions. Als sistemes agrícoles intensius de l’oest de França, el baix èxit reproductor s’ha atribuït a la destrucció dels nius durant la sega dels cultius (Bretagnolle et al. 2018) i també s’ha associat a la pèrdua de les pollicades deguda a la baixa abundància d’artròpodes (Inchausti and Bretagnolle 2005, Bretagnolle et al. 2011), els quals són essencials per a la cria dels polls (Jiguet 2002). Per altra banda, a les pseudoestepes cerealístiques del nord-est de la península Ibèrica, l’absència d’una cobertura vegetal adequada i l’escassetat d’aliment també s’han identificat com a responsables de l’alta mortalitat dels polls. No obstant, contràriament al descrit a l’oest de França, tan sols una petita proporció de les pèrdues esdevingudes durant la incubació es van poder atribuir a l’efecte directe de les operacions de sega o altres activitats agrícoles (Lapiedra et al. 2011), ja que moltes de les postes fracassades durant la incubació tenien lloc abans de la collita del cereal en aquesta regió.

D’altra banda, des d’un punt de vista demogràfic, no tan sols la productivitat i el reclutament de nous individus a les poblacions juguen un paper important en la viabilitat de les poblacions. En les espècies relativament longeves, un dels paràmetres demogràfics clau per a que una població disposi de bona salut és la supervivència dels individus adults i sexualment madurs (Newton 1998, Morales et al. 2005a). Les principals amenaces descrites fins ara que afecten la supervivència adulta són la caça il·legal i les col·lisions amb línies elèctriques (Iñigo and Barov 2010, BirdLife International 2016). Tot i que la seva importància relativa de cadascun d'aquests factors resta desconeguda.

Intensificació agrícola a Espanya

A Espanya, encara avui dia, trobem forces zones agrícoles extensives (Kleijn et al. 2006), amb un alt percentatge de la superfície arable del país ocupada per pseudoestepes (Suárez et al. 1997). Aquestes es caracteritzen per ser zones obertes i planes o ondulants, dominades per cereals d'hivern, com l'ordi i el blat (Suárez et al. 1997), en un clima mediterrani continental. Que encara perdurin zones agrícoles extensives és un dels motius per els quals les poblacions d'ocells de medis agrícoles a Espanya disposen de millor salut que en altres països europeus (Butler et al. 2010). De fet, el conjunt de la península Ibèrica és la regió més important per als ocells esteparis dins de la Unió Europea (Santos and Suárez 2005) amb una gran diversitat d'espècies a Espanya (Traba et al. 2007). Així, aquest estat té una gran responsabilitat en garantir la conservació d'aquestes espècies. Els processos d'intensificació agrícoles actuals a Espanya posen en perill algunes d'aquestes espècies. I en l'actualitat, trobem davallades poblacionals més accentuades que en altres països de l'entorn europeu (Staneva and Burfield 2017).

1. *Conversió a regadiu*

Els sistemes agrícoles extensius de secà tradicionals, dominats principalment per cereals d'hivern, tals com l'ordi o el blat, són poc productius en comparació amb els cereals que es troben en sistemes agrícoles irrigats (Mueller et al. 2012). De fet, si es deixessin de regar tots els cereals irrigats, actualment, la producció d'aquests cultius disminuiria un 47%, causant una pèrdua en la producció dels cereals a nivell mundial al voltant d'un 20% (Siebert i Döll 2010). Les diferències s'evidencien molt més si comparem la producció i rendiments econòmics dels cereals de secà amb altres tipus de cultius que requereixen d'aportació hídrica, com podrien ser els cultius de blat de moro o els cultius llenyosos de fruita dolça. A escala global, el 24% de les terres de cultiu són regades i aquestes són les responsables del 34% de la producció agrícola (Siebert and Döll 2010).

A Espanya, la construcció de nombrosos pantans a les principals con-ques hidrogràfiques a partir dels anys 50 va permetre l'emmagatzemament de grans reserves d'aigua. Aquesta disponibilitat hídrica va propiciar el desenvolupament dels sistemes de regadiu. Així, a mitjans del segle XX comença una important conversió de cultius de secà a cultius de regadiu que continua tenint lloc en l'actualitat (Fig. 2). Avui dia, el regadiu ocupa un 22.0% de la superfície agrícola espanyola i un 7.4% de la superfície geogràfica del país (MAPAMA, 2017).

El sistema de reg per gravetat va ser el primer sistema de reg utilitzat de manera generalitzada, ja que és el que necessita d'una menor infraestructura i tècnica (veure Requadre 2). Encara avui dia, aquest sistema de reg està força estès (25% de la superfície regada a Espanya; MAPAMA 2017), tot i que és poc eficient en l'estalvi d'aigua. Per altra banda, l'augment progressiu de la superfície de reg ha provocat un increment en la pressió sobre aquest recurs tan preuat. Així que, cada vegada més, es fa més necessària la modernització dels sistemes de reg menys eficients en l'ús de l'aigua per altres sistemes que permeten un major estalvi dels recursos hídrics (Tilman et al. 2002). Actualment, el reg per gravetat està sent substituït per altres sistemes de reg més eficients. A Espanya, durant l'última dècada (període 2007-2016), el reg per gravetat ha disminuït un 15%, mentre que altres sistemes de reg com són el reg per aspersió amb suport fixe, el reg per aspersió mitjançant pivot o el reg localitzat han augmentat un 18%, un 24% i un 23 %, respectivament, per al mateix període (MAPAMA, 2017).

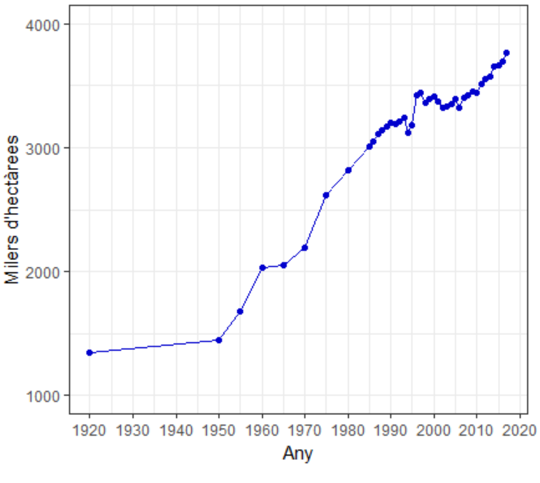
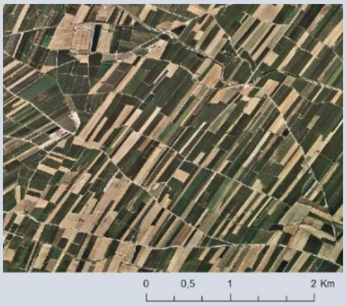


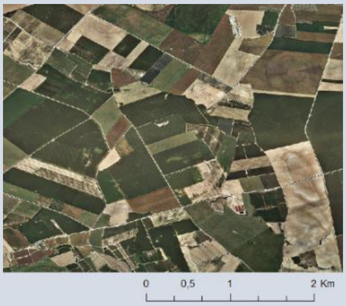
Figura 2 Evolució de la superfície de cultius de regadiu a Espanya pel període (1920-2017). Les dades emprades per generar la gràfica han estat recopil·lades de diverses fonts: *Estructura económica de España* per Tamames (2008) (període: 1920-1980); *Anuario de estadística 2002* del Ministerio de Agricultura, Pesca, Alimentación y Medio Ambiente (MAPAMA) (període: 1985-2001); *Anuario de estadística 2017,* MAPAMA (període: 2002-2017).

Requadre 2 Descripció dels sistemes de reg més comuns. A la dreta es poden observar imatges aèries de zones dominades pels diferents sistemes de regadiu descrits. Observis que l'ús dels diferents sistemes de reg pot tenir efectes en l'heterogeneïtat del paisatge agrícola.

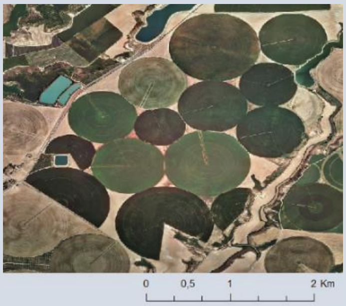
SISTEMES DE REG



Reg per gravetat: és el sistema més antic de reg i encara avui dia el més estès al món. L'aigua procedent d'un riu o font es canalitza mitjançant un seguit de canals que porten l'aigua fins als conreus. El reg es realitza amb l'obertura d'un comporta per on surt l'aigua i gràcies a un cert desnivell de la parcel·la aquesta es regada.



Reg per aspersors fixes: sistema de reg a pressió que requereix de molta energia. L'aigua es transportada per unes canonades que porten l'aigua fins a uns aspersors fixes que dispersen l'aigua simulant la pluja. Per assolir la pressió requerida normalment es necessari l'ús de bombes o bé dipòsits d'aigua elevats o sistemes similars.



Reg per pivots: tipus de reg per aspersió mòbil. El més comú és el de tipus central que rep el seu nom degut al seu moviment circular al voltant d'un punt central sobre el qual pivota. Per a que aquest sistema de reg sigui rentable es requereix que l'estructura mòbil sigui bastant llarga, generant així conreus de grans dimensions. Es considera que la mida mínima de la parcel·la per a que aquest tipus de reg sigui rentable és d'unes 16 hectàrees.

Reg localitzat per degoteig: de la mateixa manera que el reg per aspersió, aquest és un tipus de reg pressuritzat. Aquest sistema es basa en un alt aprofitament de l'aigua a través d'un sistema de petites canonades que reguen per degoteig el sistema radicular de les espècies cultivades. Generalment aquest tipus de reg s'utilitza per espècies llenyoses encara que també es poden utilitzar en cultius herbacis.

Aquests canvis poden tenir importants efectes en el paisatge agrícola, ja que cadascun d'aquests sistemes duu associat un determinat tipus de parcel·la agrícola. Per exemple, les parcel·les regades per gravetat normalment presenten una mida relativament petita, ja que és necessari que tinguin una amplada que permeti el direccionament de l'aigua amb la finalitat que la irrigació es produeixi en tots els punts de la parcel·la. Mentre que, per exemple, el reg per pivot requereix que les parcel·les ocupin grans extensions de terreny per a que aquestes explotacions siguin rendibles.

Tot això, té grans conseqüències en la configuració del paisatge. En general, els sistemes agrícoles constituïts per parcel·les de mida petita fomenten la heterogeneïtat del paisatge ja que poden propiciar una matriu paisatgística més diversa, mentre que aquells sistemes formats per parcel·les de mida més gran, sovint, són considerats com a sistemes més homogenis (Fahrig et al. 2011). No obstant això, hi ha

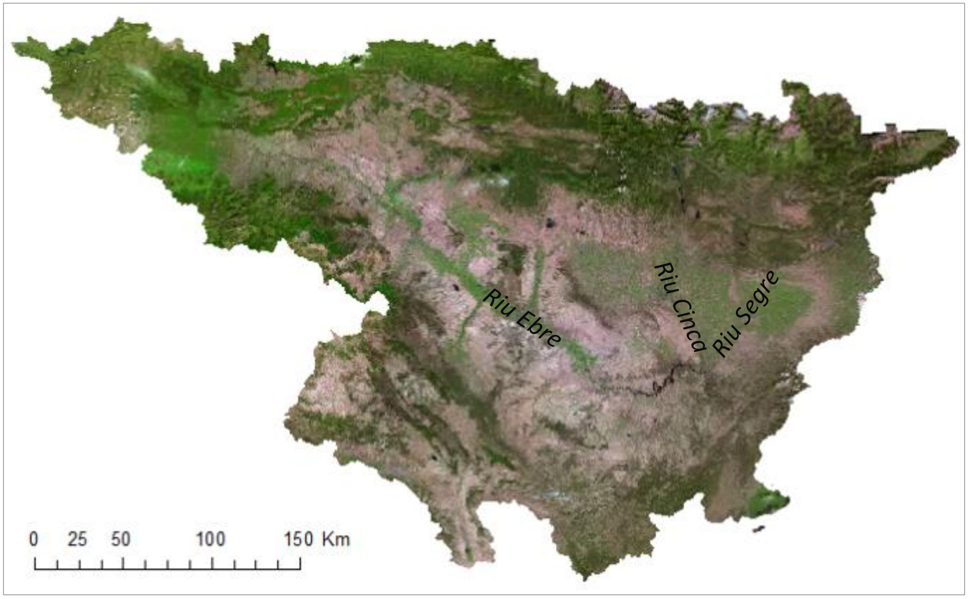


Figura 3 Ortofotomapa de la conca de l'Ebre. Mapa generat a partir de l'obtenció d'imatges satel·litals (Spot-5 a 20 m de resolució) i ortofotografies (PNOA 0.25-0.50 m de resolució). A la imatge es poden apreciar les principals àrees de regadiu (verd pàl·lid) presents a l'interior de la conca. Les principals àrees de regadiu es poden delimitar, d'est a oest, en regadius de la Plana de Lleida irrigats mitjançant el Canal d'Urgell amb aportació de cabal del riu Segre, regadius amb aportació del riu Cinca i regadius a la llera de l'Ebre i altres afluents.

gran diversitat de medis agrícoles i existeixen sistemes amb parcel·les de mida petita que són força homogenis en la seva composició.

2. *Canvis en els usos del sòl*

La producció agrícola respon a les necessitats de mercat. Així que les noves plantacions de cultius busquen satisfer les demandes del mercat interior i exterior. Tal i com hem mencionat prèviament, els sistemes agrícoles de regadiu permeten conrear cultius i varietats que d'altra manera no serien possibles en entorns on les precipitacions no són suficientment abundants. Cal destacar que les plantacions de cultius llenyosos modifiquen dràsticament els paisatges agrícoles tradicionalment caracteritzats per ser espais oberts amb cultius herbacis anuals, generant ambients molt més tancats dominats per grans extensions de monocultius gestionades de manera intensiva. Per altra banda, la modificació dels usos del sòl no tan sols es produeix per una substitució d'uns cultius per uns altres. Paral·lelament al procés d'intensificació agrícola s'ha produït una progressiva translocació de la població de les zones rurals a les ciutats que ha provocat l'abandonament de zones agrícoles menys productives (MacDonald et al. 2000, Rey Benayas 2007). Aquest abandonament ha propiciat que amb el temps la vegetació natural recolonitzi aquests espais (Cohen et al. 2011). Es dóna així, un procés de forestació natural quan les condicions de l'ambient i la pròpia vegetació natural ho permeten, aquest procés no s'hauria de confondre amb el fenòmen de reforestació efectuada per repoblacions actives d'arbres mitjançant la plantada o la sembra de llavors (Mather and Needle 1998).

Segons The Economist (2017), Espanya ha passat d'un 28% de superfície forestal a l'any 1990 a un 37% en l'actualitat. A altres països de la Unió Europea s'han observat tendències similars. No obstant, aquests increments no es deuen exclusivament a processos de forestació natural, sinó que les forestacions actives també han contribuït a l'increment de la superfície forestal en els països occidentals.

La forestació de les últimes dècades a Espanya està vinculada a l'entrada d'aquest estat a la Comunitat Econòmica Europea al 1986 i a les mesures de protecció ambiental i forestals proposades dins de la Política Agrària Comuna (PAC) aprovades a l'any 1992 (Rey Benayas 2007, Vadell et al. 2016). Els sòls objecte d'aquesta forestació van ser un 22% terres de cultiu, un 50% pastures i guarets pasturats i un 28% zones forestals obertes (Picard 2001). Durant el període 1993–1999 les zones forestades van assolir les 460.000 ha a Espanya, amb taxes d'increment anuals similars a les reforestacions dels anys 50 (Vadell et al. 2016).

Finalment, l'abandonament de les zones rurals ha conduït a una expansió de les zones urbanes i de les infraestructures, ocupant entre d'altres hàbitats, els medis agrícoles.

3. *Mecanització i concentració parcel·laria*

El desenvolupament tecnològic ha propiciat la mecanització dels sistemes de producció agrícola augmentant la mida de les explotacions agrícoles i accelerant els processos de producció. En l'actualitat, per exemple, la collita del cereal succeeix molt més ràpid que quan aquesta s'efectuava manualment o amb l'ajuda de tracció animal, a més a més, la nova maquinària agrícola permet realitzar de manera simultània diferents operacions (p. ex., la collita del cereal, la trilla del gra i l'embalatge de la palla) (Robinson and Sutherland 2002). Paral·lelament, el progressiu desenvolupament econòmic i social, junt amb l'escàs relleu generacio-nal a la pagesia, ha provocat una reestructuració en la possessió de les propietats agrícoles. Conseqüentment, avui dia tenim explotacions agrícoles de mida més gran (Stoate et al. 2001).

D'altra banda, l'aparició de tractors cada vegada més potents i altra maquinària agrícola ha facilitat l'eliminació de rodals amb vegetació natural i de marges de parcel·les. Addicionalment, en alguns casos, des de l'administració pública s'ha fomentat la concentració parcel·laria. Aquesta es basa en la redistribució espacial i concentració de les parcel·les agrícoles d'un mateix propietari en blocs de parcel·les agregades. Així que, sovint, la concentració parcel·laria provoca l'eliminació de marges i augmenta la mida de les parcel·les agrícoles. Per posar un exemple proper, si comparem en nombre i mida les parcel·les agrícoles en una mostra de 1018 hectàrees a la Zona d'Especial Protecció per a les Aus (ZEPA) dels Secans de Belianes-Preixana abans i després d'una concentració parcel·laria trobem que el nombre de parcel·les d'ús agrícola ha disminuït un 38%. Mentre que la mida de les parcel·les abans de la concentració parcel·laria era de 1.4 ± 1.6 ha (mitjana ± sd), en l'actualitat és de 2.1 ± 2.6 ha (dades pròpies obtingudes a partir de la cartografia SIGPAC 2009 i 2016). A més a més, la concentració parcel·laria al generar parcel·les agrícoles de mida més gran, redueix la densitat de marges, elements estructurals importants pel manteniment de la biodiversitat (Robinson and Sutherland 2002) i provoca la simplificació i homogeneïtzació dels paisatges agrícoles.

4. *Ús de fertilitzants*

L'augment dels rendiments en la producció de les explotacions agrícoles ha estat possible gràcies a l'aplicació de fertilitzants sintètics. A escala global, entre 1960 i 1995 l'aplicació de fertilitzants nitrogenats es va multiplicat per 7 i l'ús del fòsfor va augmentar 3.5 vegades (Tilman et al. 2002). Avui dia, l'ús de fertilitzants sintètics permet conrear varis cultius en un mateix camp per temporada agrícola. A banda dels compostos sintètics, existeixen altres productes que s'utilitzen per a fertilitzar el sòl, com poden ser els fertilitzants d'origen orgànic. La matèria orgànica acostuma a millorar l'estructura del sòl i ajuda a retenir nutrients importants per a les plantes. No obstant, a vegades porta alguns problemes associats, com és el cas dels purins generats per la indústria porcina. Els purins, rics en nitrogen, s'utilitzen com a fertilitzants dels cultius i, simultàniament, els productors de porcí es desfan d'un residu incòmode de gestionar.

A banda dels problemes de contaminació de rius i aqüífers per l'escorrentia dels compostos nitrogenats, degut a la seva alta mobilitat i de l'emissió a l'atmosfera de gasos com els òxids de nitrogen que augmenten l'ozó troposfèric, l´ús de fertilitzants ha modificat els sistemes agrícoles tradicionals basats en la rotació dels conreus i el repòs de la terra en guaret. A dia d'avui, les terres en repòs o guarets han quedat relegats dels sistemes agrícoles intensius. No obstant, aquest sistema de rotació s'ha mantingut en les zones poc productives on, per les característiques del sòl, els costos de fertilització no compensen l'escàs rendiment econòmic d'aquest tipus d'explotacions agrícoles.

Pel que fa a Espanya, els guarets s'han reduït un 16.4% durant el període 2006–2016 segons dades del Ministeri d'Agricultura del govern espanyol (MAPAMA 2017). Tot i això, és un dels països dins de la Unió Europea amb un major percentatge de guarets respecte la superfície agrícola total del país (Fig. 4). Malauradament, comprovem per a les dades disponibles per a l'any 2007, com el rang dels percentatges de guarets respecte la superfície total agrícola per als diferents països de la UE es comprèn entre el 11.2% de Xipre i el 0.2% d'Irlanda (EUROSTAT 2015).

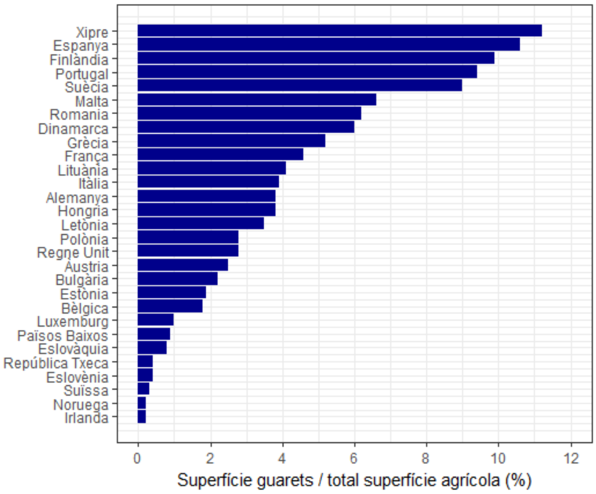


Figura 4 Percentatge de superfície en guaret respecte el total de superfície agrícola total per els diferents països de la UE per a l'any 2007 segons EUROSTAT. Per el cas de Suïssa no hi havia dades disponibles per aquest any i s'han utilitzat les dades per a l'any 2005. Font: http://appsso.eurostat.ec.europa.eu

Tradicionalment, els guarets s'empraven com un mètode de manteniment de la fertilitat del sòl i de control de les "males herbes" (Pierce and Rice 1988). En addició, les terres en repòs tenen una importància ecològica rellevant sobre la flora i fauna d'aquests ambients (Van Buskirk i Willi 2004) i també sobre els propis serveis ecosistèmics. Per posar un exemple, s'ha descrit com els sistemes de rotació amb guaret tindrien un efecte positiu sobre la pol·linització a través de l'afavoriment de la riquesa d'espècies i l'abundància dels insectes pol·linitzadors (Kuussaari et al. 2011). A més a més, els guarets podrien afavorir a altres grups d'insectes amb funcions tant importants com són l'eliminació d'excrements i el control de plagues (veure Zhang et al. 2007). Altres taxons, com són els ocells també poden exercir el servei de supressió de plagues (Boesing et al. 2017). A més a més, la vegetació seminatural redueix els danys als cultius per insectes degut a una major presència dels ocells que els depreden (Martin et al. 2013). Això últim és especialment rellevant, ja que en un sistema agrícola intensificat amb un paisatge simplificat basat en monocultius, la presència de plagues d'aquests cultius pot ser especialment important (Andow 1983, Öst-man et al. 2001). No obstant, els guarets també podrien servir com a zones de refugi i propagació d'espècies no desitjades (Rodríguez-Pastor et al. 2016).

5. *Ús de pesticides*

L'ús desmesurat d'herbicides i altres pesticides per fer front a les plantes i plagues indesitjables des d'un punt de vista agronòmic és, segurament, un dels problemes més greus que ocasiona la producció agrícola intensiva. Els seus efectes actuen en forma d'efecte cascada "bottom-up". És a dir, s'alteren els nivells basals de l'ecosistema i aquesta alteració afecta a la resta d'estrats superiors (Abrams et al. 1996). I és que els pesticides d'ampli espectre són letals per a les espècies objectiu (p.e. plagues dels cultius) però, al ser poc selectius, afecten a les altres espècies, alterant l'estructura de les comunitats (Rohr and Crumrine 2005) i amb conseqüències molt negatives per a tot l'ecosistema.

A més a més, els pesticides poden causar efectes no letals, afectant l'estat de salut i condició física dels individus, fet que pot revertir negativament en la supervivència i les taxes reproductives de les poblacions afectades (Lopez-Antia et al. 2015). D'altra banda, l'estrès fisiològic provocat per aquests agents externs pot desequilibrar la homeòstasi interna dels individus, augmentant la càrrega alostàtica que pot produir una disminució de la resposta immunitària i la susceptibilitat dels individus a patir malalties (Ramsay and Woods 2014).

Finalment, en els pesticides s'hi poden trobar altes concentracions de contaminants, com per exemple els metalls pesants, de la mateixa manera que els trobem presents en els fertilitzants inorgànics (Gimeno-García et al. 1996, Singh et al. 2017). Aquestes substàncies contaminen el sòl, són absorbides per les plantes i bioacumulades en els teixits, especialment en els organismes situats en els nivells superiors de les cadenes tròfiques (Singh et al. 2017). Fins i tot en dosis baixes, els metalls pesants poden tenir greus conseqüències sobre la salut dels organismes (Lukačínová et al. 2011).

OBJECTIUS

Els objectius generals d'aquesta tesi són aprofundir en alguns aspectes poc coneguts sobre la biologia i ecologia del sisó comú, però fonamentals per a la seva conservació en un context d'intensificació agrícola. Més concretament en aquelles qüestions més rellevants des d'un punt de vista de la dinàmica poblacional (mortalitat adulta i productivitat) o aspectes que han estat poc estudiats fins a l'actualitat, com és la dieta o les diferències interindividuals en els patrons de selecció d'hàbitat i el comportament espacial i les seves limitacions. Els objectius específics dels diferents capítols d'aquesta tesi són:

Capítol 1

1. Analitzar el comportament espacial de les femelles de sisó durant el període no reproductor definit per predictors d'hàbitat i limitacions espacials.
2. Avaluar la variació interindividual en els patrons de selecció d'hàbitat i comportament espacial.
3. Proposar mesures correctores per a la conciliació del desenvolupament agrícola i altres activitats humanes amb la conservació de les poblacions de sisó durant el període no reproductor.

Capítol 2

4. Descriure per primera vegada la composició d'espècies vegetals i animals que constitueixen la dieta del sisó en ambients agrícoles durant el període no reproductor.
5. Comparar la composició i diversitat d'espècies que conformen la dieta del sisó durant el període no reproductor sota diferents esquemes agrícoles (secà – regadiu) i gradients d'intensificació (extensiu – intensiu).
6. Discutir les possibles implicacions per a les poblacions de sisó que tenen les diferències trobades en la dieta en els diferents sistemes agrícoles.

Capítol 3

7. Avaluar les causes de mortalitat adulta i estimar la importància relativa de cadascuna de les causes de mort identificades a la península Ibèrica.
8. Plantejar solucions per tal de minimitzar els impactes negatius d'origen antròpic sobre la supervivència adulta de l'espècie.

Capítol 4

9. Caracteritzar per primera vegada els patrons d'incubació de les femelles de sisó.
10. Identificar les causes relacionades amb el fracàs reproductiu durant la fase d'incubació.
11. Investigar els factors responsables del fracassos produïts abans de l'eclosió relacionats tant amb activitats agrícoles com amb causes naturals.
12. Quantificar la taxa de reposició per aquelles femelles que fracassen durant el període d'incubació o mort prematura dels polls.
13. Suggerir mesures destinades a corregir les pressions sobre els nius de sisó per tal de contribuir a una major taxa d'eclosió i productivitat de l'espècie.

INTER-INDIVIDUAL CONSISTENCY IN HABITAT SELECTION PATTERNS AND SPATIAL RANGE CONSTRAINTS OF FEMALE LITTLE BUSTARDS DURING THE NON-BREEDING SEASON

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Identifying the factors that affect ranging behavior of animals is a central issue to ecology and an essential tool for designing effective conservation policies. This knowledge provides the information needed to predict the consequences of land-use change on species habitat use, especially in areas subject to major habitat transformations, such as agricultural landscapes. We evaluate inter-individual variation relative to environmental predictors and spatial constraints in limiting ranging behavior of female little bustards (*Tetrax tetrax*) in the non-breeding season. Our analyses were based on 11 females tracked with GPS during 5 years in northeastern Spain. We conducted deviance partitioning analyses based on different sets of generalized linear mixed models (GLMMs) constructed with environmental variables and spatial filters obtained by eigenvector mapping, while controlling for temporal and inter-individual variation. The occurrence probability of female little bustards in response to environmental variables and spatial filters within the non-breeding range exhibited inter-individual consistency. Pure spatial factors and joint spatial-habitat factors explained most of the variance in the models. Spatial predictors representing aggregation patterns at ~ 18 km and 3–5 km respectively had a high importance in female occurrence. However, pure habitat effects were also identified. Terrain slope, alfalfa and corn stubble availability were the variables that most contributed to environmental models. Overall, models revealed a non-linear negative effect of slope and positive effects of intermediate values of alfalfa and corn stubble availability. High levels of cereal stubble in irrigated land and roads had also a positive effect on occurrence at the population level. Our results provide evidence that female little bus-tard ranging behavior was spatially constrained beyond environmental variables during the non-breeding season. This pattern may result from different not mutually exclusive processes, such as cost-benefit balances of animal movement, configurational heterogeneity of environment or from high site fidelity and conspecific attraction. Measures aimed at keeping alfalfa availability and habitat heterogeneity in open landscapes and flat terrains, in safe places close to breeding grounds, could contribute to protect little bustard populations during the non-breeding season.

Cuscó, F., L. Cardador, G. Bota, M.B. Morales, and S. Mañosa. 2018. Inter-individual consistency in habitat selection patterns and spatial range constraints of female little bustards during the non-breeding season. BMC Ecology (in minor review since 24th September 2018)

Introduction

Identifying the factors that affect ranging behavior of animals is a central issue to ecology and an essential tool for designing effective conservation policies (Sutherland 1998, Tella et al. 1998). This knowledge provides the infomation needed to predict the consequences of land-use change on species habitat use, especially in regions subject to major habitat transformations, such as agricultural landscapes. However, this type of information is not always available, particularly in the non-breeding season or non-breeding areas of species with different seasonal distribution ranges (Peterjohn 2003, Suárez et al. 1997). Locations of radio and satellite telemetry provide valuable information on animal movement and are widely used for studies of habitat selection (Manly et al. 2002, Cardador and Mañosa 2011, Hooten et al. 2017). However, this type of data is frequently spatially autocorrelated (Kenward 2001, Aarts et al. 2008). Spatial autocorrelation in animal movement is often assumed to be the result of species-specific responses to spatially structured environment. However, other ecological processes, such as cost-benefit balances of animal movement across space and time, dispersal limitations or conspecific attraction, can also be involved in generating this pattern (Pinto and Macdougall 2010). Thus, accounting for spatial autocorrelation in analyses is essential to understand the ecological processes underlying ranging patterns (Hooten et al. 2017).

Among environmental factors, habitat characteristics and resource availability have been identified as major factors determining ranging behavior in birds (e.g., Cardador and Mañosa 2011, Tarjuelo et al. 2013). Other environmental factors such as risk of predation or anthropogenic conditions can also be involved (Le Cuziat et al. 2005, Alonso et al. 2012). Additionally, individuals within a population can show different strategies in the way they exploit available habitat or space (Cardador et al. 2012, Roever et al. 2013, Brown and Crone 2016). Indeed, individual differences in behavior, morphology, physiology, personality, and life history traits are common across taxa, which may lead to inter-individual differences in cost-benefit balances of different ranging strategies (Réale et al. 2007, Wilson and McLaughlin 2007, Boon et al. 2008). Behavioral variability in a population is thus an issue to take into account to develop effective conservation measures.

The little bustard (*Tetrax tetrax* L.) is a medium-sized steppe bird that inhabits natural steppes and cultivated areas of the Palearctic (Cramp and Simmons 1980). This is a ground nesting bird with a characteristic polygynic mating system based on exploded leks (Jiguet et al. 2002). During the non-breeding season the species is gregarious, forming large mixed flocks up to hundreds of individuals (Pinto 1998, García de la Morena et al. 2006, Ponjoan et al. 2011), even a few thousands in some regions (Gauger 2007). The species has been described as migrant in Russia, central Asia and northern France and as sedentary or partially migrant - with variations between and within populations - in the Iberian Peninsula, Italy and southern France (Cramp and Simmons 1980, Villers et al. 2010, García de la Morena 2015).

The species is listed as “Near Threatened” at global scale (BirdLife International 2016) and “Vulnerable” in Europe (BirdLife International 2015). The Iberian Peninsula holds one of the most important populations in the world (García de la Morena et al. 2006). There, the species is undergoing rapid declines regionally (De Juana 2009, Mañosa et al. 2015, Morales et al. 2015), leading to a global decrease of up to 50% of the Spanish population in a decade (García de la Morena et al. 2017). Contributing factors to such decline around the world are the loss and degradation of habitat related with agricultural intensification and hunting pressure (Goriup 1994, Del Hoyo et al. 1996, Iñigo and Barov 2010). Although habitat requirements during the breeding season have been the subject of much research (Martínez 1994, Salamolard and Moreau 1999, Wolff et al. 2001, Morales et al. 2005, 2008, Tarjuelo et al. 2013), studies centered on the non-breeding period are scarce (but see Leitão and Costa 2001, Silva et al. 2004, Faria and Silva 2010), even when the species spends around 3/4 of its annual cycle (from July to February) in non-breeding grounds (García de la Morena et al. 2015). In addition, most studies on the species are based on male observations, while female ecology and behavior have been scarcely studied. This is largely due to the extremely secretive behavior of females in spring and consequently the difficulty of obtaining data about them (Cramp and Simmons 1980).

In this study, we evaluate the role of environmental predictors in limiting ranging behavior during the non-breeding season of female little bustards in an intensified farmland, while considering potential spatial constraints in ranging patterns. We did so by implementing habitat selection models constructed with orographic, crop types, human-related variables and by excluding or incorporating spatial constraint variables obtained by eigenvector mapping. The inclusion of spatial constraint variables in models has recently been shown to effectively capture the effect of subjacent spatial structures that are not related to the environmental factors considered in models (De Marco et al. 2008, Estrada et al. 2016, Romero et al. 2016). We also assessed for inter-individual variation in the importance of response to ecological requirements and spatial constraints by incorporating a random structure in models. Finally, we use our results to propose some recommendations in order to design future conservation actions to reconcile agricultural development and other potentially conflicting human activities with the preservation of little bustard populations during the non-breeding season.

Methods

Study area

The study area is located in the Plana de Lleida (UTM Y: 4592-4629 km N; X: 289-341 km E), a large agricultural area situated in the northeastern Ebro basin (Iberian Peninsula) at 261 ± 65 meters over sea level. Climate is semiarid Mediterranean, with an average annual rainfall of 300-400 mm and an average temperature of 7-8 ºC in winter and 24-25 ºC in summer (AEMet 2015). In the last decades, the study area has suffered a strong process of agricultural intensification with an increase in mechanization, the use of chemical fertilizers and pesticides, land concentration processes and the transformation of dry lands to irrigated crops (Calvet et al. 2004). Nowadays, the zone is dominated by intensively irrigated cultivated farmland, although more extensive dry lands are also present in the periphery of the area, where the main breeding grounds of the species in the region are located (Fig. 1). Drylands are dominated by winter cereals (mainly barley and wheat), as well as some scattered almond and olive tree groves. Irrigated crops include fruit orchards, corn, alfalfa and spring cereals. In autumn, with

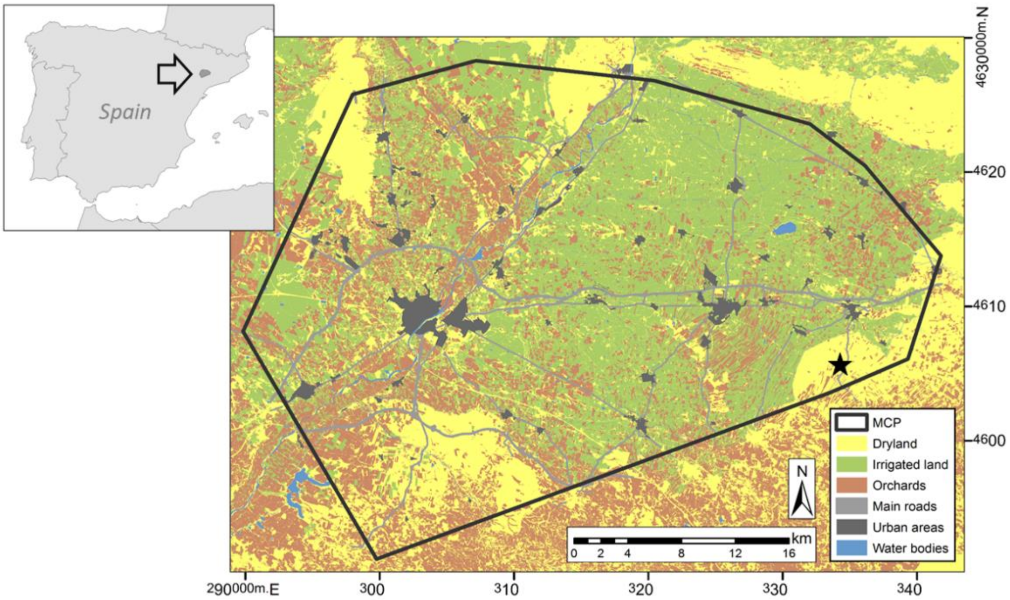

Figure 1 Location and land-use composition of the study area. Boundaries are defined by the minimum convex polygon (MCP) including the pool of locations of tagged female little bustards. Lleida is the large urban area located on the left. The black star indicates the main breeding area for the species in the study area. Reference coordinates in UTM. Map derived from SIGPAC cartography.

the beginning of a new agricultural cycle, most of cereal and corn fields are stubbles that will be plowed in the course of the season to turn into new sowings. Natural vegetation is scarce in the study area, representing around 10% of total surface.

Telemetry data

From 2009 to 2013, 18 female little bustards were captured using adapted funnel traps (see Ponjoan et al. 2010). The females were tagged with 22 g Solar Argos/GPS PTT–100 transmitters (Microwave Telemetry). The transmitter weight with harness never represented more than 5% of the body weight of the birds to avoid overload (Kenward 2001). To avoid capture myopathy, the time of capture and handling were minimized and never exceeded 15–20 minutes (Marco et al. 2006, Ponjoan et al. 2008).

A maximum of 6 locations per transmitter and day were obtained for each female in non-breeding period (23th September – 20th December) 2009-2013, with a latitude/longitude accuracy of 18 m (Microwave Telemetry). The study period was selected to ensure that all tracked birds had finished breeding or rearing chicks (the end of the breeding period and chick rearing period largely varies across individuals – from July to August – in the study area) (Calvet et al. 2004) and to maximize data quality (the long periods of fog during winter in the study area did not allow the batteries recharge, leading to important information gaps). To homogenize the data from the different transmitters (oldest devices were programed to transmit only one location during non-breeding season to avoid the drain of batteries caused by long periods of fog), only one location per day for each female was used. For location selection we chose the common hour for all transmitters (14:00 GMT). In case this was not available, the nearest location in time was used. For 7 females complete data for the study period was not available due to mortality or device failure (n=6), or abandonment of the study area (n=1). These females were excluded from analyses. Thus, final data included 1841 locations for a total of 11 female little bustard for the whole study period. Final sample size per bird and season ranged from 34 to 89 locations (mean ± sd: 76.7 ± 16.1). Locations were incorporated into a Geographic Information System (GIS) using a Universal Transverse Mercator (UTM) grid of 1-km^2 to fit environmental data resolution (see below). Duplicate samples (i.e. two or more records within the same grid cell) within same female and non-breeding season were handled as single observations, since we were interested in a presence/absence approximation of data. Association in flocks between tracked females was low (see Additional file 1) and thus data can be reasonably considered independent.

Habitat variables

We compiled landscape composition data on 5 dominant crop cover type variables to represent habitat variability in the study area as well as human influence predictors and terrain slope (Table 1). These variables are likely to affect the species ranging patterns during the non-breeding period due to their different vegetation structure and management that affect provision of food availability, food accessibility and shelter (Leitão and Costa 2001, Silva et al. 2004, Faria and Silva 2010, Bravo et al. 2017).

The habitat variables were acquired combining the information from Geographic Information Sys-

Table 1 Description of habitat variables (mean ± standard deviation), measured on each 1x1 km^2, included in occurrence probability models of female little bustards in the Plana de Lleida (2009-2013).

Variable	Description	Source	Mean ± SD
Alfalfa	Proportion of alfalfa	SIGPAC & DUN	0.11 ± 0.10
Corn stb.	Proportion of corn stubble/plow	SIGPAC & DUN	0.15 ± 0.15
D. cereal stb.	Proportion of cereal stubble/plow in dryland	SIGPAC & DUN	0.09 ± 0.20
I. cereal stb.	Proportion of cereal stubble/plow in irrigated land	SIGPAC & DUN	0.11 ± 0.10
Orchards	Proportion of orchards	SIGPAC	0.24 ± 0.19
Roads	Proportion of roads	SIGPAC	0.01 ± 0.02
Terrain slope	Standard deviation of elevation (m)	DEM (15x15 m pixel)	6.58 ± 4.80
Urban areas	Proportion of urban areas	SIGPAC	0.03 ± 0.11

tem of Farming Land (SIGPAC versions 2009 to 2013) – which provides information on large groups of land uses (such as arable lands, orchards and urban areas) and the Unique Agrarian Statement (DUN 2009-2013) – which provides specific information on cultivated crops and their varieties according to annual owners' declaration. Both data were provided by the regional Department of Agriculture, Livestock, Fisheries, Food and Environment of the Generalitat de Catalunya (http://agricultura.gencat.cat). Habitat predictors were computed using ArcGIS 10.2.2 with a 1-km^2 grid cell resolution. Human influence variables (Silva et al. 2004, Faria and Silva 2010), were also compiled considering urban areas and roads as the main ones. Terrain slope was calculated as the standard deviation of elevation in each 1-km^2 grid cell and was derived from a digital elevation model with a resolution of 15 m.

Spatial constraints

To account for spatially structured patterns on little bustard ranging behavior, we used spatial variables obtained through eigenvector mapping (hereafter called spatial filters) (Griffith and Peres-Neto 2006, De Marco et al. 2008). Filters represent spatial aggregation at different scales in the study area

(Diniz-Filho and Bini 2005). Thus, their significance when they are included in distribution models indicates spatial autocorrelation in the data (De Marco et al. 2008). We computed the spatial filters in SAM 4.0 (Rangel et al. 2010) by constructing a pair-wise distance matrix amongst all grid cells of the study area using their Universal Transverse Mercator coordinates (X and Y). The distance matrix was truncated at four times the maximum distance that connects all cells under minimum spanning tree criterion, and from this modified distance matrix 464 positive spatial filters were computed using principal coordinate analysis (Borcard and Legendre 2002). To reduce model complexity and include only relevant filters in multiple regressions assessing habitat selection patterns at the population level (see distribution modelling below), we used univariaable logistic models (a generalized linear model per female and year) and retained only significant filters after Bonferroni correction. This approach was used to retain potential temporal and inter-individual variation in spatial patterns in our final models. We used Moran's I coefficients and correlograms to evaluate spatial patterns in selected filters as a measure of their spatial scale and structure (Diniz-Filho and Bini 2005).

Distribution modelling

We built multiple regression models to estimate the probability of occurrence of female little bustard in relation to habitat variables and spatial filters at the population level using generalized linear mixed models (GLMMs) including data on all female and years. Female and year were included as random effects (intercepts) in those models to account for potential differences in occurrence probability. We then conducted variation partitioning analyses to separate the independent contribution of environment and spatial filters from their joint contribution (i.e., that due to spatial aggregation of occurrences related to responses to a spatially autocorrelated environment). Variation partitioning entails the calculation of incremental improvement in model fit due to the inclusion of a variable set (in our case, habitat variables and spatial filters) in models. As measure of model fit we used the deviance explained by models.

For this, we followed a hierarchical approach and ran GLMMs based on three different sets of the fixed variables, namely (1) a habitat

GLMM that included only habitat variables (*HAB*); (2) a spatial GLMM that included only spatial filters (*SPAT*) and (3) a habitat and spatial GLMM that included both habitat and spatial filters (*HAB+SPAT*). All continuous variables were standardized before modelling. Linear and quadratic terms of habitat variables were considered to account for nonlinear relationships.

For GLMMs development, a Bernoulli error distribution for the dependent variable (presence-absence data) and a logit-link function were fitted. Absence data were generated by random selection of 50 non-used locations per female and year within the study area, which we defined as the minimum convex polygon (MCP) including the pool of presence locations of all females and years. We selected 50 locations to ensure neutral prevalence (Araújo and Williams 2000, Brotons et al. 2004). To avoid model overfitting and an excess of nuisance in GLMM outputs due to the inclusion of a large number of predictors (Whittingham et al. 2006), we applied a backward stepwise procedure based on the Akaike Informa-tion Criterion (AIC) (Burnham and Anderson 2002). However full models provided highly consistent results (see Results). The best *HAB, SPAT* and *HAB+SPAT* models were then ranked as the models receiving higher support (models with lower AIC). Dropped variables from the best *HAB* or *SPAT* models were removed and not included in more complex *HAB+SPAT* models. 95% confidence intervals of fixed effect estimates were reported based on parametric bootstrap across 1000 iterations (Efron and Tibshirani 1986). Analyses were implemented in R software (version 3.2) through 'lme4', 'stats' and 'MuMIn' libraries. We also evaluated the independent contribution of each variable in the *HAB, SPAT* and *HAB+ SPAT* models by assessing the loss in model fit (deviance explained) when dropping that predictor. Finally, to further account for potential inter-individual differrences in habitat selection patterns, we reconduct our final GLMM models by fitting an alternative random structure (random intercepts-and-slopes models) (Nussey et al. 2007). This allows estimating a random term (slope) to the coefficient of the fixed effects, so it can be different for each female. Due to model complexity, the random slope of only one fixed effect can be fitted at a time.

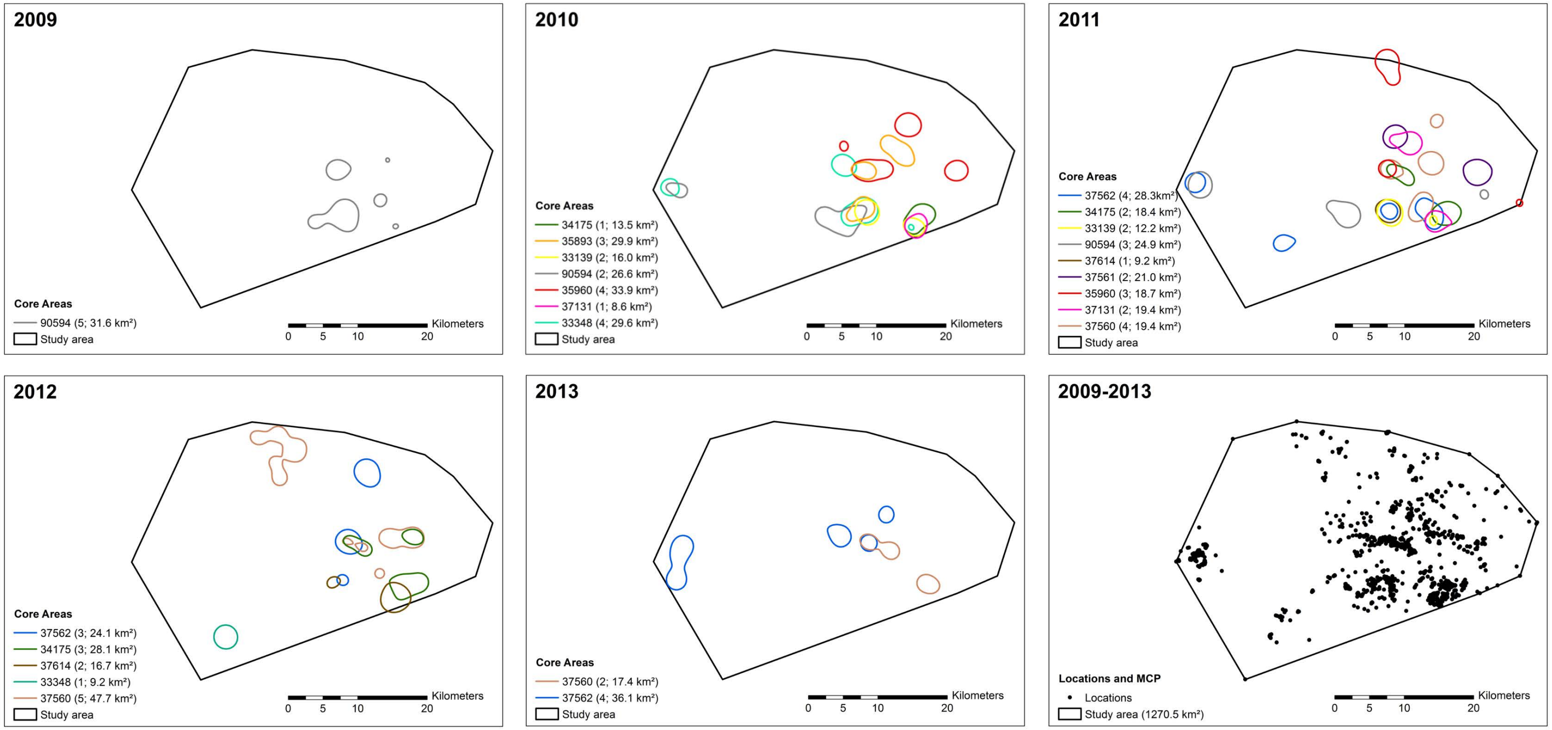

Figure 2 Occurrence distribution of tagged female little bustard in the study area. For graphical purposes, the core area (50% kernel) of occurrences of each female in different seasons is shown. In parenthesis, number of patches of the core area and size.

Results

In total, information on 24 non-breeding ranges was recorded from 11 females for the whole study period (3 repeated non-breeding ranges were recorded for 4 females, 2 for 5 females and one for 2 females). In different years, non-breeding ranges of 1 and 9 females were recorded. In total, female little bustard occurred in 271 grid-cells of 1 km^2 (20%) of the study area during 2009-2013, most of them distributed in the eastern part of the study area (Fig. 2). In 86% of occupied grid cells the predominant habitat was irrigated land (>80% of cropland), whilst in 9% it was dryland and 5% shared both habitats. The spatial overlap of presences between different females in a same year averaged 18 ± 2% (mean ± se) and between a same female in different years averaged 25 ± 3% (mean ± se).

Habitat models

At the population level, models revealed a non-linear negative effect of terrain slope on female occurrence probability and a positive effect of intermediate values of alfalfa and corn stubble availability (negative quadratic effect) and to small and high values of irrigated cereal stubble (positive quadratic effect) (Table 2 and Fig 3). These effects were overall consistent across different females (see Additional file 2). Female little bustard also showed a positive response to availability of roads and dry cereal stubble at the population level. However, individual response curves to such variables showed high variability among females (see Additional file 2). Attending to variable importance, slope, alfalfa, corn stubble and irrigated cereal stubble availability were the variables that most contributed to the habitat models at the population level (Fig. 4). The rest of variables showed a low independent contribution to the models (0.8 – 3.6% of total deviance explained by the best *HAB* model). The total percentage of deviance explained by habitat models was 35.1%.

Spatial models

24 spatial filters were selected to describe spatial structuration in occurrence data and be included in multiple regressions (Additional file 3). Spatial correlograms showed that selected filters reflected spatial aggregation from large (c. 18 km) to small (c. 3 km) spatial scales (Fig. 5a, see also the Additional file 4 for the map pattern of

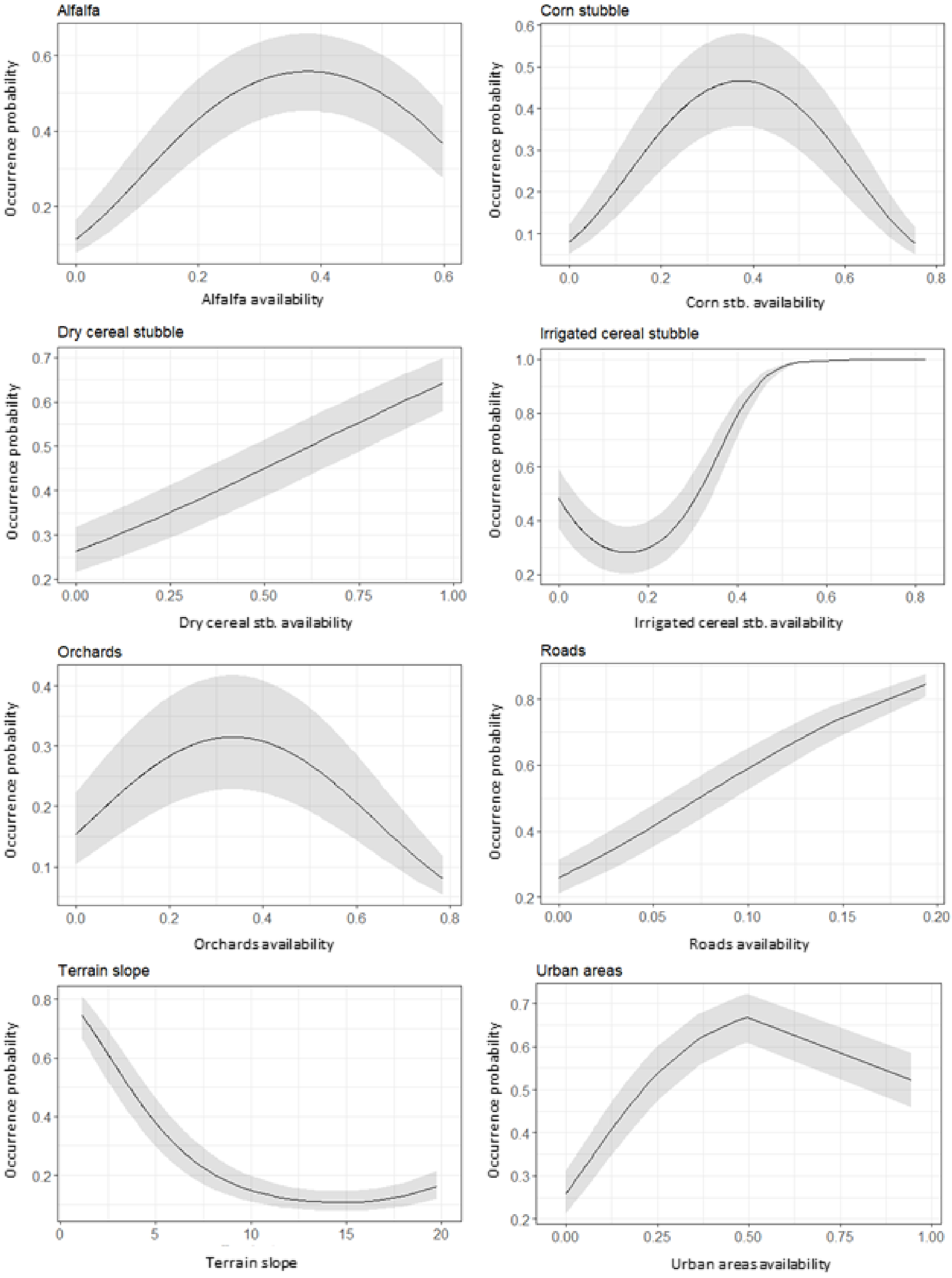

Figure 3 Responses curves for the best habitat model explaining the occurrence probability of female little bustard in the Plana de Lleida and univariate and independent contribution. Values for terrain slope response were scaled by subtracting the mean and dividing the sd.

Table 2 Results for the occurrence of female little bustard according to habitat models (GLMMs, logit link function). The table indicates the estimates ± standard error of the variables and 95% confidence intervals generated by a bootstrap procedure (1000 iterations). In bold intervals not containing the zero are marked. Results for the model containing all the predictors and for the best model based on AIC are shown.

	Best Model		**Full Model**	
AIC	1609.6		1613.4	
Fixed effects	**β ± SE**	**CI**	**β ± SE**	**CI**
Intercept	−0.88 ± 0.13	**(−1.13, −0.58)**	−0.85 ± 0.17	**(−1.18, −0.53)**
Alfalfa	0.98 ± 0.15	**(0.70, 1.31)**	1.00 ± 0.15	**(0.74, 1.38)**
Alfalfa^2	−0.22 ± 0.06	**(−0.34, −0.10)**	−0.22 ± 0.06	**(−0.35, −0.10)**
Corn stb.	1.10 ± 0.15	**(0.82, 1.46)**	1.11 ± 0.15	**(0.84, 1.46)**
Corn stb.^{2}	−0.41 ± 0.07	**(−0.56, −0.27)**	−0.41 ± 0.07	**(−0.57, −0.27)**
Dry cereal stb.	0.36 ± 0.14	**(0.09, 0.64)**	0.46 ± 0.30	(−0.09, 1.09)
Dry cereal stb.^{2}			−0.04 ± 0.10	(−0.24, 0.16)
Irrigated cereal stb.	−0.32 ± 0.14	**(−0.61, −0.06)**	−0.33 ± 0.14	**(−0.60, −0.05)**
Irrigated cereal stb.^{2}	0.43 ± 0.06	**(0.31, 0.57)**	0.43 ± 0.06	**(0.32, 0.57)**
Orchards	0.34 ± 0.14	**(0.08, 0.64)**	0.35 ± 0.14	**(0.07, 0.66)**
Orchards^2	−0.29 ± 0.10	**(−0.51, −0.10)**	−0.29 ± 0.10	**(−0.49, −0.10)**
Roads	0.39 ± 0.07	**(0.26, 0.55)**	0.36 ± 0.16	**(0.02, 0.67)**
Roads^2			0.01 ± 0.06	(−0.09, 0.15)
Terrain slope	−1.27 ± 0.13	**(−1.56, −1.05)**	−1.28 ± 0.13	**(−1.56, −1.03)**
Terrain slope^2	0.33 ± 0.08	**(0.11, 0.48)**	0.32 ± 0.08	**(0.10, 0.47)**
Urban areas	0.68 ± 0.24	**(0.24, 1.37)**	0.70 ± 0.24	**(0.31, 1.37)**
Urban areas^2	−0.07 ± 0.05	**(−0.33, −0.00)**	−0.07 ± 0.05	**(−0.35, −0.01)**

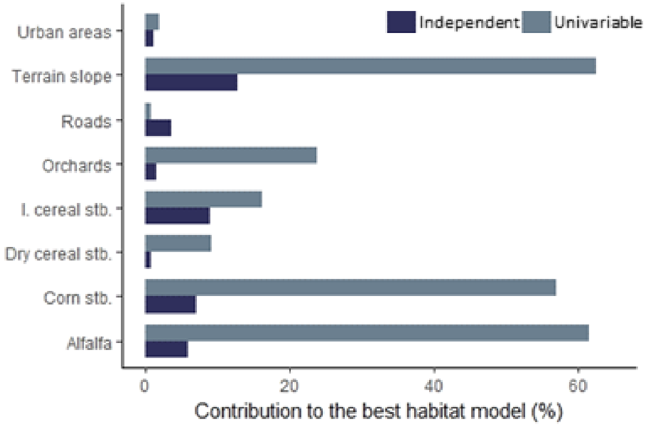

Figure 4 Univariate and independent contribution of habitat predictors in the best habitat model. Values are shown as percentage of the total explained variation by the best habitat model.

selected filters). Filters with high levels of spatial autocorrelation in the first, intermediate and last distance classes (represented by large positive and negative values of Moran's I coefficients, Fig. 5a) tended to be portrayed by a map pattern containing few major clusters of similar values as in the first eigenvectors (e.g. SF1, SF3). As the degree of positive spatial autocorrelation decreased in filters with lower eigenvalues, the map pattern became more fragmented (e.g. SF54, SF102), representing finer-resolution spatial variation in the data (Additional file 4). Post hoc variograms representing the semi-variance in positions as a function of the time lag separating observations (Additional file 5) revealed that smaller spatial-temporal aggregation (~ 3-5 km) showed by spatial filters was consistent with spatio-temporal aggregation at low time intervals. Thus, despite birds can move as long as 23 ± 2 km per day (mean ± SE of maximum distance recorded per individual and year, n = 24), average distance traversed per day was 3.1 ± 0.2 km (mean ± SE, n = 24).

When the spatial filters were considered together in multiple regression (GLMM) representing habitat selection patterns at the population level, the spatial filter representing spatial autocorrelation at the largest scale (*SF1*) had substantially greater importance in female occurrence than other filters (Fig. 5b, see also Additional file 6 for modelling results). Other broad-scale filters (such as *SF3*, *SF4*, *SF5* and *SF6* representing spatial autocorrela-tion at around 10-13 km) were also important, as well as fine-scale filters such as *SF25, SF26, SF39* and *SF60* (with autocorrelation pattern at ~ 5, ~ 4 and ~ 3 km, respectively). Overall, the response of different females to the most important filters was highly consistent (Additional file 7). The total percentage of variation explained by spatial models was 81.4%.

Habitat + Spatial models

HAB+SPAT models performed better than the *HAB* model. Total variation explained by the final *HAB+SPAT* model was 89.2% (see Additional file 8 for the results). According to variation partitioning, pure contribution of spatial filters to variation in distribution patterns was 61%. All broad-, intermediate- and fine-scale filters contributed independently to models (Additional file 9). Independent contrib-

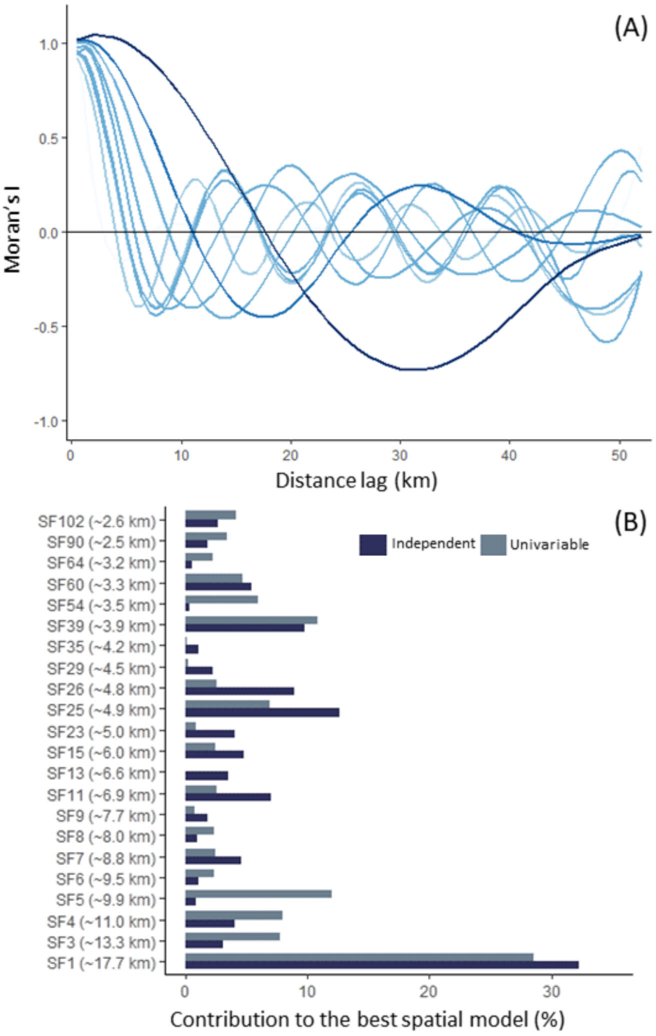

Figure 5 Spatial correlograms of spatial filters and their independent contribution to the best spatial model according to AIC. (a) Spatial correlograms of the 10 most important spatial filters (in order of importance: *SF1*, *SF25*, *SF39*, *SF26, SF11*, *SF60*, *SF15*, *SF7*, *SF4* and *SF23*) in spatial models defined by Moran's I coefficients in 5 distance classes, indicating links among points of the study area successively separated by 10 km. Spatial filters are represented in a blue gradient representing filters from broad (dark) to fine scales (light). In Fig. 5a the first distance at which Moran's I values crosses the expected value in the absence of spatial autocorrelation (0) is shown as an estimate of the scale of the spatial pattern that each filter represents. And (b), Estimate of the spatial filters in backward stepwise explaining the occurrence probability of female little bustard in the Plana de Lleida.

ution of habitat was 9% and the joint effect between habitat and spatial filters accounted for 30% (Fig. 6). Covariation between habitat and spatial variables mostly occurred at the highest scale (note the reduction in the independent effect of *SF1* in HAB+SPAT vs. SPAT models, Fig. 5b and Additional file 9).

Discussion

Animals usually show non-random spatial distributions resulting from the cumulative effects of many different factors that are often difficult to separate. By using spatial eigenvector mapping in combination with habitat models, our results showed that ranging behavior of female little bustard in the non-breeding season was affected by

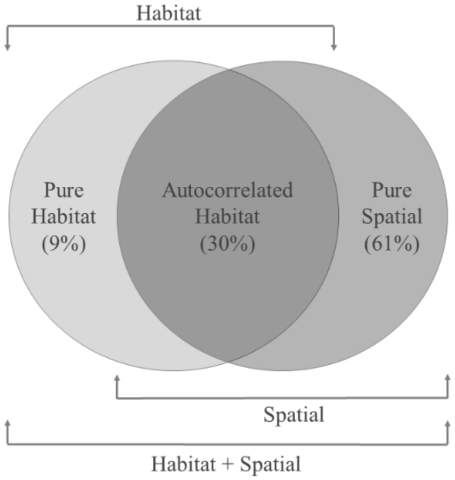

Figure 6 Results of the best habitat (HAB), spatial (SPAT) and more complex models combining both habitat and spatial variables (HAB+SPAT) based on stepwise AIC. Deviance partitioning analysis for the probability of occurrence of female little bustard. The figure shows a conceptual diagram of variance partitioning: the two circles represent the total variance explained by models with the two components (habitat + spatial), while the left and right circles show the variance explained by the habitat and spatial models, respectively. Percentage of total variation in occupancy rate explained by the pure and joint effects of habitat and spatial filters is shown.

the independent effect of habitat variables and spatial constraints, as well as by their joint effect. We found that the variance explained by the joint effect of habitat and spatial filters was high, meaning that approximately one third of the spatial aggregation observed in female little bustard distribution was related to responses to the spatially aggregated environment. The fact that different females presented, not only spatial aggregations at the same scales, but also aggregation to the same areas of the study area, suggests that observed patterns could be related with landscape configuration heterogeneity (i.e., how different crop types are interspersed at the landscape level) in the study area. Supporting the latter, female little bustards showed a negative response to filter SF1 (which mostly represent a decreasing western-eastern gradient, see Additional file 4). That is, female little bustards avoided the western parts of the study area, where irrigated arable land (suitable for females) appears interspersed in a more intensive farmland dominated by orchard crops (unsuitable for at least some females). Previous studies have already shown that landscape configurational heterogeneity can be an important determinant of habitat suitability perception for the species, beyond landscape composition (Cardador et al. 2015).

However, a remarkable result of our research was also the high importance of pure spatial effects in the distribution models, which indicates that a good deal of the ranging behavior of female little bustards within the non-breeding season could be explained by other factors not related to habitat composition or its spatial arrangement alone. In general, the broad-scale spatial constraints representing aggregation patterns at approximately 18 km were the most important in the distribution of female little bustard. However aggregation at more local scales (~ 3-5 km) was also important. This spatial structuration may result from different, not mutually exclusive processes.

First of all, cost-benefit balances between the quality of different habitat patches and the energy required to move across them may be important. Indeed, optimal foraging theory has been widely accepted when describing foraging patterns observed in birds (Charnov 1976, Alonso et al. 1995, Amano and Katayama 2009). Accordingly, post hoc variograms revealed that the smaller aggregation patterns (~ 3-5 km) showed by spatial filters were consistent with spatio-temporal aggregation at low time intervals. This suggests that aggregation at local scale is mainly related with daily activity of female little bustards. Moreover, observed daily spatial structuration occurs at higher spatial scales than that reported for the breeding season (Lapiedra et al. 2011, Ponjoan et al. 2012) - as it would be expected taking into account that during the non-breeding season individuals are no longer under the constraints related to reproduction and chick rearing (Suárez-Seoane et al. 2008).

On the second place, high concentration of little bustards in the east of the study area could be associated with the high site fidelity of the species and conspecific attraction (Gauger 2007, García de la Morena et al. 2015, García de la Morena 2016). Site fidelity could be important for little bustards to ensure resources (e.g. foraging places), reduce energy costs of search, and it contributes to flock aggregation. Finally, the spatial distribution of breeding and non-breeding areas within the region could partially explain the importance of spatial filters at larger scales, resulting in flocks using preferentially the areas closer to breeding sites. The distance from the occurrences' centroids to the main breeding grounds was 14.9 ± 0.4 km (mean ±se).

Nevertheless, even when spatial

constraints largely affected female little bustard occurrences, our results also showed an independent contribution of habitat variables to observed patterns. Our explanatory models suggest that the most suitable habitat for female little bustards during the non-breeding season in the study area is flat terrains with presence of irrigated arable land. Habitat models predicted a positive effect in the occurrence probability at heterogeneous sites, with positive effects of intermediate availabilities of irrigated alfalfa and corn stubbles, as well as sites dominated by irrigated cereal stubbles. The alfalfa crops are an attractive resource for little bustards during this period, since they provide abundant food (Bravo et al. 2017) and shelter (Cardador et al. 2014, García de la Morena 2016). Additionally, recently harvested corn and cereal stubbles, holding a varied weed community, provide interesting food resources for little bustards complementary to alfalfa crops (Bravo et al. 2017).

Regarding the effect of anthropogenic infrastructures, human disturbances caused by roads and urban areas have been reported as being avoided by little bustards during the breeding season (Suárez-Seoane et al. 2002, Arcos and Salvadores 2005) and winter (Silva et al. 2004, Gauger 2007). Meanwhile, other studies define the species as tolerant (Martínez 1994, Suárez-Seoane et al. 2008). Our results suggest that the little bustard is a flexible species, with some individuals that can exhibit habituation to human disturbances in highly humanized landscapes (Martínez-Marivela et al. 2018). Indeed, some females in the study area positively selected road vicinity areas. Positive effect of roads might be related to the fact that some roads are fenced and others have a high traffic intensity, which might hamper the crossing of predators or people, which otherwise may kill or simply flush the birds (Forman et al. 2003, Jaeger and Fahrig 2004). Additionally, in the study area roads are provided with a hunting security band where shooting is totally banned, which may act as a refuge for the species, subject to some degree of illegal killing pressure (Goriup 1994, Marcelino et al. 2017). In that way, areas in the vicinity of certain roads may provide relatively quiet places, which could be selected by some little bustards, while other individuals might be more sensitive to stress levels produced by anthropogenic disturbances (Casas et al. 2009, Tarjuelo et al. 2015).

Conclusions

Altogether, the present study increases our understanding of habitat selection patterns of a threatened steppe bird species and their associated spatial patterns at a regional scale during the non-breeding season. Individual responses to habitat and spatial variables provide evidence of a high inter-individual consistency in overall habitat selection patterns. According to such results, measures to promote flat open heterogeneous landscapes, with alfalfa and stubble availability, in safe places as close as possible to breeding sites, could contribute to benefit resident or scarcely migratory little bustard populations in non-breeding grounds. Our results also highlight the need to investigate further about the role of roads on the ranging behavior of this and other species occupying highly humanized landscapes. Although the specific process underlying the observed selection of roads is not yet well understood, promoting areas with restricted game shooting and limiting human access may help to improve the quality of the non-breeding grounds and, consequently, the condition of the birds. Finally, our results show the existence of spatial constraints in occurrence patterns beyond landscape composition. Whether site fidelity and conspecific attraction and/or configurational heterogeneity are involved in observed patterns must be addressed to anticipate potential effects of new land-use changes and provide timely advice toward long-term management planning.

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List of abbreviations

AIC: Akaike information criterion
DUN: unique agrarian statement
GIS: geographic information system
GLMM: generalized linear mixed models
GMT: Greenwich Mean Time
HAB: habitat models
HAB+SPAT: habitat and spatial models
SF: spatial filter
SPAT: spatial models
UTM: Universal Transverse Mercator

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Additional files

Additional file 1. Flock association between female little bustards in a same year. Pairwise estimates based on HWI index.

Additional file 2. Random intercepts-and-slopes habitat models. Variation in habitat predictors of the best habitat model within the female factor.

Additional file 3. Retained spatial filters. Number of times that spatial filters were retained in univariate spatial models for each female and year.

Additional file 4. Map patterns of spatial filters. Geographic patterns of the spatial filters included in univariate models testing occurrence probability of female little bustards in the non-breeding season.

Additional file 5. Variograms of distance between positions. Variograms representing the average square distance between positions (semi-variance) as a function of the time lag separating observations.

Additional file 6. Results of spatial models (SPAT). Estimates of fixed effects predicting the occurrence probability of female little bustard according to spatial models.

Additional file 7. Random intercepts-and-slopes spatial models. Variation in spatial predictors of the best spatial model within the female factor.

Additional file 8. Results of HAB+SPAT models. Estimates of fixed effects predicting the occurrence probability of female little bustard according to SPAT+HAB models.

Additional file 9. Contribution of predictors to HAB+SPAT models. Independent contribution of different predictors to the best HAB+SPAT model.

Additional file 1

Flocking

As the little bustard is a gregarious species during non-breeding season (Cramp and Simmons 1980), data can be highly aggregated among individuals. To account for possible non-independence of the data, we calculated pairwise association of females in a same flock in different years. To obtain female association we used the Half-Weight Index (HWI) (Cairns and Schwager 1987). This index measure association degree between two individuals and it can be expressed as: $HWI_{ab} = x / ½ (y_a + y_b)$, where x is the number of times in which two females (a and b) were associated in a same flock, and y_a and y_b correspond to the total of locations for the female a and for the female b. This index ranges from 0 (two females never shared a flock) and 1 (two females always detected together). Two females were considered to be in a same flock whether at time t they were located at < 500 m distance. The flock association (HWI) between females was relatively low (0.04 ± 0.06; mean ± SD), where in the 50% of pairwise comparisons HWI showed a value equals to 0 and in the 38% was below 0.1 (see the upper hemi-matrices in Table S1).

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Table S1 Results for the flock association between female little bustards (HWI: Half-Weight Index) in a same year.

Year	*Female*	90594
2009	90594	-

Year	*Female*	**34175**	**35893**	**33139**	**90594**	**35960**	**37131**	**33348**
2010	**34175**	-	0.08	0.15	0.00	0.00	0.18	0.02
	35893		-	0.02	0.06	0.03	0.00	0.15
	33139			-	0.01	0.00	0.23	0.03
	90594				-	0.00	0.00	0.15
	35960					-	0.00	0.00
	37131						-	0.01
	33348							-

Table S1 Continued.

Year	Female	37562	34175	33139	90594	37614	37561	35960	37131	37560
2011	**37562**	-	0.04	0.15	0.00	0.09	0.00	0.00	0.00	0.09
	34175		-	0.04	0.00	0.03	0.02	0.00	0.01	0.04
	33139			-	0.00	0.33	0.05	0.00	0.07	0.00
	90594				-	0.00	0.00	0.00	0.00	0.00
	37614					-	0.00	0.00	0.03	0.00
	37561						-	0.06	0.00	0.05
	35960							-	0.00	0.03
	37131								-	0.00
	37560									-

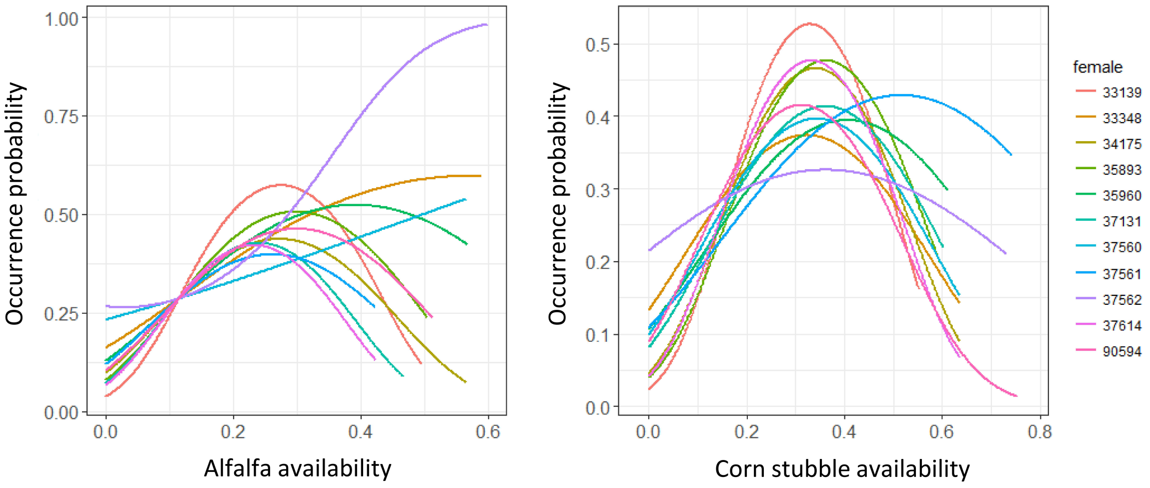
Year	Female	37562	34175	37614	33348	37560
2012	**37562**	-	0.01	0.00	0.02	0.00
	34175		-	0.01	0.00	0.14
	37614			-	0.00	0.01
	33348				-	0.00
	37560					-

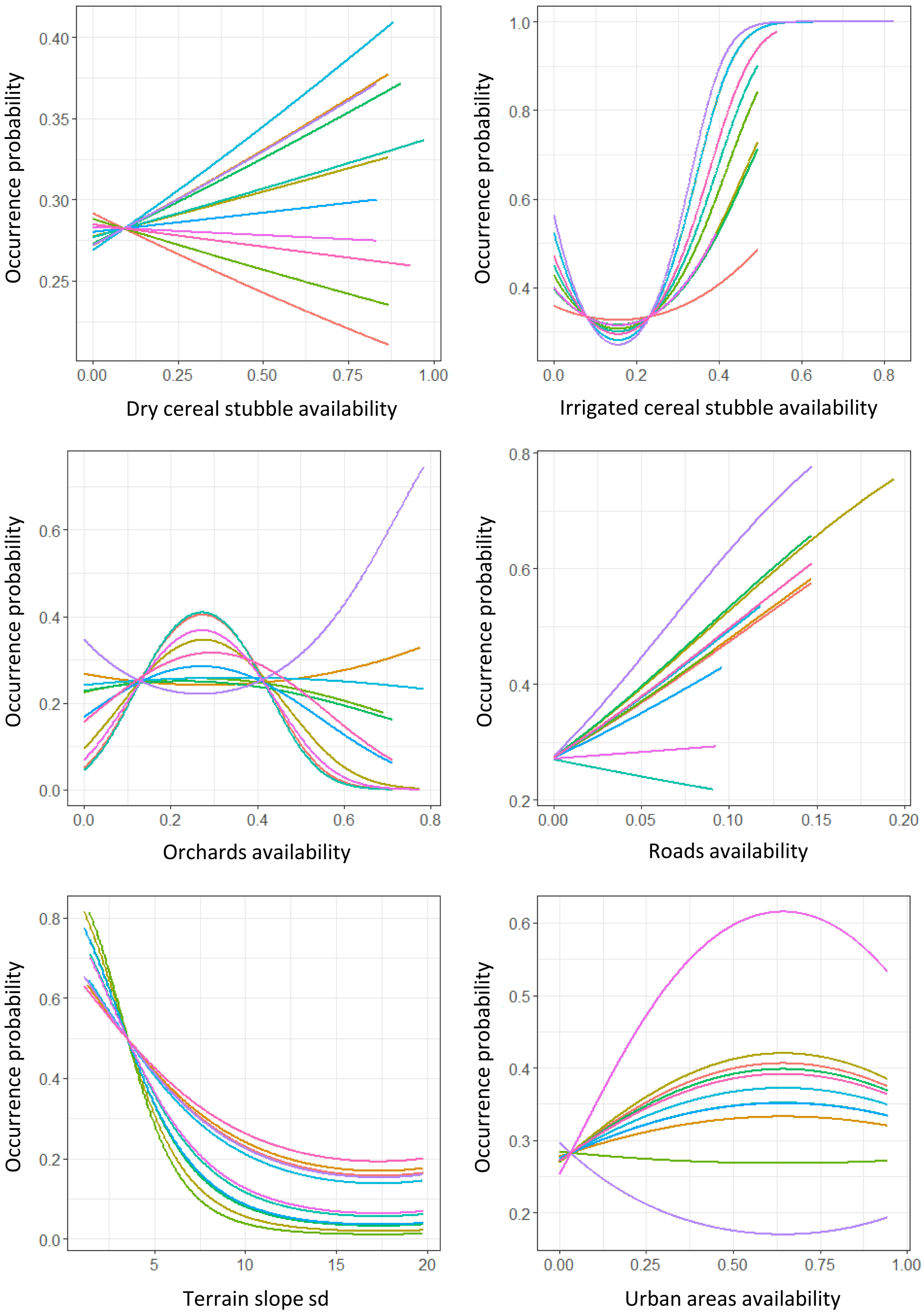
Year	Female	37562	37560
2013	37562	-	0.00
	37560		-

Additional file 2

Inter-individual variation

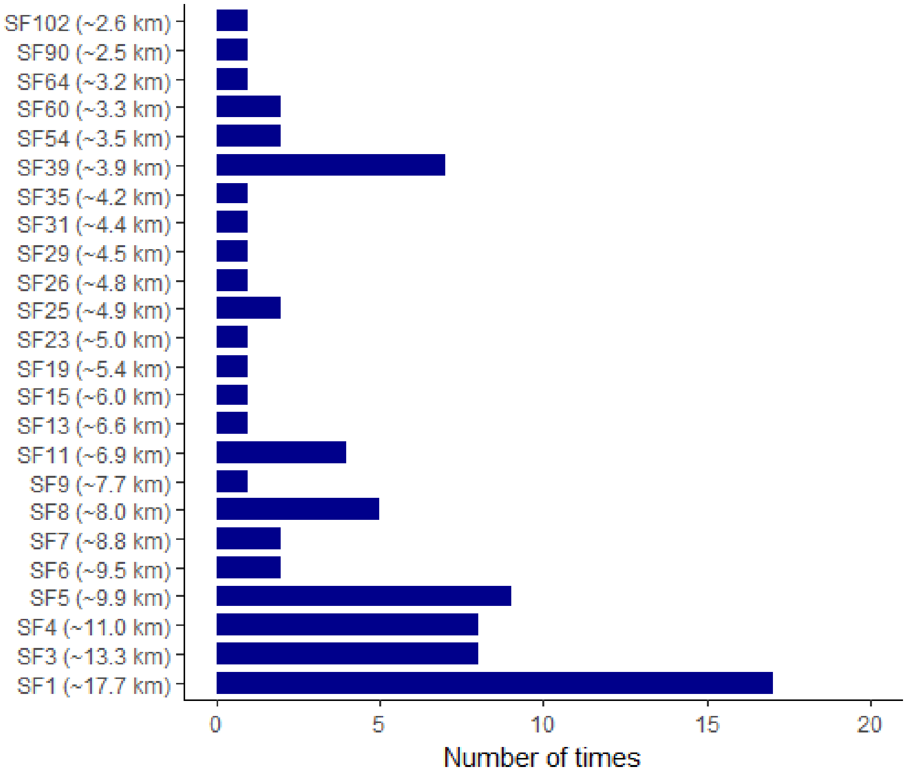
Figure S2 Partial response curves showing individual responses of female little bustard to habitat predictors based on random intercepts-and-slopes models.




Occurrence probability
0.40
0.35
0.30
0.25
0.00
0.25
0.50
0.75
1.00
Dry cereal stubble availability
Occurrence probability
1.0
0.8
0.6
0.4
0.0
0.2
0.4
0.6
0.8
Irrigated cereal stubble availability
Occurrence probability
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
Orchards availability
Occurrence probability
0.8
0.6
0.4
0.2
0.00
0.05
0.10
0.15
0.20
Roads availability
Occurrence probability
0.8
0.6
0.4
0.2
0.0
5
10
15
20
Terrain slope sd
Occurrence probability
0.6
0.5
0.4
0.3
0.2
0.00
0.25
0.50
0.75
1.00
Urban areas availability

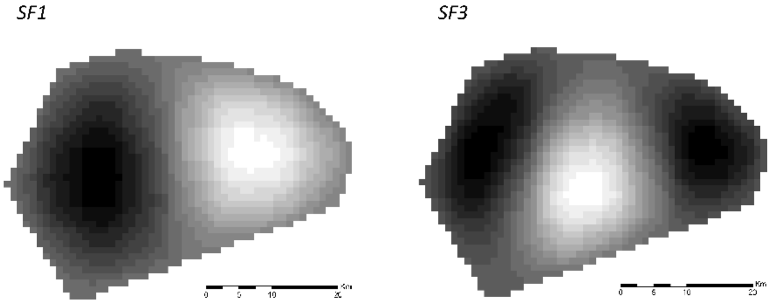
Additional file 3

Figure S3 Spatial filters retained to be included in multivariate regression (N=24). Number of times that each spatial filter was retained in univariate spatial models conducted for each female and year.

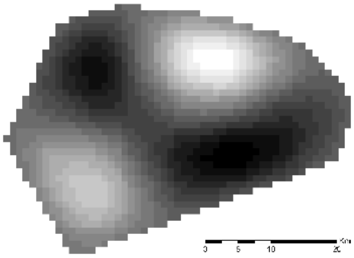


Additional file 4

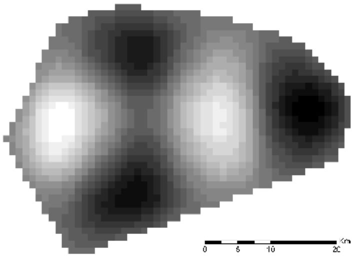
Figure S4 Geographic patterns of 24 spatial filters resulting significant in univariate test for occurrence distribution of at least one female and non-breeding season. Positive values are represented in a dark gradient and negative values in clear.



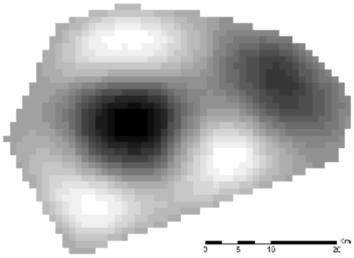
SF4



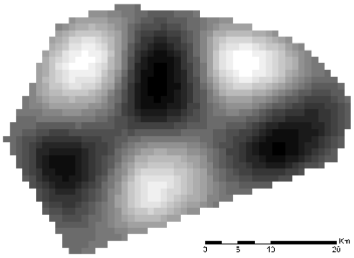
SF5



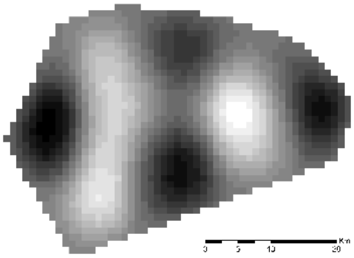
SF6



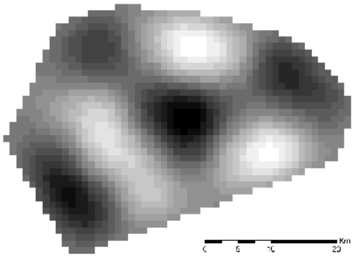
SF7



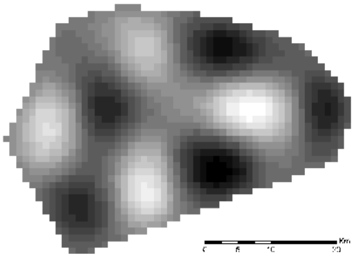
SF8



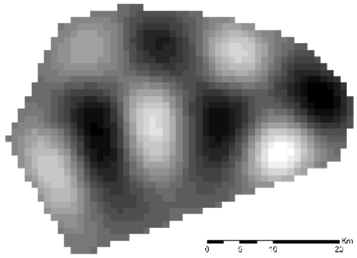
SF9



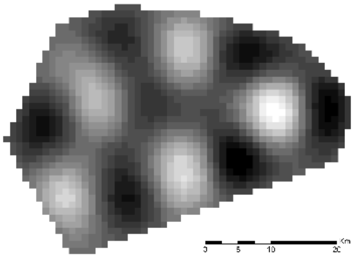
SF11



SF13



SF15



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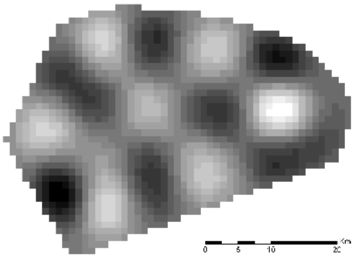
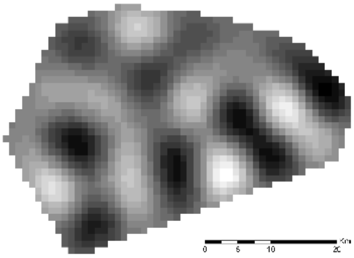
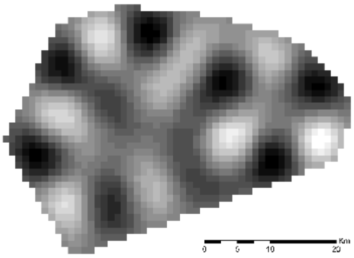


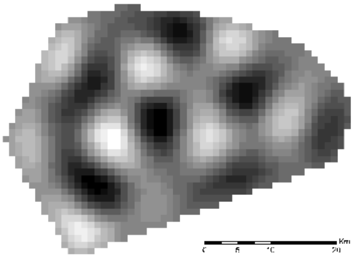
SF23



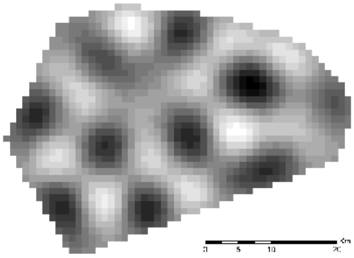
SF25



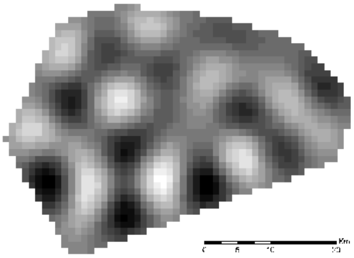
SF26



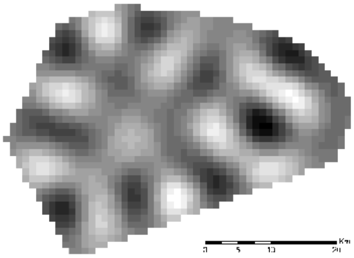
SF29



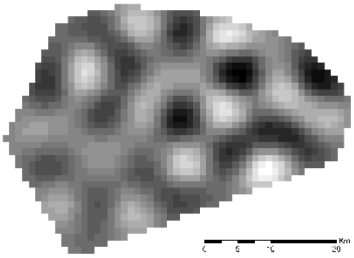
SF31



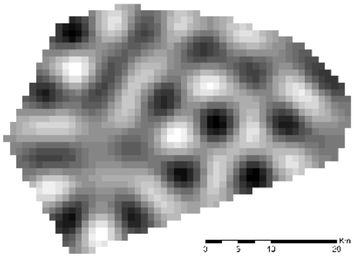
SF35



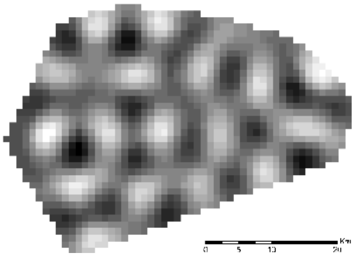
SF39



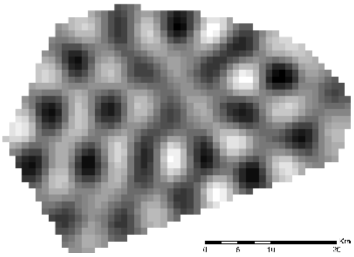
SF54



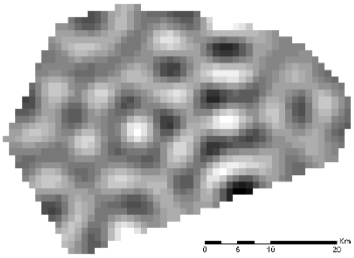
SF60



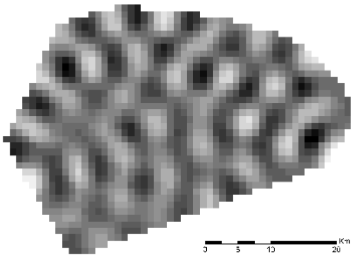
SF64



SF90



SF102



Additional file 5

Figure S5.1 Independent contribution to the best habitat+spatial model explainedby habitat and spatial predictors.

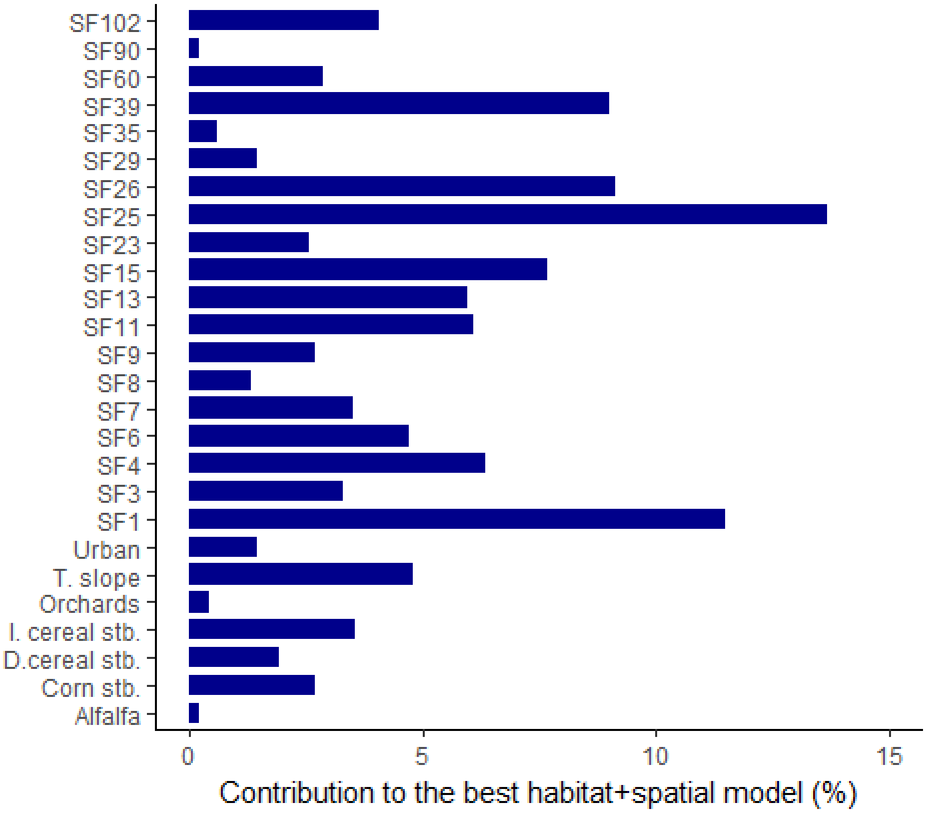


Table S5.1 Results for the occurrence of female little bustard according to habitat+spatial models (GLMMs, logit link function). The table indicates the estimators ± standard error and confidence intervals for predictor estimates. Confidence intervals at 95% for fixed effects were generated by bootstrap procedure (1000 iterations). In bold intervals not containing the zero are marked. Standard deviation of random effects are also provided. Results for the model containing all the predictors and for the best model based on AIC are shown.

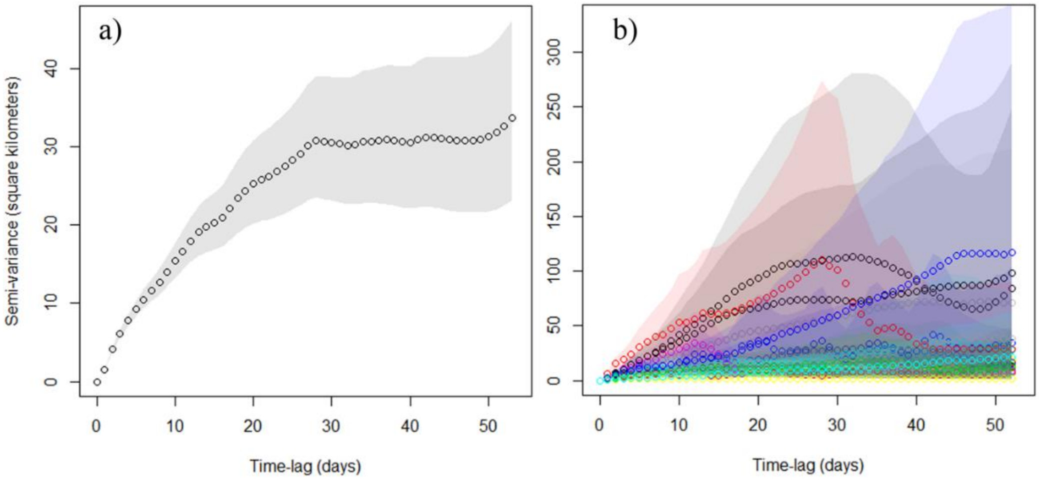
	Best Model		**Full Model**	
AIC	331.1		338.4	
Random effects				
Female intercept	sd = 0.324		sd = 0.336	
Year intercept	sd = 0.000		sd = 0.000	
Fixed effects	**β ± SE**	**CI**	**β ± SE**	**CI**
Intercept	−2.32 ± 0.84	(−5.52, 0.10)	−2.68 ± 0.97	(−6.96, 1.15)
Alfalfa	0.87 ± 0.51	(−0.31, 2.63)	0.92 ± 0.53	(−0.36, 2.93)
Alfalfa^2	−0.44 ± 0.20	**(−1.09, −0.01)**	−0.44 ± 0.20	(−1.21, 0.02)
Corn stb.	−2.15 ± 0.77	**(−4.99, −0.46)**	−2.04 ± 0.80	**(−5.16, −0.23)**
Corn stb.^{2}	−0.57 ± 0.28	**(−1.54, −0.04)**	−0.60 ± 0.29	**(−1.74, −0.03)**
Dry cereal stb.	−4.17 ± 0.72	**(−7.74, −2.94)**	−4.33 ± 0.77	**(−8.36, −3.27)**
Irrigated cereal stb.	−3.71 ± 0.54	**(−6.41, −3.05)**	−3.68 ± 0.58	**(−6.93, −2.92)**
Irrigated cereal stb.^{2}	1.78 ± 0.31	**(1.38, 3.30)**	1.76 ± 0.31	**(1.36, 3.47)**
Orchards	−1.63 ± 0.58	**(−3.83, −0.14)**	−1.73 ± 0.65	(−4.27, 0.11)
Orchards^2	0.60 ± 0.42	(−0.43, 2.16)	0.64 ± 0.43	(−0.58, 2.38)
Roads			0.13 ± 0.36	(−0.84, 1.41)
Terrain slope	−6.44 ± 0.89	**(−12.17, −5.68)**	−6.69 ± 1.00	**(−13.82, −5.95)**
Terrain slope^2	2.94 ± 0.46	**(2.36, 5.61)**	3.08 ± 0.52	**(2.41, 6.32)**
Urban areas	−8.91 ± 1.70	**(−16.03, −5.27)**	−9.42 ± 1.79	**(−18.09, −5.50)**
Urban areas^2	1.55 ± 0.45	**(0.14, 2.82)**	1.66 ± 0.41	**(0.15, 3.33)**
SF1	−11.54 ± 1.45	**(−22.78, −10.83)**	−11.59 ± 1.51	**(−26.90, −11.13)**
SF3	−3.68 ± 0.59	**(−7.27, −3.10)**	−3.66 ± 0.62	**(−8.35, −2.96)**
SF4	5.10 ± 0.63	**(4.57, 9.33)**	5.16 ± 0.66	**(4.78, 10.33)**
SF5			0.37 ± 0.65	(−2.88, 2.58)
SF6	−5.49 ± 0.74	**(−11.32, −4.89)**	−5.90 ± 0.97	**(−13.55, −4.94)**
SF7	2.64 ± 0.37	**(2.29, 5.35)**	2.62 ± 0.37	**(2.27, 6.26)**
SF8	−3.62 ± 0.71	**(−7.09, −1.98)**	−3.59 ± 0.74	**(−8.04, −2.06)**

Table S5 Continued.

	Best Model		Full Model	
Fixed effects	**β ± SE**	**CI**	**β ± SE**	**CI**
SF9	−3.43 ± 0.51	**(−6.90, −2.55)**	−3.41 ± 0.56	**(−7.94, −2.63)**
SF11	−5.85 ± 0.80	**(−11.83, −5.29)**	−5.82 ± 0.86	**(−13.80, −5.55)**
SF13	−4.27 ± 0.52	**(−8.30, −4.00)**	−4.47 ± 0.61	**(−9.74, −4.15)**
SF15	4.71 ± 0.62	**(4.33, 9.06)**	4.68 ± 0.65	**(4.47, 10.34)**
SF23	3.41 ± 0.58	**(2.80, 7.13)**	3.35 ± 0.60	**(2.91, 8.26)**
SF25	8.75 ± 1.09	**(8.06, 16.02)**	8.90 ± 1.11	**(8.44, 18.96)**
SF26	5.77 ± 0.75	**(5.23, 10.55)**	5.89 ± 0.80	**(5.46, 12.85)**
SF29	−2.26 ± 0.49	**(−4.60, −1.58)**	−2.24 ± 0.54	**(−5.44, −1.57)**
SF35	1.84 ± 0.53	**(0.79, 4.10)**	2.01 ± 0.59	**(0.83, 4.89)**
SF39	−6.24 ± 0.83	**(−11.68, −5.73)**	−6.21 ± 0.84	**(−13.61, −5.77)**
SF54			−0.16 ± 0.52	(−2.37, 1.37)
SF60	−2.57 ± 0.38	**(−4.93, −2.20)**	−2.53 ± 0.40	**(−5.92, −2.16)**
SF64			−0.12 ± 0.36	(−1.39, 1.12)
SF90	−0.76 ± 0.38	**(−2.28, −0.03)**	−0.65 ± 0.41	(−2.76, 0.25)
SF102	−3.18 ± 0.44	**(−5.96 ± −2.81)**	−3.34 ± 0.50	**(−6.90 ± −3.01)**

Additional file 6

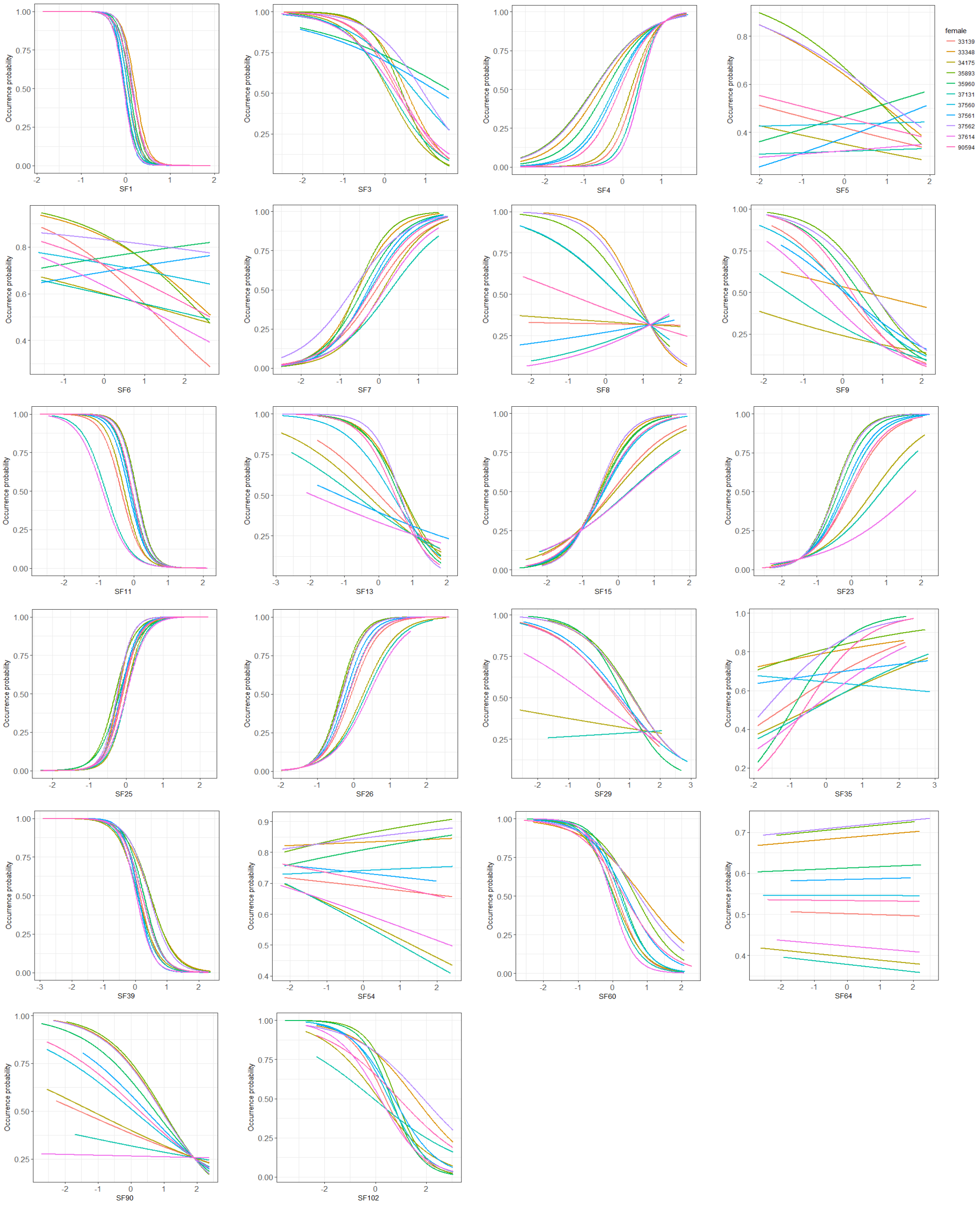
Figure S6 Variograms representing the average square distance between positions (semi-variance) as a function of the time lag separating observations. Mean semi-variance values across all individuals and years (a) and individual values (b) are shown. Shadow areas represent 95% confidence intervals around the semi-variance estimates.



Additional file 7

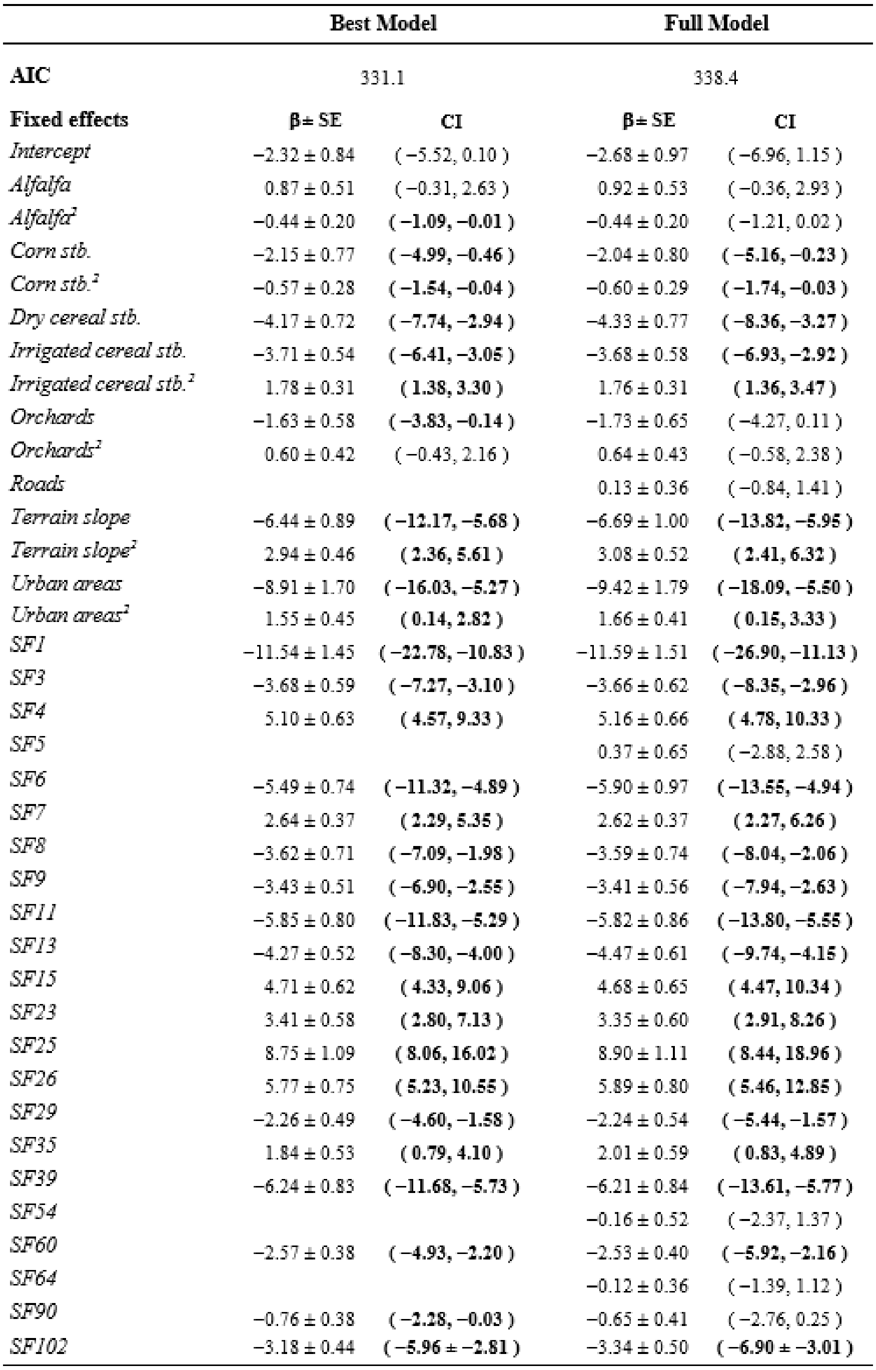
Inter-individual variation

Figure S7 Partial response curves showing individual responses of female little bustard to spatial predictors based on random intercepts-and-slopes models.



Additional file 8

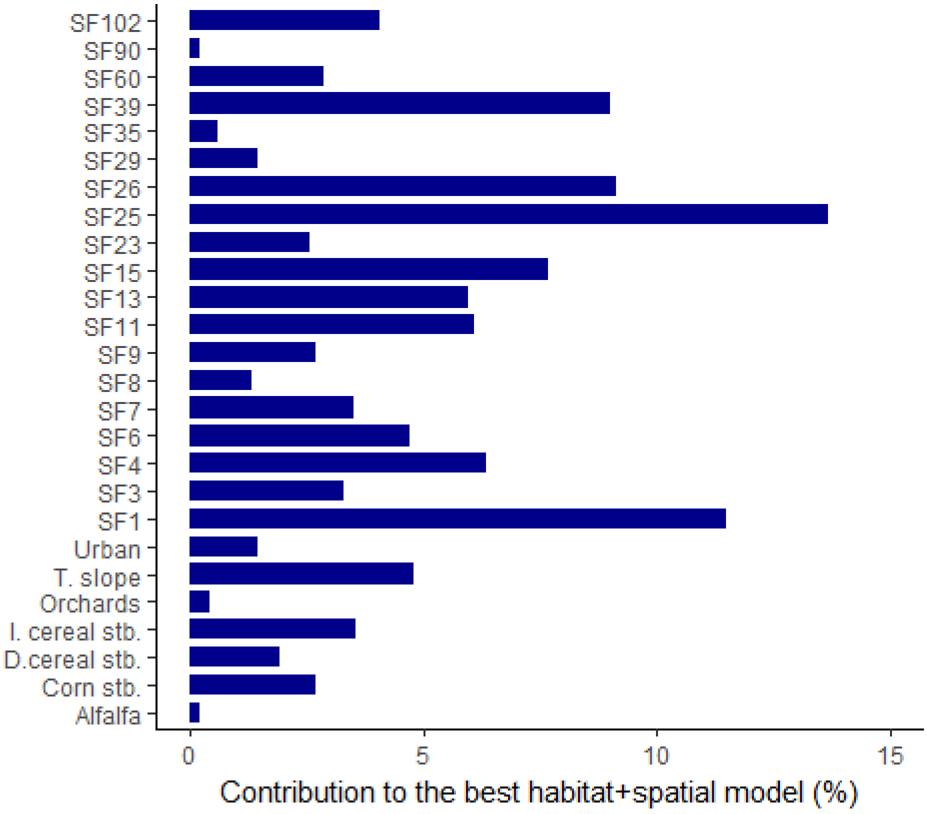
Figure S8 Results for the occurrence of female little bustard according to habitat+spatial models (GLMMs, logit link function). The table indicates the estimates ± standard error and 95% confidence intervals generated by bootstrap procedure (1000 iterations). In bold intervals not containing the zero are marked. Results for the model containing all the predictors and for the best models based on AIC are shown.



	Best Model		**Full Model**	
AIC	331.1		338.4	
Fixed effects	**β± SE**	**CI**	**β± SE**	**CI**
Intercept	−2.32 ± 0.84	(−5.52, 0.10)	−2.68 ± 0.97	(−6.96, 1.15)
Alfalfa	0.87 ± 0.51	(−0.31, 2.63)	0.92 ± 0.53	(−0.36, 2.93)
Alfalfa^2	−0.44 ± 0.20	**(−1.09, −0.01)**	−0.44 ± 0.20	(−1.21, 0.02)
Corn stb.	−2.15 ± 0.77	**(−4.99, −0.46)**	−2.04 ± 0.80	**(−5.16, −0.23)**
Corn stb.^{2}	−0.57 ± 0.28	**(−1.54, −0.04)**	−0.60 ± 0.29	**(−1.74, −0.03)**
Dry cereal stb.	−4.17 ± 0.72	**(−7.74, −2.94)**	−4.33 ± 0.77	**(−8.36, −3.27)**
Irrigated cereal stb.	−3.71 ± 0.54	**(−6.41, −3.05)**	−3.68 ± 0.58	**(−6.93, −2.92)**
Irrigated cereal stb.^{2}	1.78 ± 0.31	**(1.38, 3.30)**	1.76 ± 0.31	**(1.36, 3.47)**
Orchards	−1.63 ± 0.58	**(−3.83, −0.14)**	−1.73 ± 0.65	(−4.27, 0.11)
Orchards^2	0.60 ± 0.42	(−0.43, 2.16)	0.64 ± 0.43	(−0.58, 2.38)
Roads			0.13 ± 0.36	(−0.84, 1.41)
Terrain slope	−6.44 ± 0.89	**(−12.17, −5.68)**	−6.69 ± 1.00	**(−13.82, −5.95)**
Terrain slope^2	2.94 ± 0.46	**(2.36, 5.61)**	3.08 ± 0.52	**(2.41, 6.32)**
Urban areas	−8.91 ± 1.70	**(−16.03, −5.27)**	−9.42 ± 1.79	**(−18.09, −5.50)**
Urban areas^2	1.55 ± 0.45	**(0.14, 2.82)**	1.66 ± 0.41	**(0.15, 3.33)**
SF1	−11.54 ± 1.45	**(−22.78, −10.83)**	−11.59 ± 1.51	**(−26.90, −11.13)**
SF3	−3.68 ± 0.59	**(−7.27, −3.10)**	−3.66 ± 0.62	**(−8.35, −2.96)**
SF4	5.10 ± 0.63	**(4.57, 9.33)**	5.16 ± 0.66	**(4.78, 10.33)**
SF5			0.37 ± 0.65	(−2.88, 2.58)
SF6	−5.49 ± 0.74	**(−11.32, −4.89)**	−5.90 ± 0.97	**(−13.55, −4.94)**
SF7	2.64 ± 0.37	**(2.29, 5.35)**	2.62 ± 0.37	**(2.27, 6.26)**
SF8	−3.62 ± 0.71	**(−7.09, −1.98)**	−3.59 ± 0.74	**(−8.04, −2.06)**
SF9	−3.43 ± 0.51	**(−6.90, −2.55)**	−3.41 ± 0.56	**(−7.94, −2.63)**
SF11	−5.85 ± 0.80	**(−11.83, −5.29)**	−5.82 ± 0.86	**(−13.80, −5.55)**
SF13	−4.27 ± 0.52	**(−8.30, −4.00)**	−4.47 ± 0.61	**(−9.74, −4.15)**
SF15	4.71 ± 0.62	**(4.33, 9.06)**	4.68 ± 0.65	**(4.47, 10.34)**
SF23	3.41 ± 0.58	**(2.80, 7.13)**	3.35 ± 0.60	**(2.91, 8.26)**
SF25	8.75 ± 1.09	**(8.06, 16.02)**	8.90 ± 1.11	**(8.44, 18.96)**
SF26	5.77 ± 0.75	**(5.23, 10.55)**	5.89 ± 0.80	**(5.46, 12.85)**
SF29	−2.26 ± 0.49	**(−4.60, −1.58)**	−2.24 ± 0.54	**(−5.44, −1.57)**
SF35	1.84 ± 0.53	**(0.79, 4.10)**	2.01 ± 0.59	**(0.83, 4.89)**
SF39	−6.24 ± 0.83	**(−11.68, −5.73)**	−6.21 ± 0.84	**(−13.61, −5.77)**
SF54			−0.16 ± 0.52	(−2.37, 1.37)
SF60	−2.57 ± 0.38	**(−4.93, −2.20)**	−2.53 ± 0.40	**(−5.92, −2.16)**
SF64			−0.12 ± 0.36	(−1.39, 1.12)
SF90	−0.76 ± 0.38	**(−2.28, −0.03)**	−0.65 ± 0.41	(−2.76, 0.25)
SF102	−3.18 ± 0.44	**(−5.96 ± −2.81)**	−3.34 ± 0.50	**(−6.90 ± −3.01)**

Additional file 9

Figure S9 Independent contribution to the best habitat+spatial model explained by habitat and spatial predictors.



DIET COMPOSITION OF A DECLINING STEPPE BIRD THE LITTLE BUSTARD (*TETRAX TETRAX*) IN RELATION TO FARMING PRACTICES

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Foraging strategies and diet selection play an essential role in individual survival and reproductive success. The study of feeding ecology becomes crucial when it concerns endangered species such as the Little Bustard (*Tetrax tetrax*), whose populations are suffering strong declines as a consequence of agricultural intensification. Despite the fact that several populations are overwintering in areas affected by agricultural transformation, nothing is known about how feeding behavior responds to these changes. We studied for the first time the winter diet composition of the Little Bustard in Spain and compared it between areas with two different farming systems: dry and irrigated farmland. Diet was studied through the micro-histological analysis of 357 droppings collected in 16 locations across the wintering range of the Little Bustard in Spain. Up to 62 plant species were identified. Most consumed species were cultivated legumes (46.7%) and dicotyledon weeds (45.6%), while monocotyledons were scarcely consumed (7.7%). Diet composition differed significantly between dry and irrigated farmland areas. In irrigated areas, diet was mainly composed of legumes, in particular alfalfa (*Medicago sativa*). In contrast, in dry farmland areas diet was more diverse, composed mainly of weeds (Compositae, Papaveraceae, and Cruciferae) and also cultivated legumes, particularly vetch (*Vicia sativa*). These results suggest that legume crops could be an effective measure to improve habitat quality in areas with scarce food resources. However, in the case of irrigated areas, the strong reliance on alfalfa could make the Little Bustard more vulnerable to changes in land

use. This study is the first step to understand the winter trophic requirements of the endangered Little Bustard, but further research is necessary to understand the food requirements of this species during the entire annual cycle.

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Introduction

The Little Bustard, *Tetrax tetrax*, is a medium-sized Paleartic steppe bird from the Otididae family that has suffered a strong population decline during the last century. It is classified as "Near threatened" at the global scale and "Vulnerable" in Europe (BirdLife International 2004, 2016). Nowadays, a signifycant proportion of the world's population is concentrated in the Iberian Peninsula (García de la Morena et al. 2006, Iñigo and Barov 2010), where it inhabits extensive pastures and cereal farmland (Martínez 2008). Studies determining habitat selection and population trends suggest that the species population decline has been mainly caused by recent agricultural changes affecting their foraging habitats (Goriup 1994, Wolff et al. 2001, Bretagnolle et al. 2011). Land irrigation is one of the most important alterations in agricultural farmland, mainly through crop change and intensification, and it is considered one of the major threats for the conservation of this steppe bird (Brotons et al. 2004). The negative effect of agricultural transformation through irrigation schemes has been reported in Little Bustard and several steppe species (Tella and Forero 2000, Brotons et al. 2004, De Frutos et al. 2015). However, although landscape transformations and other potential threats in their areas are thought to contribute to this decline, it is unknown how the feeding ecology of Little Bustards is affected by these changes. In fact, although there are numerous studies on Little Bustard ecology, little is known about the species' diet. Little Bustards are omnivorous, their diet consisting mainly of green plant material followed by arthropods and seeds (Cramp and Simmons 1980). The only previous studies on the diet of the Little Bustard were carried out in Russia during the breeding and post-breeding seasons (Shlyakhtin et al. 2004) or focused only on the animal component (Jiguet 2002). Most studies of Little Bustard ecology have focused on breeding and postbreeding ecology (Martínez 1994, Salamolard and Moreau 1999, Wolff et al. 2001, 2002, Silva et al. 2007, Morales et al. 2008, 2013, Traba et al. 2008, Delgado et al. 2010), but little information is available on its habitat requirements during winter (but see Silva et al. 2004, García de la Morena 2016), when it is congregated in large flocks and food availability could be a critical factor. Indeed, winter diet composition, which is presumably mostly herbivorous, is completely unknown. We studied for the first time the winter diet composition of the Little Bustard in two of the main wintering areas for the species in Spain (Ebro valley and Southern Plateau; García de la Morena et al. 2006). Furthermore, we explored the effects of irrigation schemes on diet composition. To do this, we compared the diet composition between areas under two different farming systems: dry and irrigated farmland. Our studied dry farmland areas were characterized by cereal crops in a two-year rotation system, which generates a mosaic-like agricultural landscape of stubbles, ploughs, fallows, and sown cereal, along with to a lesser extent, other crops such as legumes, olive groves, and vineyards. On the contrary, irrigated farmland areas were dominated by intensively managed herbaceous crops, e.g., maize, alfalfa (*Medicago sativa*), and irrigated cereal, along with fruit-tree orchards, and characterized by smaller field sizes, and thus greater amount of field margins, than dry farmland (Table 1). Based on the different characteristics of each system, we hypothesized that Little Bustards should change their feeding behavior with the conditions of each agroecosystem. On the one hand, because the Little Bustard strongly selects legume crops (Martínez 1994, Salamolard and Moreau 1999, Bretagnolle et al. 2011), we expected that their diet should be mainly composed of legumes, especially in irrigated landscapes where legume crops of alfalfa are highly available. On the other hand, optimal foraging theory proposes that as a preferred resource becomes scarce, individuals tend to open their trophic niche behaving as opportunistic (Stephens and Krebs 1986), hence in areas with low legume availability such as dry farmland, we expected that diet diversity of Little Bustards should be higher. We provide a more comprehensive understanding of the winter requirements of the Little Bustard, and other herbivorous birds inhabiting cultivated farmland in a rapidly changing environment. In this context, the study of the feeding behavior of an endangered species could be an essential tool to reverse its negative trend. A precise knowledge of the diet of species living in changing environments can help to identify key environmental resources for designing reliable conservation strategies.

Methods

Study area

The study was conducted on irrigated and dry wintering farmland areas within the Spanish Little Bustard range, where populations of the species have been intensively studied (Fig. 1; García de la Morena et al. 2007, Ponjoan et al. 2012, Tarjuelo et al. 2013). Irrigated farmlands were covered by a large variety of crops, although dominated by winter-sown cereal and maize crops, as well as alfalfa fields and fruit-tree orchards (Table 1). Sampling of these irrigated areas was carried out in seven locations of Lleida Plains (Anglesola, Arbeca, El Poal, Torregrossa, Castellnou de Seana, Sidamon, Miralcamp), situated on the northeastern edge of the Ebro Valley and dominated by small fields linked to gravity-irrigated agriculture, and one location

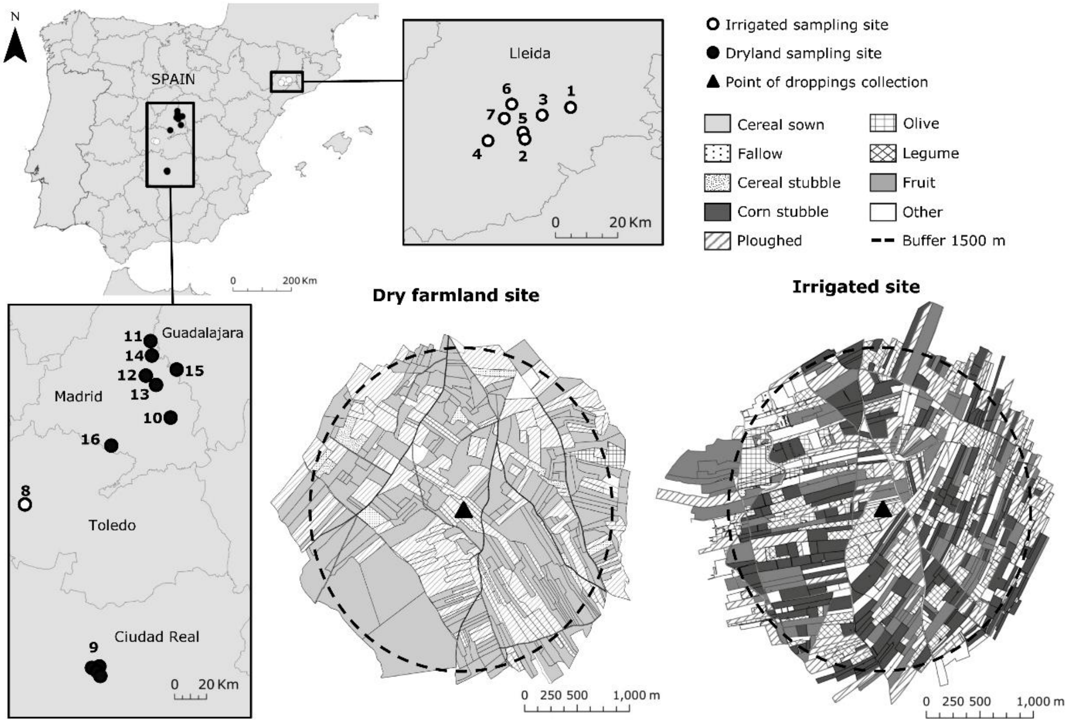

Figure 1 Map of the study area showing the irrigated sampling sites (1: Anglesola; 2: Arbeca; 3: Castellnou de Seana; 4: Torregrossa; 5: Miralcamp; 6: El Poal; 7: Sidamon; 8: La Puebla de Montalbán) and the dry farmland sampling sites (9: Campo de Calatrava; 10: Campo Real; 11: Valdepiélagos; 12: Cobeña; 13: Daganzo de Arriba; 14: Valdetorres de Jarama; 15: Villanueva de la Torre; 16: Torrejón de Velasco). Agrarian land-use composition in 1500 m buffers around the point of dropping collection is shown for two of the 16 sampling points (Torrejón de Velasco and Arbeca), as an example of each farmland system.

Table 1 Averaged (±SD) habitat and configuration of the study sites composition on grouped by irrigated and dry farmland areas.

	Irrigated areas (n=8)	Dry farmland areas (n=8)	Mann Whitney U-test	*p*
Habitat configuration				
Shannon index habitat	1.6 ± 0.2	1.5 ± 0.3	54	0.024
Field size (ha)	1.3 ± 1.4	2.5 ± 1.6	9	0.015
Land uses (%)				
Fallows	4.0 ± 2.6	6.1 ± 6.2	27	0.645
Sown cereal	9.4 ± 5.1	50.8 ± 18.0	1	<0.001
Ploughs	31.0 ± 18.6	15.0 ± 11.5	50	0.065
Maize stubble	11.5 ± 7.5	--		
Cereal stubble	2.0 ± 3.7	26.1 ± 25.3	9.5	0.018
Fruit-tree orchard	18.3 ± 14.9	--		
Legume crops†	19.4 ± 10.2	0.9 ± 1.6	64	<0.001
Olive and vineyard	3.1 ± 3.2	1.2 ± 1.9	47	0.122

†Legume crops in irrigated areas corresponded to irrigated alfalfa crops (*Medicago sativa*), whereas in dry farmland corresponded to dry legume crops of *Vicia sativa, Vicia* spp and *Pisum sativum*.

in the Tagus valley (La Puebla de Montalbán) sited in the Iberian Southern Plateau, dominated by large pivot-irrigated fields. Dry farmland was mostly dedicated to cereal production (> 80%), with some olive groves, vineyards, and leguminous crops (*Vicia sativa* and *Vicia* spp.; Table 1). Sampling of the dry farmland area was carried out in eight locations of the Southern Plateau in Madrid, Guadalajara, and Ciudad Real provinces (Valdepiélagos, Valdetorres de Jarama, Cobeña, Daganzo de Arriba, Campo Real, Villanueva de la Torre, Torrejón de Velasco, Campo de Calatrava).

Diet analysis

The diet was studied using 357 droppings collected in late November–January between 2003–2013 (Table A1.1.), in the above-mentioned eight irrigated and eight dry farmland sites within the study area (Fig. 1). On each site, fresh droppings were collected at roosting sites at dawn from cereal sown (25.5%), stubble (37.7%), and leguminous crops (36.8%). Each morning, we randomly collected 13.2 ± 5.1 (mean±SD, range: 6 – 25) fresh individual droppings per flock (127.5 ± 182.1 individuals per flock, range: 13 – 500). To avoid pseudoreplication, we collected fewer droppings than individuals per flock and only those that were at least 10 m apart. Each dropping was individually stored in a labeled bag, oven-dried at 60°C within 48 hours, and weighed afterward (accuracy: 0.001 g). Each dropping was partitioned into green plant material, arthropods, and seeds with the aid of a binocular microscope (20×). These components were weighed separately and the dry weight proportion calculated per dropping. Plant species were identified and quantified by microhistological techniques using our reference collection of tissues from the study area (Bravo et al. 2016; C. Bravo, O. Jordi, F. Cuscó and S. Mañosa 2016, unpublished data). From each sample, 80 fields, i.e., the visible circle that is observed through the microscope, were examined with a microscope (40×), recording the presence or absence of each plant species. We calculated the diet composition as the occurrence percentage of each plant species per dropping, $OD = n_i*100/80$, where n_i is the number of microscope fields in which species *i* occurred in the 80 microscope fields. All identified plants and their occurrence percentage in the diet (OD) are shown in Table A1.2.

Habitat configuration and land uses

To describe habitat configuration and proportion of land-use types of the study area, we delimited a 1500 m buffer around each dropping collection site (n = 16). Based on ecology movement of the Little Bustard in the study area (F. Cuscó and S. Mañosa 2016, unpublished data, personal observation), we assumed that this buffer provides characteristic information of the feeding areas on each sampling point. Indeed, habitat configuration and proportion of land-use types were also calculated for buffers of 1000 m and 500 m radius to determine whether results were sensitive to radius choice. Because similar results were obtained, only results of 1500 m radius are presented. In each buffer area, the habitat composition was assessed by recording the land-use type in each field and calculating the proportion of different land-use types using ArcView 10.2.2 (ESRI 2014). The land-use types considered were sown cereal crops, cereal stubbles, maize stubbles, ploughs, fallows, irrigated legume crops (*Medicago sativa*), dry legume crops (*Vicia sativa* and *Vicia spp.*), olive and vineyards, fruit-tree orchard crops, and nonused land (shrubland, infrastructures, etc.; Table 1). Farmers usually plow stubble during this period. To record the land-use types actually available for foraging Little Bustards, land-use data were collected on the same day or a few days around the date of dropping collection. Habitat configuration on the same buffer areas were estimated using FRAGSTATS 4.2 (McGarigal et al. 2012) by calculating the following variables: (i) habitat diversity (SHDI; computed using the Shannon index and considering the proportional abundance of each land-use types); and (ii) mean field size (ha) as a measure of edge density.

Statistical analysis

We examined the overlap in diet composition (percentage of each plant species per dropping) between and within dry and irrigated farmland areas using non-metric multidimensional scaling (NMDS). NMDS is an ordination technique that uses a Bray-Curtis matrix of ranked similarities and displays samples in lowdimensional space while retaining as nearly as possible the similarity rankings between groups. We chose this method for the following reasons: (i) avoids the assumption of linear relationships among variables; (ii) non-normal and nonlinear data can be used; and (iii) the ordination based on ranks relieves the "zero-truncation problem" (McCune and Grace 2002). The stress criterion was used to evaluate goodness of fit for the final NMDS model. NMDS results were considered to represent a useful model if two-dimensional stress was less than 0.2 (Kruskal 1964, Clarke 1993). We then used analysis of similarities (ANOSIM), a nonparametric test that uses permutations to calculate significance between groups, to determine if there were differences in diet composition of dry and irrigated farmland area. The test statistic was the global R, which can range from -1 to +1, with a value close to -1 indicating that the variation within groups is higher than the variation between groups and a value close to +1 indicating that the variation between groups is higher than the variation within groups (Clarke 1993). If a significant result ($p < 0.05$) was obtained using ANOSIM, we used analysis of similarity percentages (SIMPER) to determine which particular plant species were responsible for the dissimilarity between areas (Clarke 1993). All analyses above were conducted with vegan package for R 2.15 (Oksanen et al. 2013). Diet diversity in the droppings was calculated using the

Shannon diversity index H' = -∑(*pi* ˙ln *pi*), where pi is the proportion of species *i* (plant, animal and seed species) per dropping. Differences in diet diversity between dry and irrigated farmland areas were analyzed by the nonparametric Mann-Whitney U test, based on the mean diversity per sampling site. Also, differences of diet diversity among sampling sites of dry farmland and among sampling sites of irrigated farmland were analyzed by KruskalWallis test followed by Dunn's post hoc multiple comparison test. Differences in habitat configuration variables, land-use availability, and differences in dry weight of droppings in the two agroecosystems were analyzed by means of a nonparametric Mann-Whitney U test. Results are reported as mean±SD in the text and tables; and mean±SE in the figures.

Results

Dry weight of droppings was 0.95± 0.86 g, showing no differences between the two agrosystems (Mann-Whitney U = 16573, p = 0.43). The dry weight proportions of droppings were 99.998% of green plant material, 0.001% of arthropod, and 0.001% of seeds. Most droppings were composed exclusively of green plant material (96.4%), whereas only 2.8% and 0.8% of total droppings contained arthropod and seed remains, respectively. Up to 62 plant species were identified, with an average of 6±4 species per dropping and 15.8± 9.8 species per sampling area (n = 16). Overall, most species were cultivated legumes (46.7% of diet composition) and weeds (45.6% of diet composition), with reduced presence of graminoid species (7.7% of diet composition; Table A1.1). Arthropod remains corresponded to Coleoptera and Hymenoptera (Formicidae), 2.2% and 0.6% of droppings, respectively. Seeds belonged to undetermined weeds, but did not belong to any cultivated cereal or legume.

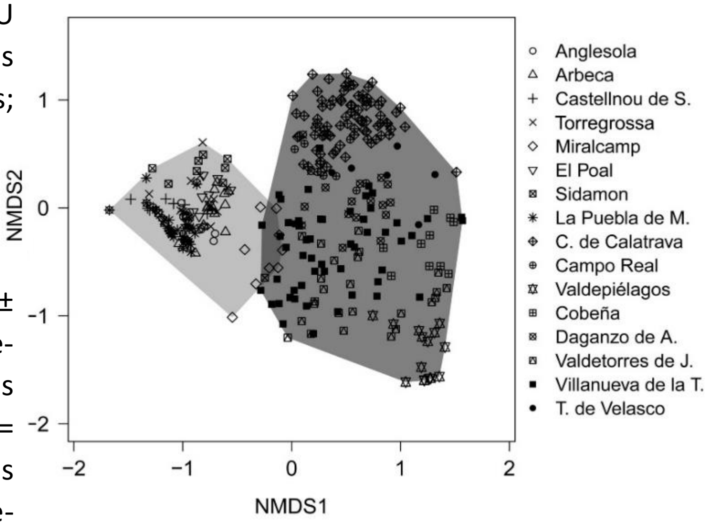

Figure 2 Nonmetric multidimensional scaling (NMDS) plot representing diet similarity for dry farmland (dark grey) and irrigated areas (light grey).

Among plants, the high consumption of cultivated legumes was highlighted (83.2% of total legumes), mainly *Medicago sativa* and *Vicia sativa*. Among weeds, Compositae, Papaveraceae, and Cruciferae were the most frequent families consumed (Table A1.1). The main species eaten were *Anacyclus clavatus*, *Papaver rhoeas*, *Capsella bursa-pastoris*, *Diplotaxis erucoides,* and *Convolvulus arvensis* (Table A1.2). Regarding graminoid plant species, *Hordeum vulgare* was the most common in the diet of Little Bustard (4.9% of diet composition; Table A1.2). The NMDS analysis of the diet composition showed a clear spatial separation between diet composition of dry farmland and irrigated areas (Fig. 2). This was statistically verified with ANOSIM test, which showed a significant difference in the degree of separation between the two assemblages ($R = 0.56$, $p < 0.05$). An additional post hoc analysis, SIMPER, found that the 38% of the dissimilarity between the assemblages was attributed to the proportion of *Medicago sativa*, 11.7% attributed to *Capsella bursa-pastoris*, and 6.8% to *Vicia sativa*. Among dry farmland sampling sites, ANOSIM test showed no significant difference in the degree of separation between assemblages of dry farmland sites ($R = -0.011$, $p > 0.05$). Also among irrigated sampling sites, ANOSIM test showed no significant difference in the degree of separation between assemblages of irrigated sites ($R = -0.072$, $p > 0.05$).

Diet diversity was significantly higher in dry farmland area (H': 1.34±0.47) than in irrigated area (H': 0.59±0.33, Mann-Whitney $U = 2938.5$, $p < 0.001$). Diet in irrigated areas mainly consisted of legumes (67.1±28.3% of diet composition), followed by Cruciferae (25.2± 25.5 % of diet composition; Fig. 3), whereas in dry farmland area diet was characterized by the presence of species from Leguminosae, Compositae, Papaveraceae, and Cruciferae species (Fig. 3). Among irrigated areas, diet diversity was significantly different between sampling sites ($H_7 = 131.5$, $p < 0.05$); being Arbeca and El Poal significantly more diverse than Anglesola, Castellnou de Seana, and La Puebla de Montalbán (Dunn's test $p < 0.05$). Whereas among dry farmland areas, diet diversity was also significantly different between sampling sites ($H_7 = 39.4$, $p < 0.05$); being Campo de Calatrava and Campo Real significantly more diverse than the remaining sites, except

Torrejón de Velasco (Dunn's test $p < 0.05$).

Discussion

In agreement with previous studies conducted in France and Russia (Jiguet 2002, Shlyakhtin et al. 2004) on the diet in the breeding and postbreeding seasons, the winter diet of the Little Bustard in Spain fundamentally consisted of green plant material, mainly cultivated legumes (46.7%) and weeds (45.6 %). Monocotyledon species were only seldom consumed (<8%), in accordance with what has been reported for related species, such as the Great Bustard (Lane et al. 1999, Bravo et al. 2016). This low consumption is remarkable because the availability of wild or cropped monocotyledons is very high in the studied farmland habitats, and is probably the consequence of its low digestibility and nutritional value compared to weeds and legumes (Smith et al. 1972).

Microhistological analysis is a method widely used to assess diet composition of herbivorous species (La Morgia and Bassano 2009, Blanco-Fontao et al. 2010, Whitney et al. 2011, Kobayashi and Takatsuki 2012, Xu et al. 2012, Freschi et al. 2014). However, results from microhistological analysis of droppings could have a potential bias derived from differential digestibility of plant species. For example, graminoids or ligneous species are generally over-represented in faecal samples (Vavra and Holechek 1980, Alipayo et al. 1992). Our results showed that diet consisted mainly of dicotyledon weeds, with smaller proportion of graminoids. Therefore, unless there are large differences in digestibility between dicotyledon weed species of our study area, our results should not differ significantly from the composition of true diet. In any case, any potential bias should not affect the comparisons between farming systems, which supports the reliability of our conclusions. On the other hand, although our sample of droppings was collected over a long period of time, sample size did not allow to test for interannual variation. Nevertheless, this study is the first step to understand the trophic requirements of Little Bustards and further studies are needed to address the changes in diet across years as agricultural intensification and land-use changes are the main threat to this species. Cultivated legumes were an important winter food resource for Little Bustard in both irrigated (67%, alfalfa) and

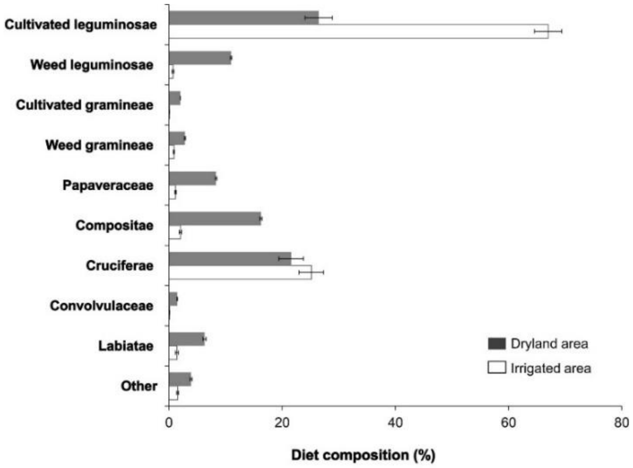

Figure 3 Percentage (mean±SE) of the main plant families in the diet of Little Bustards (*Tetrax tetrax*) in irrigated (white columns) and dry farmland areas (grey columns) in Spain. Infrequent families (Caryophyllaceae, Boraginaceae, Dipsacaceae, Euphorbiaceae, Malvaceae, Plantaginaceae, Primulaceae, Resedaceae, Rubiaceae, Scrophulariaceae) have been grouped in the "other" category.

dry farmland (26%, mainly vetch *Vicia sativa*). This was not surprising on irrigated farmland, where alfalfa covers up to 19% of land (Table 1), but it was somehow unexpected on dry farmland, with only a meagre 1% of legume crop availability (Table 1). This indicates a strong preference for feeding on legumes, as already suggested by the reported selection of legume crop areas exhibited by the Little Bustards (Martínez 1994, Salamolard and Moreau 1999, Bretagnolle et al. 2011). In spite of this apparent preference for cultivated leguminous plants, noncultivated plants were also very important in the winter diet of the Little Bustard. This dominance of weeds was remarkable on dry farmland, where *Anacyclus clavatus*, *Papaver rhoeas*, *Diplotaxis erucoides*, and *Capsella bursa-pastoris* formed the bulk of the diet. But it was somehow surprising in irrigated habitats, where the Little Bustards consumed a remarkable 32% of noncultivated plants despite that alfalfa crops seemed to provide a virtually unlimited high quality food supply. We hypothesized that nutrient requirement cannot be met from a single plant species (Stephens and Krebs 1986, Raubenheimer and Simpson 1997) and, consequently, Little Bustards try to incorporate a greater variety of plant species in their winter diet to meet a complete range of nutrient needs. The fact that there were no significant differences in diet composition between sampling sites among irrigated areas, or among dry farmland areas, suggests a consistent feeding behavior within each agroecosystem, regardless of the region (Ebro Valley or Southern Plateau), hence highlighting the robustness of the pattern described and indicating that diet composition varied between agrarian systems rather than between regions. Likely these differences in diet were the consequence of different land-use availability between agrosystems (Table 1). On dry farmland areas, diet composition was much more diverse, being composed mainly of weeds and legumes. These plants were probably provided by cereal stubble (Table 1), which hold higher availability of weeds (Ponce et al. 2014; personal observation). Also, the higher global dietary diversity on dry farmland areas was both the result of a higher between and within site variation (Figs. 2 and 3, Table A1.1). At some sites, such in Valdepiélagos and Valdetorres, cultivated legumes in diet were dominant (Table A1.1), because in these areas there was about 2% of surface occupied by *V. sativa* crops provided by the agri-environmental scheme programs (Ponce et al. 2014). In other areas, where these crops were less available, diet was more diverse, based on a mixture of legumes and weeds (Campo Real, Villanueva de la Torre), cereals and weeds (Cobeña), or mainly on weeds (Campo de Calatrava, Daganzo de Arriba, and Torrejón de Velasco), likely depending on the land-use composition on each site. The Little Bustard therefore seems to follow the prediction of optimal foraging theory, which proposes that diet diversity decreases as the abundance of the preferred resource increases (Stephens and Krebs 1986). On the contrary, in irrigated areas, despite having higher edge density and habitat diversity (Table 1), which could counteract a potentially constrained diet by providing a wider variety of food resources (Ottens et al. 2014), the dietary spectrum and diet diversity were always low, mainly composed of legumes alfalfa or, in one location (Miralcamp), cruciferae (Figs. 2 and 3, Table A1.1). Therefore, we cannot preclude the possibility that the low diversity in the diet of Little Bustard in irrigated farmland is reflecting the reduced availability of alternative resources as a consequence of agricultural intensification as has been reported in other species (Britschgi et al. 2006, Moorcroft et al. 2006, Cardador et al. 2012). Although cultivated legumes seem to provide a good food resource for Little Bustards in winter, we would like to warn about some potential drawbacks of this dependence. First, the strong reliance on legumes as a winter food resource, particularly in irrigated areas, could result in a vulnerable system, being very sensitive to changes in land uses, because of the lack of alternative suitable food resources. Alfalfa crops seem to act as a habitat island surrounded by unsuitable habitat for Little Bustards, such as fruit-tree orchard and ploughs (Silva et al. 2004), hence a decrease in the surface of alfalfa or isolation from each other could entail the abandonment of the area by the Little Bustard (Saunders et al. 1991, Brotons et al. 2004), as has been recently described by Morales et al. (2015) for the Tagus valley. Second, the benefits of a diverse diet on the fitness, growth, or survivorship has been reported for several species, particularly herbivorous ones (Lefcheck et al. 2013) so it is likely that a narrow diet composed mainly of alfalfa does not meet the complete range of nutrients needed by Little Bustards. In fact, as stated above, our results suggest that, even in alfalfa-dominated areas, a high proportion of weeds are included in the diet, suggesting that the Little Bustard needs to equilibrate their winter diet with a variety of plants. Finally, alfalfa monocultures are intensively managed crops, involving the use of high amounts of pesticides (Barker et al. 1980, Almacellas and Perdiguer 2007, Cantero and Moncunill 2012). It is well known that the use of these compounds has direct or indirect effects on avian wildlife, compromising bird survival or breeding success because of intoxication by the ingestion of contaminated food, soil, or water (Fry 1995, Lemly et al. 2000). Thus, the potential negative effects that a high reliance on alfalfa as a winter food resource may have on the Spanish Little Bustard population and those of other farmland birds deserve further attention from an ecological, nutritional, and toxicological point of view. In the meantime, although the effectiveness of providing legume crops as a measure to increase habitat quality and carrying capacity for bustards in agricultural landscape has been well established (Wolff et al. 2001, Ursúa et al. 2005, Bretagnolle et al. 2011, Kovács-Hostyánszki and Báldi 2012, Ponce et al. 2014), we suggest that these crops should be included within a web of a diverse habitat matrix providing different suitable and complementary habitats such as fallow land (Silva et al. 2004) to supply alternative and varied food resources. To summarize, our results show that Little Bustards show a great trophic plasticity, being able to change their foraging behavior with the conditions prevailing on each agrarian system. The conservation of this species in Spain requires the adequate management of agricultural farmland aiming to meet its food requirements. In winter, this would involve providing diversified landscapes, containing large amounts of wild or cropped legumes, but also many weeds to complement the diet. In areas dominated with cultivated legumes, fallow land should be promoted. On the contrary, on cereal- and fallow-dominated areas, plots of legume crops should be provided. Finally, practices associated to the intensive treatment of fallows such as repeated tillage of rotatory fallows should be avoided. This study is the first step to improve our knowledge about feeding behavior of the Little Bustard in a changing farmland environment. However, there is still much work to be done to understand to what extent the variable availability of trophic resources might explain the decline of Little Bustard populations in Spain. This requires improving our knowledge of the species feeding behavior during the breeding season and identifying the trade-offs between food intake and fitness.

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Additional files

Appendix 1. Diet composition and diet diversity of the Little Bustard sorted by irrigated and dry farmland areas.

Appendix 1

Table A1.1 Diet diversity (H') and green plant families identified in Little Bustard diet sorted by irrigated and dry farmland area. Diet composition is shown as the average (±SD) percentage of microscope fields with presence of each family per dropping. Infrequent families (Caryophyllaceae, Boraginaceae, Dipsacaceae, Euphorbiaceae, Malvaceae, Plantaginaceae, Primulaceae, Resedaceae, Rubiaceae, Scrophulariaceae) are grouped in "other" category. N represents the total number of collected droppings and Date represents date of collection.

	Date	N	Diversity (H')	Cultivated legumi-nosae (%)	Weedy legumi-nosae (%)	Cultivated gramineae (%)	Weedy gramineae (%)	Papave-raceae (%)	Compositae (%)	Cruciferae (%)	Convolvu-laceae (%)	Labiatae (%)	Other (%)
Irrigated area		**138**	**0.6 ± 0.2**	**67.0±28.4**	**0.1±0.1**	**0.7 ± 1.7**	**0.9±1.1**	**1.2±1.6**	**2.0±2.4**	**25.2±25.5**	**0.1±0.5**	**1.4±3.4**	**1.5±2.1**
1. Anglesola	Jan. 2013	20	0.4 ± 0.3	86.7±11.5		0.5 ± 2.1			0.1±0.3	9.3±8.3		2.4±3.8	1.1±2.3
2. Arbeca	Nov/Dec. 2011/12	20	0.8 ± 0.2	60.6±14.2	0.2±0.6	0.1 ± 0.3		0.4±0.9	3.9±3.9	31.8±14.8	0.4±1.1	0.7±2.9	2.1±4.1
3. Castellnou S.	Jan. 2012	10	0.3 ± 0.3	90.0±10.6		4.9 ± 9.6	0.1±0.4	0.2±0.8		3.3±5.2		1.2±1.5	0.2±0.5
4. Torregrossa	Dec. 2011	10	0.7 ± 0.4	79.1±12.7	0.8±1.6			1.7±2.9	0.1±0.4	9.3±5.5	0.1±0.4	8.0±5.3	1.0±1.2
5. Miralcamp	Nov. 2011	13	0.6 ± 0.4	0.8±2.0	0.3±0.5	0.1 ± 0.4	2.5±4.6	2.6±7.0	5.2±5.5	83.9±12.8	0.3±0.8	3.0±5.0	1.3±1.6
6. El Poal	Nov. 2013	10	0.8 ± 0.2	68.4±10.6			1.6±4.9	4.3±5.2	1.4±2.5	23.9±7.9			0.5±1.1
7. Sidamon	Jan. 2012	10	0.7 ± 0.5	72.4±30.7			2.3±6.4	0.0±0.0	5.5±4.7	18.0±20.0		0.2±0.5	1.7±2.9
8. La Puebla de M.	Dec/Jan. 2003/05	45	0.5 ± 0.3	77.3±13.2	0.0±0.1		0.5±0.9	0.1±0.4	0.0±0.3	21.8±12.7		0.2±0.5	0.1±0.2
Dryland area		**219**	**1.3 ± 0.4**	**26.5±28.4**	**2.0±4.2**	**11.0 ± 10.6**	**2.8±2.5**	**8.3±19.2**	**16.3±15.2**	**21.6±15.1**	**1.5±5.1**	**6.3±13.2**	**3.9±3.4**
9. C. de Calatrava	Dec. 2011	84	1.7 ± 0.3	15.4±14.7	12.0±10.4	0.0 ± 0.2	1.3±1.4	9.4±9.5	29.3±20.7	23.0±17.2	1.6±4.5	4.9±9.7	3.2±3.8
10. Campo Real	Nov. 2012	8	1.7 ± 0.2	20.8±20.0		0.2 ± 0.4	7.0±3.8	0.2±0.4	1.9±2.1	35.0±11.1	1.0±0.9	27.9±16.3	6.1±7.4
11. Valdepiélagos	Jan. 2012	15	0.7 ± 0.2	69.6±16.0		26.8 ± 16.9	0.9±1.4		0.9±2.6	0.2±0.6		0.2±0.4	1.6±3.1
12. Cobeña	Dec. 2011	10	1.3 ± 0.3	0.4±0.8	3.2±3.0	22.3 ± 16.5	1.5±2.2		21.8±17.4	47.1±15.9	2.6±4.5	0.1±0.4	1.1±0.8
13. Daganzo de A.	Jan. 2011	17	1.2 ± 0.2	1.5±6.4	0.3±0.7	14.6 ± 10.3	0.8±1.6	55.2±12.6	15.8±12.6	9.5±9.9	0.1±0.6	0.5±1.2	1.7±2.9
14. Valdetorres J.	Jan. 2010	25	0.9 ± 0.4	70.6±23.2			4.7±5.4		7.3±8.5	13.7±15.2		3.2±6.3	0.6±2.0
15. Villanueva T.	Dec/Jan. 2011/13	54	1.2 ± 0.4	25.9±23.9	0.6±3.3	16.0 ± 25.6	5.5±7.6	0.6±2.2	8.1±8.7	28.6±26.5	0.4±1.3	13.2±19.5	1.1±2.2
16. T. de Velasco	Nov. 2012	6	1.4 ± 0.2	7.3±8.2		7.9 ± 6.0	1.0±1.9	1.2±1.5	45.0±22.6	15.5±8.2	21.8±16.2		0.2±0.5
TOTAL		**357**	**0.9 ± 0.4**	**46.7±34.5**	**1.0±3.0**	**5.8 ± 9.0**	**1.9±2.1**	**4.7±13.7**	**9.1±12.8**	**23.4±20.3**	**1.8±5.4**	**4.1±7.3**	**1.5±1.5**

Table A1.2 Plant species identified in Little Bustard diet sorted by irrigated (n=8) and dry (n=8) farmland areas. Frequency of each plant species is expressed as the average percentage (±SD) of droppings in which the species appears, and diet composition is shown as the average (±SD) percentage of microscope fields with presence of each species per dropping. Averages were based on the mean of the 8 sampling sites per agroecosystem.

		Frequency (%)		Diet composition (%)	
Family	**Species**	**Irrigated area**	**Dry farmland area**	**Irrigated area**	**Dry farmland area**
Boraginaceae	*Echium plantagineum*		4.0 ± 9.3		0.17 ± 0.39
	Heliotropium europaeum		0.1 ± 0.4		
	Lithospermum apulum	1.3 ± 3.3	0.7 ± 2.1	0.04 ± 0.12	0.01 ± 0.02
	Lithospermum arvensis	1.7 ± 3.6	1.2 ± 2.3	0.05 ± 0.14	0.09 ± 0.16
Caryophyllaceae	*Stellaria media*	1.3 ± 3.3	7.4 ± 18.8	0.03 ± 0.08	0.14 ± 0.34
Compositae	*Anacyclus clavatus*	28.2 ± 29.2	58.3 ± 42.6	1.68 ± 2.00	11.53 ± 15.06
	Andryala integrifolia		25.4 ± 28.4		2.62 ± 4.30
	Bellis perennis	0.6 ± 1.7		0.01 ± 0.02	
	Calendula arvensis		0.2 ± 0.7		0.00 ± 0.01
	Carthamus lanatus		6.7 ± 11.8		0.16 ± 0.34
	Cnicus benedictus		2.1 ± 5.9		0.12 ± 0.35
	Crepis sancta		0.4 ± 1.3		0.00 ± 0.01
	Crepis vesicaria	1.4 ± 3.7	11.8 ± 16.0	0.03 ± 0.09	0.30 ± 0.44
	Filago sp		7.0 ± 13.4		0.65 ± 1.71
	Picris echinoides		19.7 ± 25.7		0.53 ± 0.67
	Picris sp		1.9 ± 4.2		0.04 ± 0.09
	Senecio vulgaris	2.5 ± 4.3	0.1 ± 0.4	0.03 ± 0.06	0.00 ± 0.01
	Silybum mariamum	0.3 ± 0.7	0.5 ± 1.0	0.00 ± 0.01	0.01 ± 0.02
	Tolpis barbata		0.1 ± 0.4		0.01 ± 0.02
	Undetermined	7.0 ± 13.0	9.1 ± 20.4	0.60 ± 1.07	3.30 ± 4.09
Convolvulaceae	*Convolvulus arvensis*	3.9 ± 5.0	35.0 ± 36.2	0.09 ± 0.14	3.45 ± 7.48
Cruciferae	*Alyssum minus*		0.9 ± 2.5		0.03 ± 0.08
	Biscutella auriculata		9.7 ± 21.7		1.11 ± 2.59
	Brassica repanda		0.1 ± 0.4		0.02 ± 0.05
	Camelina micrarpa	1.3 ± 3.3		0.01 ± 0.04	
	Capsella bursa-pastoris	91.1 ± 7.8	42.3 ± 24.5	24.34 ± 25.62	5.24 ± 5.88
	Cardaria draba		3.1 ± 8.8		0.64 ± 1.80
	Descurainia sophia	0.3 ± 0.7	0.7 ± 2.1	0.00 ± 0.01	0.01 ± 0.03
	Diplotaxis erucoides		36.6 ± 38.5		8.47 ± 15.89
	Malcolmia africana		0.1 ± 0.4		
	Neslia paniculata		13.4 ± 19.6		1.77 ± 3.69
	Raphanus raphanistrum		2.9 ± 4.5		0.27 ± 0.48
	Sisymbrium irio	4.5 ± 6.9	3.6 ± 6.8	0.20 ± 0.45	0.71 ± 1.35
	Undetermined	20.1 ± 26.3	26.9 ± 32.3	0.22 ± 0.50	0.64 ± 1.67
Dipsacaceae	*Scabiosa sp*		3.2 ± 5.1		0.06 ± 0.11
	Scabiosa stellata	1.3 ± 3.3	0.2 ± 0.7	0.02 ± 0.06	0.00 ± 0.01
Euphorbiaceae	*Euphorbia helioscopia*		0.5 ± 1.4		0.03 ± 0.08
Geraniaceae	Undetermined	3.8 ± 7.0	8.0 ± 17.7	0.09 ± 0.18	1.86 ± 2.53
Gramineae	*Bromus diandrus*		2.4 ± 4.5		0.09 ± 0.22
	Bromus sp		0.7 ± 2.1		0.02 ± 0.05
	Hordeum murinum	6.9 ± 18.4	32.4 ± 11.8	0.31 ± 0.89	0.84 ± 0.38
	Hordeum vulgare	2.6 ± 3.8	55.5 ± 44.5	0.08 ± 0.17	10.79 ± 10.40
	Lolium rigidum	3.8 ± 7.0	0.7 ± 2.1	0.46 ± 0.87	0.01 ± 0.04
	Triticum aestivum	3.8 ± 9.9	1.5 ± 2.8	0.61 ± 1.73	0.18 ± 0.35
	Undetermined	6.9 ± 11.6	27.9 ± 34.8	0.01 ± 0.02	0.00 ± 0.01
Labiatae	*Lamium amplexicaule*	32.8 ± 27.7	34.4 ± 33.0	1.95 ± 2.67	6.24 ± 9.83
Leguminosae	*Astragalus hamosus*		10.3 ± 29.0		1.16 ± 3.27
	Astragalus sp	2.8 ± 7.3		0.03 ± 0.09	
	Medicago polymorpha	2.5 ± 6.6		0.03 ± 0.08	
	Medicago sativa	89.0 ± 25.5		66.90 ± 28.34	

Table A1.2

		Frequency (%)		Diet composition (%)	
Family	**Species**	**Irrigated area**	**Dry farmland area**	**Irrigated area**	**Dry farmland area**
	Medicago sp		37.2 ± 28.3		5.39 ± 7.63
	Ornithopus compressus		11.9 ± 27.7		0.48 ± 1.10
	Trifolium angustifolium		3.5 ± 7.1		0.04 ± 0.07
	Trigonella monspeliaca	0.3 ± 0.7	9.4 ± 26.5	0.00 ± 0.01	0.31 ± 0.89
	Vicia sativa		25.0 ± 45.1		17.15 ± 31.39
	Vicia sp	3.8 ± 7.0	24.0 ± 30.4	0.10 ± 0.21	3.91 ± 6.22
Malvaceae	*Malva sylvestris*		3.5 ± 5.1		0.04 ± 0.06
Papaveraceae	*Papaver hybridum*		6.3 ± 17.7		0.15 ± 0.42
	Papaver rhoeas	24.4 ± 23.3	27.6 ± 43.6	1.17 ± 1.58	8.17 ± 19.29
Plantaginaceae	*Plantago lagopus*	0.9 ± 1.7	1.2 ± 2.3	0.02 ± 0.06	0.01 ± 0.02
Primulaceae	*Anagallis arvensis*		0.2 ± 0.7		0.01 ± 0.02
Resedaceae	*Reseda alba*		0.3 ± 0.8		0.01 ± 0.02
Rubiaceae	*Galium tricornutum*		4.0 ± 11.4		0.11 ± 0.31
	Sherardia arvensis		0.3 ± 0.8		0.00 ± 0.01
Scrophulariaceae	*Veronica heredifolia*	6.3 ± 10.2	15.6 ± 18.3	0.13 ± 0.20	0.29 ± 0.36
	Veronica polita	1.4 ± 3.7	0.1 ± 0.4	0.02 ± 0.05	
Undetermined	Undetermined	20.6 ± 13.0	12.3 ± 10.3	0.26 ± 0.62	0.29 ± 0.69

TRACKING DATA OF THE LITTLE BUSTARD (*TETRAX TETRAX*) IN IBERIA SHOWS HIGH ANTHROPOGENIC MORTALITY

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The Little Bustard *Tetrax tetrax* (Linnaeus, 1758) is a medium-sized, "Near Threatened" steppe bird, whose Iberian population has been alarmingly declining over recent decades. Although this population loss has been mainly attributed to agricultural intensification, there is no information on Little Bustard adult mortality levels and their drivers. Based on a joint effort combining all the tracking data on adult Little Bustards collected over a period of 12 years by all research teams working with the species in Iberia, we found that annual anthropogenic mortality is likely to have a critical impact on the species, with values almost as high as the mortality attributed to predation. Collision with power lines was found to be the main anthropogenic threat to the adult population (3.4–3.8%/year), followed by illegal killing (2.4–3%/year), which had a higher impact than initially foreseen. Our work shows how poorly understood and previously unknown threats are affecting the survival of the most important Little Bustard population in Europe.

Marcelino, J., F. Moreira, S. Mañosa, F. Cuscó, M.B. Morales, E.L. García de la Morena, G. Bota, J.M. Palmeirim, J.P. Silva. 2017. Tracking data of the Little Bustard *Tetrax tetrax* in Iberia shows high anthropogenic mortality. Bird Conservation International, 1–12. doi:10.1017/S0959270917 00051X

Introduction

Identifying causes of death and assessing their prevalence is fundamental in understanding species' population dynamics, and targeting the reduction of mortality in endangered populations. A good understanding of the causes and rates of mortality is therefore of vital importance for the conservation of endangered species.

Compared to other demographic parameters of wildlife populations, mortality is difficult to estimate (McCallum 2000) due to difficulties in capturing and monitoring animals, which usually results in small sample sizes, and the uncertainty about the fate of a large proportion of tracked individuals. Nevertheless, the increasing use of remote tracking devices and the improvement in capture techniques has facilitated mortality and survival studies in free-ranging animals (Krebs 1999, Kenward 2001, Millspaugh and Marzluff 2001).

While natural threats are less subject to human control, sources of anthropogenic mortality can be challenging to manage (Loss et al. 2012). This is the case with mortality caused by overhead power lines, wind farms and buildings, or hunting and illegal killing (Erickson et al. 2005, Tourenq et al. 2005, Loss et al. 2014, Silva et al. 2014).

The Little Bustard *Tetrax tetrax* (Linnaeus, 1758) is currently classified as globally "Near Threatened" (BirdLife International 2016). Its present breeding distribution is fragmented and concentrated in two main regions: one centered in south-eastern European Russia and Kazakhstan, and a second in the Iberian Peninsula, France, Sardinia and Morocco (Cramp and Simmons 1980, del Hoyo et al. 1996, Palacín and Alonso 2009, BirdLife International 2016). Over recent decades the population has been declining mainly in its western range. In western France, for example, between the 1980s and late 1990s the population suffered an estimated decline of 92% (Jolivet 1997). Because of this declining trend, the species is classified as "Vulnerable" in the Iberian Peninsula (Madroño et al. 2004, Cabral et al. 2005) and is considered a priority species under the European Union Wild Birds Directive (2009/147/EC), which has led to the designation of many steppe areas as Special Protection Areas (SPA).

The Iberian Peninsula holds the main stronghold of the species in Europe (Iñigo and Barov 2010). The

Spanish population was estimated between 29,000 and 48,000 individuals (García de la Morena et al. 2006), and the Portuguese population was estimated at 17,500 males (Silva and Pinto 2006). Over the last 10 years, alarming declines have been reported for several regions of Iberia, such as Catalonia, Central Spain and Extremadura, with regional losses between 50% and 70% of the breeding population (Morales et al. 2006a, 2015, De Juana 2009, Mañosa et al. 2015).

A number of factors are contributing to the Little Bustard's decline. A major overall threat is agricultural intensification, which leads to habitat loss and degradation (e.g. Goriup 1994, Morales et al. 2005a, 2006b, García et al. 2007). In Iberian landscapes, agricultural intensification leads to the decreasing use of traditional crop rotation systems and suppression of fallow land, which is a key breeding habitat for the species (Martínez 1994, Morales et al. 2005b, Moreira et al. 2012). In France, nest destruction during harvesting has also been reported as a main factor of decline (Inchausti and Bretagnolle 2005).

Adult survival has also been pointed out as one of the most important demographic parameters affecting Little Bustard population viability (Morales et al. 2005a, Inchausti and Bretagnolle 2005), highlighting the importance of knowing mortality rates as well as their underlying causes. There is, however, a great dearth of information on these topics. Exceptions include the study by Schulz (1987), who found that predation is the most common natural cause of death for Little Bustard. In fact, its behaviour seems to be determined, in great measure, by an anti-predator strategy that includes flocking outside the breeding season and selecting habitats with a vegetation structure that provides both cover and visibility (Silva et al. 2004, García de la Morena 2016). Collisions with overhead power lines have also been described as an important source of nonnatural mortality (Silva et al. 2010, unpubl. data). A rough estimate based on the number of dead birds found next to power lines indicated that 1.5% of the Portuguese national population could be killed annually by these structures (Silva et al. 2014). Other sources of human induced mortality, such as illegal killing, have also been identified as threats, but have never been quantified (Iñigo and Barov 2010).

The purpose of this paper is to assess the causes of adult mortality and estimate the relative importance of each of the identified causes in the Iberian Peninsula. This information is essential to outline a future strategy aiming to set a conservation plan to reverse the decline of this threatened steppeland bird. Based on a joint effort, all tracking data on adult Little Bustards collected by the Iberian research teams over a period of 12 years were used for this paper.

Methods

Study area

The study was carried out in the Iberian Peninsula, within several areas holding important populations of Little Bustard, namely north-eastern Iberia (Catalonia and Aragón), central Iberia (Madrid, Castilla-La Mancha, Castilla-León) and south-western Iberia (Extremadura in Spain and Alentejo in Portugal). In central and north-eastern Iberian areas, the agricultural landscape is dominated mainly by dry cereal farmland of varying degrees of intensification (Mañosa et al. 2015, Morales et al. 2015). Conversely, in south-western Iberia the landscape is characterised by larger fields and considerable amounts of grasslands, especially in Portugal (Moreira et al. 2012).

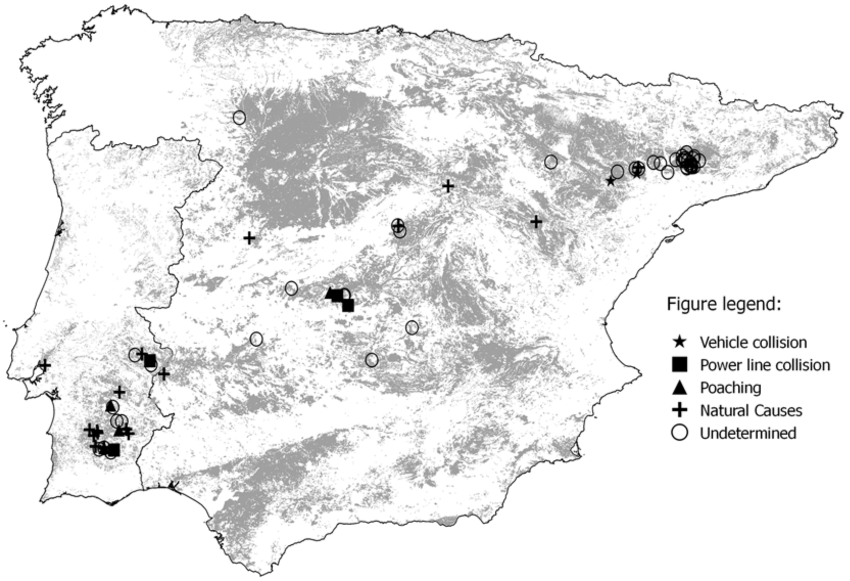
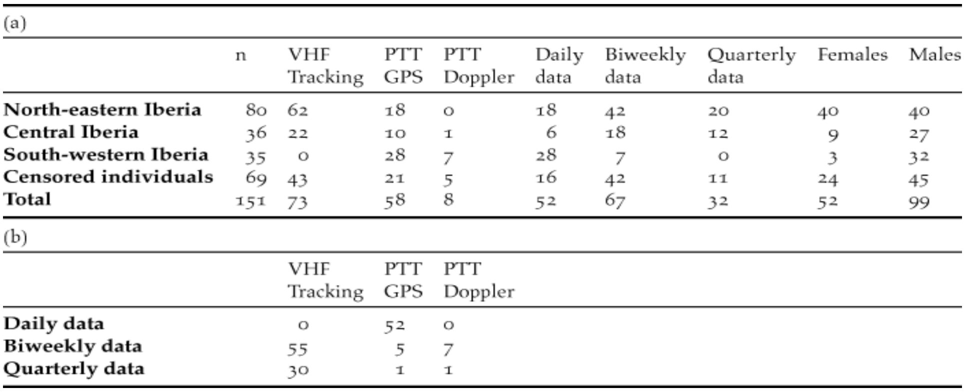


Figure 1 Symbols indicate the location of dead individuals recorded between 2001 and 2013 used in the cause-specific analysis. The areas in light grey represent the potential habitat for the Little Bustard, i.e. land uses most frequented by the species (Martínez, 1994, Silva et al. 2004, 2007, Morales et al. 2006b).

Table 1 (a) Number of birds, tracking methods, data frequency and sex per region; censored individuals. (b) Number of individuals per tracking method and data frequency.



(a)

	n	VHF Tracking	PTT GPS	PTT Doppler	Daily data	Biweekly data	Quarterly data	Females	Males
North-eastern Iberia	80	62	18	0	18	42	20	40	40
Central Iberia	36	22	10	1	6	18	12	9	27
South-western Iberia	35	0	28	7	28	7	0	3	32
Censored individuals	69	43	21	5	16	42	11	24	45
Total	151	73	58	8	52	67	32	52	99

(b)

	VHF Tracking	PTT GPS	PTT Doppler
Daily data	0	52	0
Biweekly data	55	5	7
Quarterly data	30	1	1

Data collection

We collected mortality data from 151 adult individuals that were tagged in several areas of the Iberian Peninsula (Figure 1) from 2001 to 2013. A total of 52 females and 99 males were tracked by different technologies in different areas: VHF tracking, PTT–GPS and PTT–Doppler, and with different data acquisition frequencies (Table 1). Life expectancy of the transmitters ranged between one and three years for VHF tracking and above three years for solar PTT–GPS and PTT–Doppler. For males, the capture was made with a stuffed female used as a decoy, with trap loops around it. Individuals that were attracted and fell into the traps were fitted with harnesses with transmitters attached. Females were captured with the funnel trap method (Ponjoan et al., 2010). In all cases the tracking device was fitted to the bird using Teflon ribbon harnesses (Kenward 2001). When a tracking signal was lost, or when the mortality sensor was activated or indicated immobility for a long period of time (Burnside et al. 2016), the individual's last position was field-checked. The individual's status was set to censor-ed (lost to follow-up) if no carcass, remains or transmitter were subsequently found, or when the tag reached the end of its functional time. In these cases, the individual was accounted as alive until the last day of appearance. Instead, if a carcass, a feather spot or a transmitter were located, the likely cause of death was assessed based on the signs found on the remains or the transmitter, combined with local evidence and the circumstances surrounding the place and time of death. Causes of death were categorised as human or natural. Anthropogenic deaths were classified as (a) collision with overhead transmission lines, if the bird was found near or underneath overhead transmission power lines with clear signs of trauma; (b) vehicle collision, if the carcass was found next to a road, with hard trauma injury, no evident signs of illegal killing nor near power lines; or (c) illegal killing, if the carcass was found with pellets or showing pellet wounds; transmitter with pellet impacts or Teflon ribbon showing pellet marks.

Natural deaths corresponded to predation events, and for most cases it was possible to distinguish predation by birds of prey from predation by mammals. In the presence of broken bones, or feathers still attached to the remains or without remaining feather quills, or even bite marks on the tag's plastic cover, the predator was presumably a mammal (Brown et al. 2003, Fraigneau 2008). In contrast, if the carcass was left whole, with feathers with remaining broken section quill around it, a bird of prey was the probable predator (Brown et al. 2003). In cases when there was information on whether the predated carcass was near a power line of road, the cause of dead was assigned to collisions with the latter, as many dead carcassses resulting from collisions are scavenged. If the cause of death was not clearly identified, it was set to "undetermined" or, in case of obvious signs of human manipulation (birds with Teflon ribbon cuts or manipulation or buried tags without signs of the carcass), to "undetermined with human manipulation".

Given that it is not always possible to distinguish between a transmitter failure/end of natural battery life or actual death, mortality rate estimation was carried out using two models: model 1 – where we followed the classification above and censored individuals were not considered to be mortalities (Pollock and Winterstein 1989) being accounted until the last day of appearance; and model 2 – where all censored cases were classified as undetermined deaths.

Because the Little Bustard in particular is susceptible to capture myopathy (Marco et al. 2006, Ponjoan et al. 2008), which can affect the bird's mobility up to 11 days after capture and consequently rendering it vulnerable to predation (Ponjoan et al. 2008), we only analysed mortality events that occurred after a first tracking period of 25 days to avoid confounding effects between natural death and capture myopathy. Our total sample of 151 tracked animals does not include those cases.

Data analysis

The date of death or disappearance was assumed to be the median time between the date of the last live record and the date when the carcass was found (range 0–67 days, mean = 2.32, SD = 8.97). Censored individuals were not considered to be mortalities (Pollock and Winterstein 1989) and were only accounted for until the last day of appearance.

Transmitter weight can influence animal mortality, and consequently affect the final study results (Wilson and McMahon 2006, Brooks et al. 2008, Casper 2009). Backpack transmitters, like those used in our study, fitted with a full harness, have the advantage of not affecting the bird's balance (Irvine et al. 2007). The medium weights of the backpacks (i.e. transmitter plus harness) was 4.54% (SD ± 0.69) of the weight of the bustards, therefore below the maximum recommended 5% of body weight for harness mounts (Kenward 2001). In order to evaluate if there was a bias effect of the tracking device weight on mortality, we carried out a Kaplan-Meier analysis (Kaplan and Meier 1958), and a Log-Rank Test (Harrington and Fleming 1982), to compare the distributions of the backpack weights.

Descriptive statistics were used to characterise the relative prevalence of anthropogenic and natural deaths in the adult population. The Heisey and Fuller estimator (Heisey and Fuller 1985) was used to compute annual mortality rates, i.e. the percentage of the population that died each year due to each type of causal factor. When extended for multiple causes of death, the Heisey and Fuller estimator states that the daily mortality rate due to a particular death cause (j) is the probability that an animal alive at the beginning of a day in interval i dies during the day due to this cause. The maximum likelihood estimator of this probability m_{ij} is the number of deaths in interval i due to cause j (y_{ij}), divided by the total number of transmitter days in the interval (x_i): $\hat{m}_{ij} = y_{ij}/x_i$. The probability that an animal dies from cause j during the interval i

(M_{ij}) is the sum of the probabilities that it survives to a particular day, and then dies on that day from cause j. This result is expressed as:

$$M_{ij} = m_{ij} + s_i m_{ij} + s_i^2 m_{ij} + \ldots + s^{(L_i - 1)} m_{ij} = \left(\frac{m_{ij}}{1 - s_i}\right)\left(1 - s_i^{L_i}\right),$$

where s_i is the daily survival rate for the interval and L_i is the length in days of interval i. This estimator was computed using the software MICROMORT 1.3 (Heisey and Fuller 1985).

Results

Out of the 151 tracked individuals followed over a total of 76,182 radio-tracking days, and after censoring individuals whose transmitter stopped working, we recorded 82 mortality events and 69 censored individuals that entered the analysis - a summary of the data is presented as a Kaplan-Meier survival curve (Figure 2). Cases of possible failed transmit-ters were a small percentage (8.6%). Predation was responsible for 26% of the total recorded mortality. Birds of prey were the main predators identified, with a prevalence of 55.6%, while mammals were responsible for 38.9% of predation events. Cases classified as natural deaths but for which it was not possible to recognize the type of predator corresponded to 5.6%. Anthropogenic death causes repre-

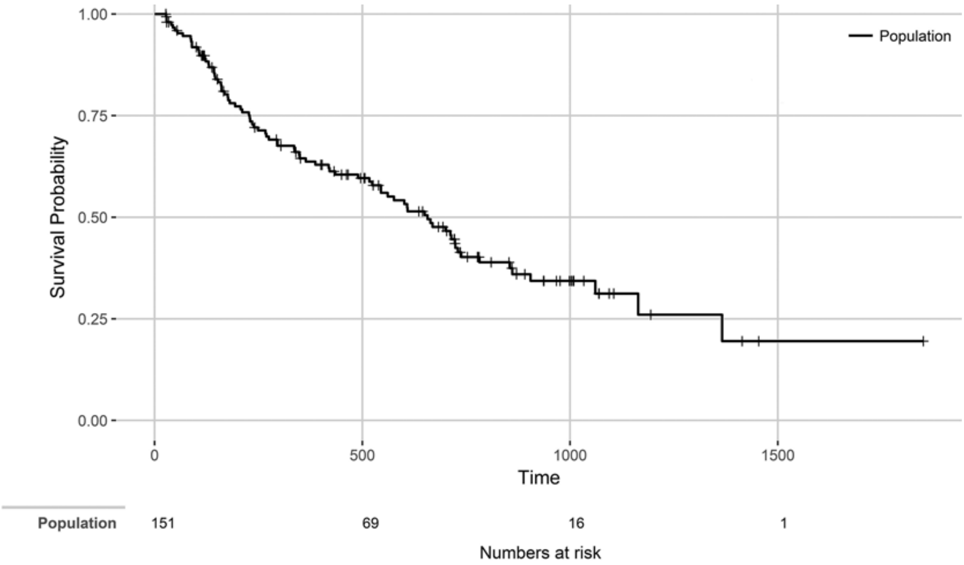
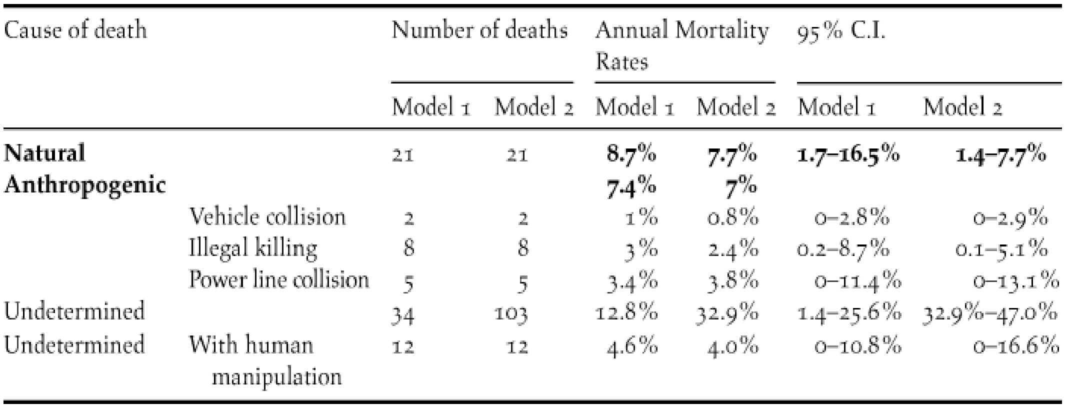


Figure 2 Plot of Kaplan-Meier product limit estimator of survival for the 151 Little Bustards with 82 mortality events. Time is displayed in days and the number of birds at risk at day 0, 500, 1000 and 1500 is represented below.

Table 2 Annual cause-specific mortality rates and 95% confidence intervals estimated using Heisey and Fuller method (1985) for adult Little Bustards *Tetrax tetrax* in the Iberian Peninsula. Annual rates were computed based on a 12-year period (2001–2013).



Cause of death		Number of deaths		Annual Mortality Rates		95% C.I.	
		Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Natural		21	21	**8.7%**	**7.7%**	**1.7–16.5%**	**1.4–7.7%**
Anthropogenic				**7.4%**	**7%**		
	Vehicle collision	2	2	1%	0.8%	0–2.8%	0–2.9%
	Illegal killing	8	8	3%	2.4%	0.2–8.7%	0.1–5.1%
	Power line collision	5	5	3.4%	3.8%	0–11.4%	0–13.1%
Undetermined		34	103	12.8%	32.9%	1.4–25.6%	32.9%–47.0%
Undetermined	With human manipulation	12	12	4.6%	4.0%	0–10.8%	0–16.6%

sented 18% of the detected mortality events. Illegal killing was the most common source of anthropogenic mortality (10%), followed by power line collision (6%) and vehicle collision (2%). Undetermined mortality corresponded to 57% of the mortality cases.

Using the Heisey and Fuller estimator, the estimated overall annual survival rate was 66.5% (C.I. 95%: 48–82%) for model 1 and 48.3% (C.I. 95%: 32–66%) for model 2. Annual cause-specific mortality rates are presented in Table 2. Both models produced similar results for cause-specific mortality rates - the yearly mortality rate of Little Bustards due to anthropogenic causes was 7% while 8% died from natural causes. Power line collision represented 3.4–3.8% of population deaths, followed by illegal killing (3–2.4%) and vehicle colision (1–0.8%) (Table 2). The estimates presented above correspond to model 1 and model 2, respectively. The Log-Rank Test did not detect a statistically significant relation between mortality and the weight of the tracking device ($\chi^2 = 0.6$, df = 1, $P = 0.436$).

Discussion

This is the first time that mortality rates of adult Little Bustard were estimated based on a relatively large sample of tagged birds. Previous estimates, used for the development of demographic models in France, were based on resighting data of colour-ringed birds (Inchausti and Bretagnolle 2005), and might therefore be subject to different sorts of biases. This new dataset is particularly important since it relates to the species’ stronghold in Europe, contributing to an assessment of its global conservations needs.

Animal tracking allowed us not only to estimate mortality rates, but also to obtain some information on the causes of death. Although we were not able to determine with absolute certainty the cause of death of many birds, the evidence was usually enough to assess the most probable cause of death and, at the very least, to distinguish between anthropogenic and predation-related mortality. The fact that we did not find any significant effect of the weight of the transmitters on the survival of the tracked Little Bustards, indicates that our results were not affected by the tagging protocol. Although with the current tracking equipment, failure is not common, it does occur. We were not able to distinguish between possible transmitter failure and natural end of battery life and both situations were treated as censored cases. In any case, when censored data were classified as mortality by unknown causes, they yielded similar mortality estimates compared to model 1, showing that possible undetermined censored data did not represent a source of bias in the analysis. White and Garrott (1990) refer that a low number of possible transmitter failures will not influence the analysis. Premature cessation of transmission (defined by us as < 365 days) occurred in 13 cases (8.6%).

Here we adopted a simple approach to distinguish anthropogenic from natural mortality. It is also important to note that we are assuming that the identification of the causes of death is reliable, even though it is a probable cause of death, in the absence of necropsy. In addition, we also assume that the probability of detecting anthropogenic death is the same as of detecting natural death.

We estimated an overall annual survival rate of adult Little Bustards of just 67%, similar to the 68–72% estimated for western France when the population was declining between 1998 and 2003 (Inchausti and Bretagnolle 2005). It is also lower than in other vulnerable Eurasian bustards: Great Bustard *Otis tarda* with 90% (Palacín et al. 2017) and Houbara bustard *Chlamydotis undulata* with 75–86% in non-hunting areas (Hardouin et al. 2015). As lower confidence intervals seem highly unlikely to represent the reality of the Little Bustard's survival rates, the upper confidence intervals of both models in terms of annual survival rate (model 1: 82% and model 2: 66%), probably indicate the best-case estimates for the survival of this species. Given that only 54% of the chicks seem to survive to become adult (Schulz 1987), the overall annual population mortality (considering both juvenile and adult together) is likely to be higher. Productivity is a key demographic parameter for the viability of animal populations. A productivity of less than one fledging per female a year could lead to a decline in the Little Bustard population of 15% a year (Bretagnolle et al. 2011). Other factors are likely to worsen this scenario in areas with more intensive agriculture, such as low productivity (Bretagnolle et al. 2011, Lapiedra et al. 2011), or a biased sex ratio towards males (Inchausti and Bretagnolle 2005, Morales et al. 2005a, 2008), that may result in a decrease in productivity due to female shortage (Tarjuelo et al. 2013). Morales et al. (2005a) used simulations to show that in declining populations like those in western France, adult survival values close to 70% result in population survival probabilities of 60%, a low value for a species with "Near Threatened" classification. Additional analyses are needed to assess how this level of mortality could be affecting the Iberian Peninsula population dynamics.

Anthropogenic mortality of the Iberian Little Bustard population was, surprisingly, almost as high as the annual mortality recorded by predation. These high estimated mortality rates are consistent with the species' overall declining trend (Morales et al. 2015).

Power line collision was the main anthropogenic cause of mortality identified in both models, estimated to cause the death of 3.4% (model 1) and 3.8% (model 2) of the population, yearly. These values could reach up to 11.4% and 13.1% in the highest intervals of model 1 and model 2, respectively. A comparison with previous studies (Infante et al. 2005, Jenkins et al. 2010, Silva et al. 2010) shows that the annual rate of mortality due to collisions with power lines is one of the highest ever recorded for a particular species. Previous estimates of mortality caused by linear infrastructure are based on counts of Little Bustard carcasses found next to power lines or roads, and may thus be biased by factors like removal by scavengers, difficult detection and limited search area

(APPLIC, 2012). Survival analysis using tracked birds provide more robust estimates of mortality rates as it is subject to fewer biases (e.g. Naef-Daenzer et al. 2017).

Illegal killing was identified as the second main threat to Little Bustard's survival, with an estimated annual mortality rate of 2.4 (model 2) and 3% (model 1) by this cause. These values could reach up to 8.7% in the highest interval of the most conservative model. Even though this threat was identified as important by Iñigo and Barov (2010), its importance has never been quantified. There are few references to Little Bustard hunting tradition or illegal killing in Iberia (Smith 1868), in contrast to other Otididae species such as the Great Bustard or Houbara Bustard, for which there is a long and well documented hunting tradition (Palacín and Alonso 2009, Sehhatisabet et al. 2012, Brochet et al. 2016). In fact, hunting and illegal killing have been identified as one of the main negative factors affecting the population viability of both species in areas of North Africa and Asia (Tourenq et al. 2005, Alonso et al. 2005), in spite of legal protection of the Great Bustard in Morocco.

As regards predation, even though birds of prey were responsible for most of the identified cases, it was not possible to ascertain statistically if they were more important predators than mammals. However, it should be noted that the Little Bustard in Iberia is depend-ent on man-made landscapes and farming practices. Changes in landscapes or how these habitats are managed can play a decisive role in the rate of predation (Whittingham and Evans, 2004). For example, overgrazeed pastures may lead to birds being more exposed to predation due to reduced vegetation cover. Also, more intensified irrigation crops may lead to higher rates of disturbance and, finally, increased urbanisation of the rural landscape may promote increasing numbers of human-associated predators. Therefore, our designated "natural" mortality may be highly dependent on how the habitat is being transformed and/or managed.

Our work shows how poorly understood and previously unknown threats are affecting the survival of the most important Little Bustard population of Western Europe. Reducing anthropogenic mortality can thus have a major positive impact on the species' viability, particularly for populations that show low breeding productivity (Lapiedra et al. 2011, Bretagnolle et al. 2011). Anthropogenic deaths seem to have higher importance than what was initially foreseen in this species. Low awareness of the species' conservation status amo-ng hunters is a problem, and the unfavourable population trends should be better communicated. The unexpectedly high impact of collision with power lines high-lights the importance of adapting the overhead electric power line network to conservation needs. This may include the relocation of existing hazardous power lines and the routing of new ones away from areas with greater collision risk (Silva et al. 2014). New power line designs that minimise collision risk, should also be considered, includ-ing underground cabling (Raab et al. 2012, Silva et al. 2010, 2014, Barrientos et al. 2012, Alcazar 2013). Legislation should be drawn up at national level to ensure the integration of these preventive measures into the design of new power lines nationwide and not limited to the Natura 2000 netwok.

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INCUBATION BEHAVIOR OF THE LITTLE BUSTARD (*TETRAX TETRAX*) HENS: NEST SITE, INCUBATION PATTERNS AND HATCHING SUCCESS

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The viability of little bustard (*Tetrax tetrax*) populations has been shown to be particularly sensitive to breeding rates. However, little is known about the reproductive biology of hens and their requirements during the breeding season. In 2010-2016, we monitored 28 clutches of eight little bustard females tracked by GPS in the Ebro Depression (NE Spain) with the objective of elucidating those essential factors concerning the incubation behavior of this species. In addition to describing the incubation pattern, we evaluated the factors that determine the hatching probability (by generalized linear mixed models) and the risk to fail by unit of time (by Cox models with mixed effect) as a function of breeding timing, nest habitat and incubation behavior. Overall, nest failure accounted for 67.9% of clutches, influenced by the low hatchability of replacement clutches (16.7%). Farming practices accounted for 36.8% of nest failures. The main cause of failure was nest desertion/predation (58%). The increased risk to fail by desertion/predation towards the end of incubation may indicate that nest desertion/predation may be facilitated by other factors, such as hen exhaustion. Laying date had a negative effect on the hatching probability of clutches and on the risk to fail among first clutches. The size of nesting field (negative effect) was the most important predictor for the hatching probability, but the home-range size (positive effect) also contributed to this. Measures aimed at improving food provision by increasing field edge density and fallow availability may facilitate hens to keep body-

condition prior and during incubation, as well as providing suitable habitat for replacement clutches. Adaptive irrigation and mowing patterns in alfalfa fields during the nesting season would also contribute to increase the hatchability of replacement clutches.

Cuscó, F., A. Llovet, G. Bota, S. Mañosa. 2018. Incubation behavior of the Little Bustard (*Tetrax tetrax*) hens: nest site, incubation patterns and hatching success. (*In preparation*).

Introduction

Incubation is a critical process in the reproduction of birds, allowing for the correct development of the embryo. It involves the provision of suitable temperature and humidity conditions to the eggs, as well as protection against predators or adverse weather conditions (Deeming 2002). It is a very demanding activity involving high costs for the incubating birds (Williams 1996, Monaghan and Nager 1997), which have to care and protect the nest and the eggs as well as satisfy their own needs, mainly feeding, at the same time. This may involve leaving the nest unattended for some periods of time which may entails risk to the eggs (see Inglis 1977, Conway and Martin 2000). To reduce this constraint, incubation is often shared by both members of the pair or, if only one incubates, the mate provides food and vigilance for the incubating partner. But this is not the case for some species, in which care of the eggs and young is conducted solely by a single bird, which has to incubate and satisfy its own needs at the same time, without any help. For these species, the incubation phase might be still a more critical period in the reproduction cycle as it already is for the majority of birds.

The Little Bustard (*Tetrax tetrax*; Linnaeus, 1758) is one of such bird species. It is a medium sized steppe bird of Palearctic distribution (Del Hoyo et al. 1996), inhabiting both natural steppes as well as cultivated areas and pastures (Morales et al. 2005a, Silva et al. 2010). It is a polygynous lekking species in which males do not provide any sort of parental care (Jiguet et al. 2000) and incubation is conducted solely by the female. The nest is a simple depression on the ground garnished with dry grass (Boutinot 1957), located among low herbaceous vegetation, often in fallow or arable fields. In the Iberian Peninsula the clutch, usually of 3–4 eggs (Cramp and Simmons 1980, Shlyakhtin et al. 2004), is laid in late April–May. Effective incubation probably begins before the last egg is laid and the clutch is incubated for 20–22 days. Although after nesting failure hens are able to lay replacement clutches, these clutches have been described as infrequent (Lapiedra et al. 2011, Bretagnolle et al. 2018). Chicks are precocial and are cared by the female alone (Cramp and Simmons, 1980).

Nowadays, the Little Bustard is experiencing a rapid decline in the Western area of its distribution range, mainly due to habitat loss and degradation by agricultural intensification and infrastructures development. However, poaching effects and bird collisions with power lines have also been described as threatening factors (Iñigo and Barov 2010, BirdLife International 2016, Marcelino et al. 2017). Although the current status and trends of Eastern populations is uncertain, the rapid reduction of European populations is alarming enough to list the species as "Vulnerable" in Europe and "Near Threatened" at a global scale (BirdLife International 2016, Collar et al. 2017).

The specific processes linking agricultural intensification and population decline in this species are surely complex and multifactorial. Research conducted in Western France (Bretagnolle et al. 2011) and Northeastern Spain (Lapiedra et al. 2011) indicates that breeding success is below the demographic viability threshold (Inchausti and Bretagnolle 2005, Morales et al. 2005b) in both populations. In the intensive farming systems of Western France, low breeding success has been attributed to nest destructtion during harvest operations (Bretagnolle et al. 2018), as well as to brood losses associated to low abundance of arthropods (Inchausti and Bretagnolle 2005, Bretagnolle et al. 2011), which are essential for chick rearing (Jiguet 2002). In the cereal pseudosteppes of Northeastern Spain, lack of adequate cover and shortage of food has also been found responsible of high chick mortality, but only a minor proportion of the losses taking place during the incubating phase were attributed to the direct effect of harvest operations or other farming activities (Lapiedra et al. 2011). Many incubation failures have been recorded before harvest in this area, which might suggest that some internal or external factors affecting the incubation behavior of the hens, facilitating high levels of desertion or predation, precludes the correct outcome of incubation.

The aim of this study was to describe the incubation behavior of the little bustard hens and to explore whether the analysis of the timing of breeding, the nest location and substrate and the incubation behavior can give some cues on the factors explaining the high levels of clutch losses reported in the study area. With this purpose, we modelled the hatching probability and the risk of failure by unit of time in an attempt to determine the mechanisms linked with clutch survival, in order to better explain the factors affecting the final reproductive outcome.

Methods

Study area

The study was based on the monitoring of female little bustards which were captured and equipped with GPS transmitters in the Secans de Belianes–Preixana SPA (Special Protection Area; Fig. 1), NE Iberian Peninsula, in 2009−2013. Subsequent nesting attempts of tagged hens were followed from 2010 to 2016. Most nests were situated in the Secans de Belianes–Preixana, but some were distributed on a wider region within the Ebro Depression (Fig. 1). Nest location latitude and longitude ranged from 41.39 – 41.85º N and 0.67º W – 1.03º E, respetively, and altitude ranged from 164−489 m a.s.l. The climate of the area is Mediterranean with continental characteristics in most of the basin and semiarid in the center of the depression (Romaní et al. 2011).

The Secans de Belianes–Preixana SPA (41.59º N, 0º 59’ E) is ranked as an important area for the conservation of birds in Spain, mainly for the relevance of its steppe bird populations (Traba et al. 2007), notably for the Little Bustard, which reaches densities of up to 6 males/ km^2 (Tarjuelo et al. 2017). The area occupies an expanse of 6,519 ha and it is dominated by a pseudosteppe of winter cereal crops, mainly barley, but also wheat and some fallow fields (< 10% of cultivated land). In this area, the traditional 2−year rotation cycle for cereal crops has almost disappeared completely due to a farmland intensification process and the use of chemical fertilization. Most existing fallow land is left as compulsory countervailing actions of the Segarra−Garrigues irrigation project and of the pit-gravel industry. West to the area there is a wide expand of irrigated land dominated by maize, alfalfa and orchards. Although most of nests were located in the Secans de Belianes–Preixana SPA, some hens nested in other nearby rainfed farmland SPAs, such as Secans del Mas de Melons−Alfés (7,617 ha) and Secans del Segrià i Utxesa (7,718 ha), both in Lleida plains, or in the vicinity of the Sierra de Alcubierre SPA (42,108 ha) in the Monegros (Fig. 1). Cereal harvest usually starts in early June in the study area.

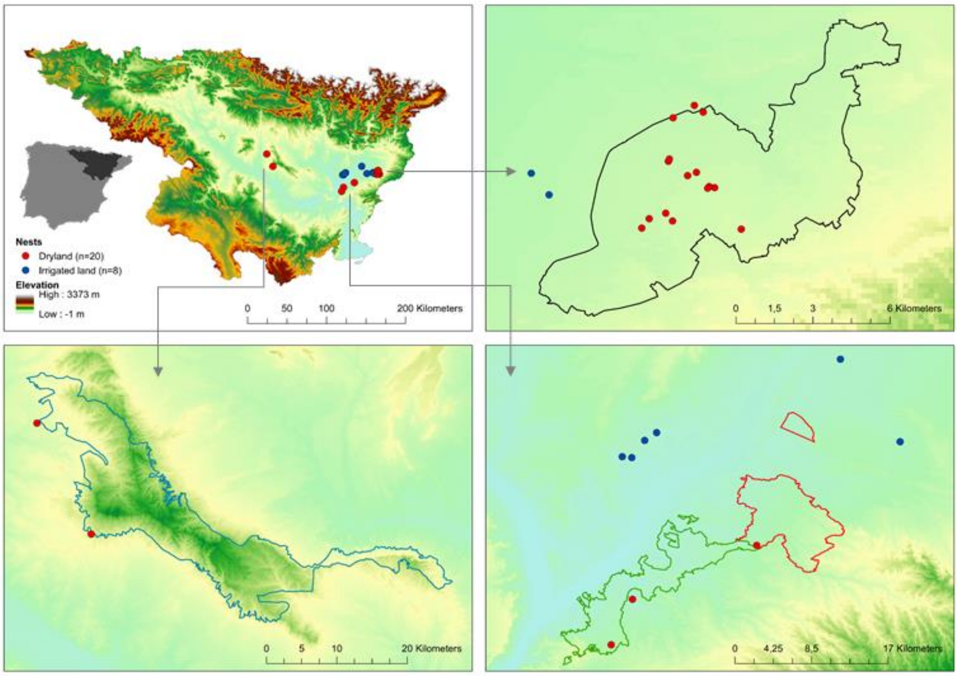


Figure 1. Study area. Digital elevation model (DEM) with a resolution of 200 m of the Ebro Basin in Iberian Peninsula (top-left). Boundary delimitation of ZEPAs: Secans de Belianes–Preixana in black (top-right), Sierra de Alcubierre in blue (bottom-left), Secans del Segrià i Utxesa in green and Secans del Mas de Melons–Alfés in red (bottom-right). Clutches occurring in rainfed farmland are shown in red and clutches occurring in irrigated farmland in blue.

Capture and monitoring

Between 2009-2013, 18 little bustard hens were captured using funnel traps as described by Ponjoan et al. (2010). This method was specially designed to capture hens and it has been reported to perform better than previous methods both in terms of efficiency and animal welfare. All hens were tagged with 22 g Solar Argos/GPS PTT–100 transmitters (Microwave telemetry). The relationship between the weight of the transmitter and the weight of hens (646 ± 63 g; mean ± SD; range: 522–760 g) never exceeded the 5% safety threshold for harness mounted tags and rings (Kenward 2001). Capture and handling of hens followed the recommendations of Ponjoan et al. (2008) and no capture myopathy occurred following capture and release. As captured hens were females with offspring, gathering data on incubation behavior could only start in successive breeding seasons, in years 2010–2016. Only in one case, a replacement clutch

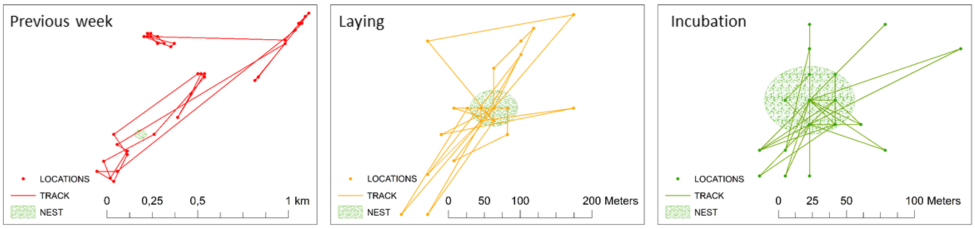


Figure 2. Fixes and movement patterns of a hen little bustard during breeding season (PTT-34175; clutch Id 11). We distinguished 3 stage: previous week, laying and incubation stage. The previous week was defined as the period occurring seven days before the first visit to the nest. Laying stage as the period between the first visit to the nest until the hen sits to incubate. And incubation stage was defined as the period from the laying of the last egg in a clutch to the hatching of the first chick.

was monitored after the loss of the brood on the same year of capture (PTT–33139, 2010). For each transmitter, we obtained up to 6 diurnal fixes daily (± 18 m Lat/Long GPS accuracy; maximum error: $\sqrt{(18^2+18^2)} = 25$ m) between 5:00 – 22:00 hours GMT (Greenwich Mean Time). Fixes were provided on a regular grid of $0.0001\hat{6}$ degrees.

Incubation patterns and nest attendance

We analyzed the behavior of the hens during the laying period (from laying of the first egg to the start of incubation) and during the incubation period (from the start of incubation to hatching or failure). In order to avoid disturbances, we never tried to flush the hens, so the exact location of the nests was not determined. The start of laying and the nest-point were determined from GPS fixes, as they concentrated around a central point, assumed to be the nest, drawing a star-shaped movement pattern. The onset of incubation (Julian date) was estimated based on an increase of the nest attendance and hourly differences in the attendance pattern (see nest attendance in Results section). Nest attendance for each period and clutch was determined as the percentage of fixes in which the hen was considered to be in the nest in relation to the total number of fixes. Females were assumed to be on the nests if they were located on the central point (usually with the highest frequency of fixes) or in the immediate surrounding points (Fig. 2). Considering that all fixes are referred to daytime period, there may be a certain bias in nest attendance on a 24 h basis (probably underestimated), since we would expect a higher attentiveness overnight in order to avoid the cooling of eggs.

Hatching success and causes of nest failure

Clutch fate (hatched or failed) was evaluated once data provided by GPS fixes indicated that a hen did not return to the nest anymore. At that point, we tried to locate the nest and to find evidences on the potential nest outcome. We considered that a clutch was successfullly hatched if chicks were observed or if, after 19.5 days of incubation (minimum time a clutch was successfully hatched in our study), the movement pattern of the hen suggested that it was accompanied by chicks (see Lapiedra et al. 2011). Alternatively, we considered a nest as failed if it was abandoned before 19.5 days of incubation or, if abandoned shortly later, the female movements (distance covered) were incompatible with the existence of chicks. In this case, we tried to determine the cause of failure. If we found clear signs of recent agricultural activities on the nest field, such as cereal harvest, alfalfa mowing or field irrigation, we assumed the nest was abandoned or destroyed because of the farming practice. If no sign of farming practices was noticed and the eggs were found broken with yolk remains, some eggshells out of the nest or ticking signals, we assumed the nest has been deserted or depredated. However, it was impossible to ascertain whether predation occurred during incubation or after desertion, so desertion and predation were clumped in the analysis on a single cause category ("natural causes").

Ranging behavior

Home ranges were defined as the 100% Minimum Convex Polygons, and were calculated for the week previous to laying (PRE_MCP), the laying period (LAY_MCP), the incubation period (INC_MCP) and the laying+incubation periods together (TOT_MCP). We also delineated the 80% MCP for the laying and the first week of incubation together (80L1_MCP) as a measure standardized by time. Home-range eccentricity for the laying and for the incubation period were calculated by obtaining the geometric center of the home-range (defined by LAY_ MCP or INC_MCP) and dividing the distance between the centroid and the nest by the distance-between the centroid and the farthest point of the home-range.

Habitat selection

We measured the proximity of every nest to the field edges (m), the size of the field where the nest was located, and the index of electivety (Ivlev 1961) of the selected nesting habitat *vs* the total available habitat. For the nests occurring in cereal, we also calculated nest proximity to the nearest fields with permanent or semi-permanent herbaceous vegetation (i.e. fallows, legume fields, unplowed almond/olive cultivations), henceforward called HVF. Spatial nest location was compared with random distribution points in relation to field edge proximity (all clutches) and to HVF (only for cereal clutches). For edge proximity we generated 100 points distributed randomly within each nest field and for distance to HVF we selected 100 random points within a 300 m buffer around each nest. In both, we compared nest distances and random distributions by a Kolmogorov-Smirnov test.

To evaluate habitat selection and habitat preferences of hens in off-nest bouts during the laying and the incubation, a compositional analysis (Aebischer et al. 1993) was performed. This method highlights whether the utilization of habitat types is disproportionate in relation to its availability or whether habitat is used randomly. For this, the method compares log-ratios between the used and the available habitats, measuring the disproportionality between them at individual level. In our study, habitat use and its availability was calculated for each of the clutches. We performed a third-order habitat selection analyses where fixes were used to determine the utilization of different habitat types and the proportional areas of each habitat within the home-range (TOT_MCP) as a measure of habitat availability (Johnson 1980). In a third-order habitat selection, zero values could be found in the matrix of available habitats. So, in some clutches, some habitat types could not be used by the hens. Under these conditions, a randomization test, which compares a matrix containing the mean difference between the used and available log-ratios, is needed. In this procedure, weighted mean lambda (λ) is used instead of the usual Wilk's λ. If a habitat type was available but not used by the hen, we replaced these 0 values in the utilization matrix by a small positive value (0.01%) in order to obtain a valid log-ratio transformation (Aebischer et al. 1993). Fixes located at lower distance than 4 meters to a field edge were assigned as to be in the field edge, since edges act as source of weed propagules, exerting a greater influence in the first meters of their vicinity, both at abundance level and number of species (Wilson and Aesbischer 1995).

Considering that home-range size commonly increases with number of fixes before reaching an asymptote (Seaman et al. 1999, Powell 2000), that some clutches failed prematurely and that not always an asymptote was reached, certain biases related to sampling effort may occur. In order to avoid these possible biases, we estimated the number of fixes for which most of home-ranges reached an asymptote (Harris et al. 1990). Thus, we selected only home-ranges (TOT_MCP) with a minimum of 20 off-nest fixes for the compositional analysis (n = 22). Additionally, to test differences in habitat selection related to the nesting habitat this analysis was also performed for only clutches occurring in dryland (n = 16) and for only clutches occurring on cereal (n = 13).

Factors affecting incubation behavior

We explored the relationships between nest attendance, home-range size (80L1_MCP) and food availability around the nest. Because home-range estimation increases as more days are considered, we restricted these analyses to the laying stage and the first week of incubation for the 23 clutches for which we had complete information for this period. Food availability was measured as the percentage of HVF + Field Edges within 300 m buffer around the nest. This buffer encloses 91% and 98% of off-nest fixes during the laying and the incubation periods, respectively, for the global of the clutches.

Nest survival analysis

We calculated the probability of clutch survival by means of a Kaplan-Meier estimate and confidence intervals for the set of clutches, comparing first and replacement clutches, and for those clutches that were hatched or failed by natural causes. The Gehan’s test, a generalization of the Wilcoxon rank sum which allows for censored data, was used to prove if the risk of failure changed along the incubation stage (i.e., by comparing the risk to fail between the two halves, first half and last, of incubation stage). This analysis was also conducted for first clutches that did not fail by agricultural causes.

The analysis of the factors that explained hatching success was conducted through generalized linear mixed models (GLMMs) with binomial error structure and logit link function. Female and year factors were included to the models as random effects. Preliminarily, we performed univariate models explaining hatching success in relation to the timing of breeding, habitat, and behavioral patterns (see Table S1 in Appendix 1 for the description of predictors used in univariate analysis). To avoid high correlation ratios among predictors, we selected those predictors that were not affected by multicollinearity through the variance inflation index. Finally, five predictors were retained for more complex models: the laying date, the size of the nest field, the 80% home-range of the laying and the first week of incubation (80L1_MCP), the mean size of the fields within 300 m of the nest, and the land use richness in a 300 m buffer around the nest.

Additionally, the hazard rate to fail (i.e., rate of clutch lost per day since laying started) was investigated by Mixed Effects Cox models with random effects, including same predictors and random structure as in GLMMs. These models had the advantage of predicting the hazard rate over time as a baseline of risk (Therneau 2015).

Model selection was based on a multi-model inference approach for both sets of models (GLMMs and Cox models). This implied building models by combining the different selected predictors. Once models were generated, we ranked them according to the Akaike's Information Criterion corrected for small samples (AICc) and a probability of being the best model was computed (w_i) (Burnham and Anderson 2002). Final models were then calculated as averaged values of models receiving higher support (models within the 90% probability of cumulative w_i). In hatching probability model averaging, estimates were standardized based on partial standard deviations to avoid scale problems across models (Cade 2015).

Statistical analysis were carried out using the following packages of the R v.3.4.2 software (R Development Core Team 2016): 'survival' for Kaplan-Meier estimates (Therneau and Grambsch 2000), ‘adehabitat’ for compositional analysis (Calenge 2006), ‘lme4’ for generalized linear mixed models (Bates et al. 2015), ‘coxme’ for mixed effect Cox models (Therneau 2015) and ‘MuMIn’ package for model averaging (Barton 2017).

Results

From a total of 20 breeding opportunities (i.e. GPS tagged hens alive at the start of each breeding season from 2010-2016), laying was initiated in 16 and it was not in three of them, corresponding to two different hens. In another case, the start of laying could not be determined with certainty, giving a global laying rate of 84% (n = 19). Hens were able to lay up to three different clutches in a same breeding season after nest lost during incubation or immediately after hatching. In total, we managed to monitor 28 clutches from eight of these females, corresponding to 16 first clutches, 8 second clutches and 4 third clutches (Appendix 2). The replacement rate was 67% for first clutches that failed during incubation (n = 9) and 57% for failed second clutches (n = 7). No third fail-ed clutch (n = 3) was replaced. Fled-glings (>30 days old chicks) were produced only in 2011 (five fledglings, 0.83 chicks/laying hen, n = 6), giving an average of 1.67 chicks per successful hen (n = 3), 0.31 chicks/ laying hen (n = 16) and 0.25 chicks/ hen (n = 20) for all considered years. Globally, nine broods were produced of which only three (33%) survived to fledgling.

Timing of breeding and nest site selection

Considering all 28 clutches, laying occurred between 17 April and 13 July. First clutches (n = 16) took place in dry farmland between 17 April and 22 May, 12 in cereal and 4 in fallow. Second clutches (n = 8) were initiated between 15 May and 13 July and occurred both in the dry pseudoesteppe (n = 4) or in alfalfa fields within the irrigated farmland area (n = 4). Finally, third clutches (n = 4) took place between 2 and 18 June, always in alfalfa fields in the irrigated farmland (Fig. 3a; Appendix 2). Time to replace a lost nest was 5.0–18.8 days (9.6 ± 4.0, n = 12). Distance between consecutive nests of a hen during a breeding season ranged from 0.2–100.7 km (median: 5.3 km of 11 nest comparisons). Distance between first clutches of a hen in consecutive years ranged from 0.2 to 133.7 km (median: 3.3 km of 8

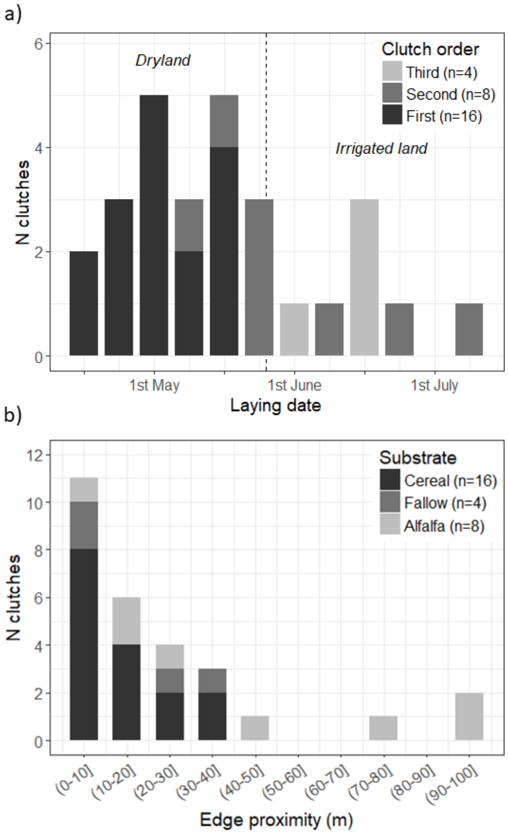


Figure 3 Incubation behavior of hen Little Bustard based on 28 clutches in the Ebro Depression: a) Timing of laying depending on the clutches sequence. Time is shows by weeks; b) Edge proximity of nests. The graph shown the number of clutches by distance classes (10 m intervals) to the nearest field edge.

comparisons). And distance between the last clutch of a hen occurring in dryland and the first clutch of the next breeding season ranged from 0.0 to 142.9 km (median: 3.0 km of 8 comparisons). Finally, successive clutches between dryland and irrigated land in a breeding season ranged from 4.0 to 100.7 km (median: 21.7 km of 6 comparisons) (Appendix 3).

In dry farmland, hens showed a stronger positive selection to nest in fallow fields (Ivlev's electivity index = 0.21) than in cereal fields (Ivlev's electivity index = 0.11). In irrigated farmland, alfalfa was positively selected (Ivlev's electivety index = 0.38, Figure S4 in Appendix 4). Nests were located at 23.6 ± 25.3 m (mean ± SD) to the field edges (Fig. 3b), but they were not distributed differently than random points (D = 0.146, *P* = 0.598). Distance to field edges showed significant differences between substrates (ANOVA; F = 5.697, *P* = 0.009). According to Bonferroni post-hosc test, clutches in cereal occurred closer to the field edges (13.5 ± 10.1 m, n = 16) than clutches in alfalfa (45.2 ± 37.1 m, n = 8) (*P* = 0.007). No significant differences were found between clutches occurring in cereal or fallow (21.2 ± 14.6 m, n = 4), nor between clutches in fallow and alfalfa. However, clutches in cereal fields (n = 16) were not closer to edges than random points (13.5 ± 10.1 m) (D = 0.108, *P* = 0.993). Clutches in cereal were located between 1.8–402.9 m (116.5 ± 104.1 m, n = 16) from HVF, but this was not different

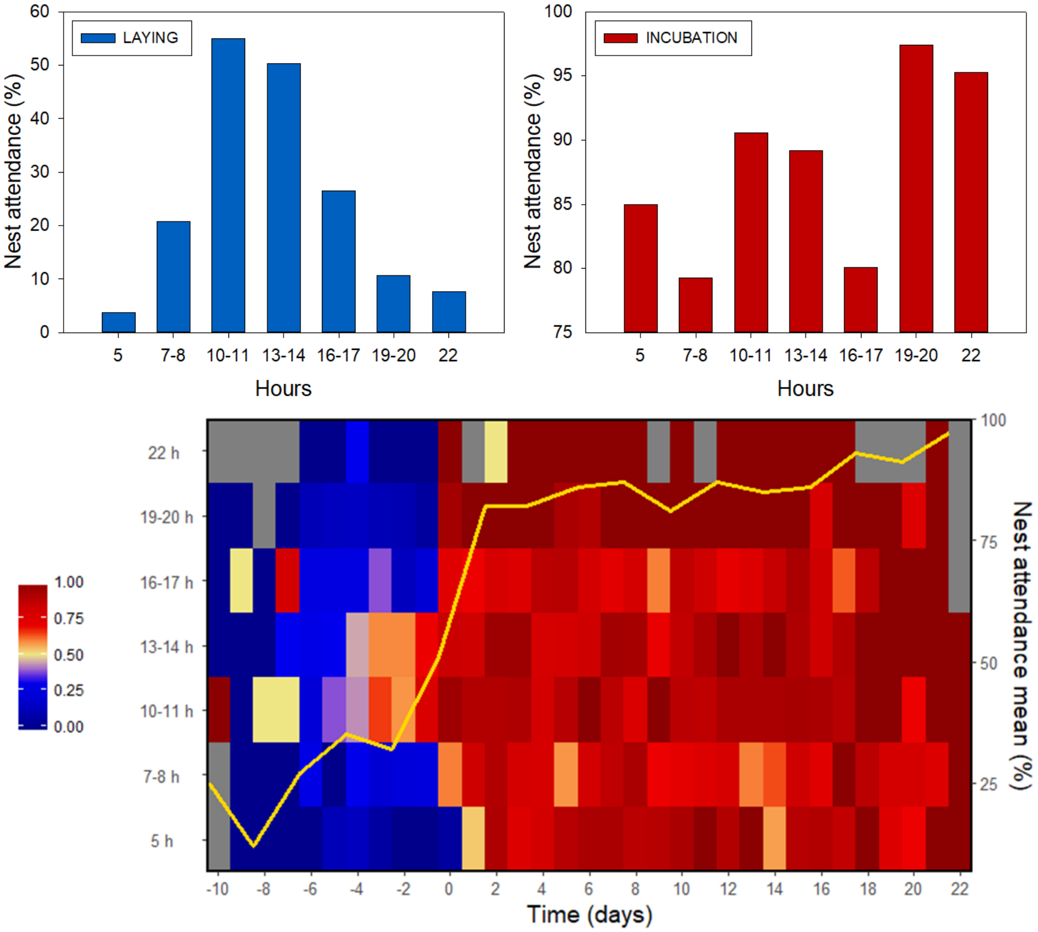


Figure 4. Frequency distribution of nest attendance of laying (top-left) and incubation stage (top-right) for each hour interval. Below, actogram of nest attendance pattern (bottom) based on frequency distribution of nest attendance by hour range (main axis). Nest attendance mean is represented on a bi-daily basis (secondary axis). Incubation start is centered at time 0 (horizontal axis) and negative values refer to laying stage. The time is shown as GMT (Greenwich Mean Time). Spanish time during summer equals to GMT+2. No available data are presented in white rectangles.

from random (D = 0.223, *P* = 0.409). Field size showed a marginal trend toward significant differences between substrate type (4.1 ± 5.3 ha, n = 28) (F = 3.198, *P* = 0.058).

Laying and incubation length

Laying lasted for 4.9 ± 1.8 days and was similar for first clutches (5.3 ± 1.8 days, n = 16) and replacement clutches (4.3 ± 1.6 days, n = 12) (F =

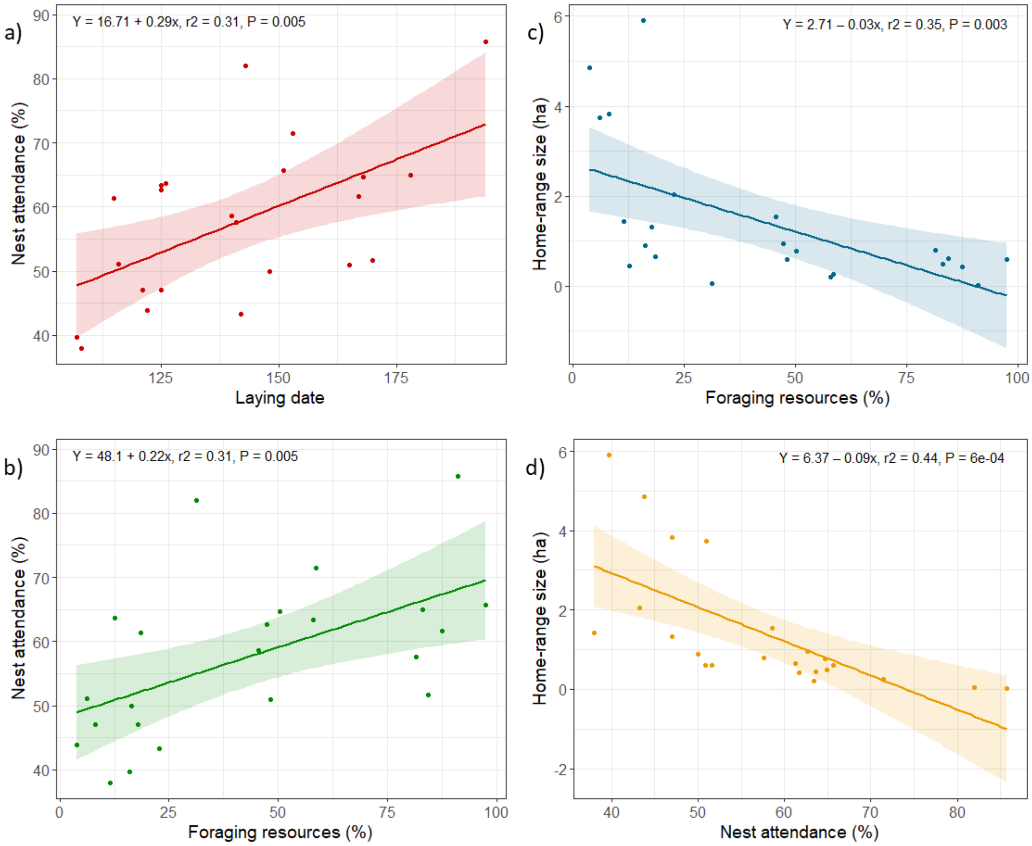


Figure 5. Factors affecting incubation behavior for 23 clutches of Little Bustard in the Ebro Depression. a) Linear regression between laying date (Julian days) and the percentage of nest attendance. b) Linear regression between the percentage of foraging resources and the percentage of nest attendance. c) Linear regression between the percentage of foraging resources and the home-range size (ha). d) Linear regression between the percentage of nest attendance and the home-range size (ha). Foraging resources availability were measured as the percentage of permanent or semi-permanent vegetation within 300 m buffer around the nest. Nest attendance and home-range size (80% MCP) were calculated for the laying and first week of the incubation stage.

2.298, *P* = 0.142). Estimated incubation time of successful clutches was 20.7 ± 1.0 days (19.5–22.3 days, n = 9). In one case, a clutch failed after 5.4 days after the first visit to the nest and we cannot be sure if incubation had started. For clutches that failed after the start of incubation, incubation was interrupted on average after 11.1 ± 4.8 days (2.6–18.0, n = 18) of incu-

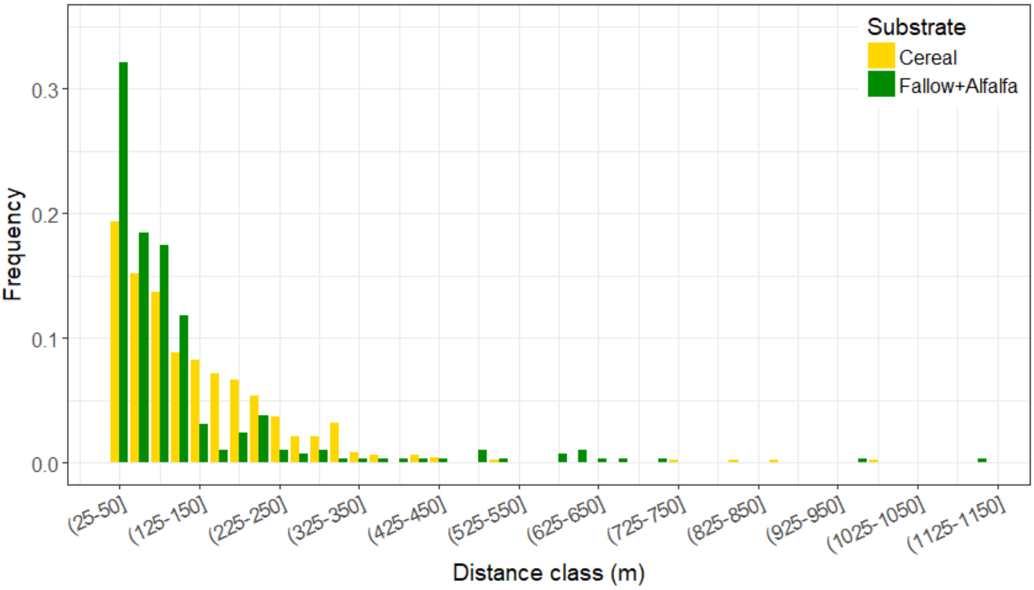


Figure 6. Frequency distribution of off-nest fixes grouped by nest substrate of 28 little bustard clutches during both, laying and incubation stages. The frequency of off-nest fixes is shown in distance classes of 25 m. Nest locations (0–25 meters) are not shown.

bation. Time to failure showed significant differences in relation to clutch sequence (F = 9.283, *P* = 0.002). According to Bonferroni post-hosc test, time to failure was significantly longer for first clutches (14.5 ± 3.7 days, n = 9) than for second clutches (6.9 ± 2.7 days, n = 7, *P* = 0.002), but none of these were significantly different from third clutches (11.8 ± 4.2 days, n = 3).

Nest attendance

Nest attendance during laying was 30.8 ± 11.5%, (9.5–53.3%) and 86.8 ± 6.4% (72.5–95.7%) during incubation. Nest attendance tended to increase as incubation progressed, particularly in the last days (Fig. 4). During laying, nest attendance that peaked at midday (10–14 h), while during incubation, this showed a peak at late evening showed a normal daily distribution bimodal pattern with a maximum (19–22 h) and a lower peak at midday. Thus, incubation recesses were concentrated in early morning and during the afternoon (Fig. 4). Considering only the clutches which completed the first week of incubation (n = 23, including one that failed at day 6.88 of incubation), nest attendance during laying+first week of incubation increased as the Julian date of laying progressed (Fig. 5a). Similarly, we found a positive effect of food availability (measured as the percentage of permanent or semi-permanent vegetation, HVF+Field Edges, within 300 m buffer around the nest) on nest attendance during laying+first week of incubation (Fig. 5b).

Ranging behavior during laying and incubation

The median TOT_MCP for the 28 incubation events was much smaller (3.4 ha; IQR: 2.1–13.1 ha) than the median 100% MCP of the week previous to laying (PRE_MCP: 355.0 ha; IQR: 63.7–1900.0 ha), in which some females can make long movements (i.e., a hen abandoned the breeding ground, traveling a linear distance of 219 km and returning to the starting area 3.4 days later). The LAY_MCP (mean ± SD: 8.4 ± 10.3 ha; n = 28) was 15 times larger than the INC_MCP (1.4 ± 2.0 ha; n = 27) (Wilcoxon paired-data test: W = 377; $P < 0.001$). Considering only the successful clutches (n = 9), the median TOT_MCP was 6.8 ha (IQR: 3.2–10.5 ha), the median PRE_MCP was 132.1 ha (IQR: 34.7–344.1 ha), the median LAY_ MCP was 4.6 ha (IQR: 3.2–9.9 ha) and the median INC_MCP was 1.3 ha (IQR: 1.2–2.5 ha).

The average overlap between the LAY_MCP and the INC_MCP was 73.1 ± 30.7% of the INC_MCP (n = 27). Similarly, average overlap between the LAY_MCP and the PRE_MCP was 72.8 ± 30.8% of the LAY_MCP (n = 27). Home range eccentricity during laying (0.486 ± 0.247) was not different than during incubation (0.387 ± 0.212) (Paired t-student test: 1.499, P = 0.146, n = 27). A negative relation-

Table 2. Ranking matrices for breeding hen little bustards based on comparing proportional habitat use (off-nest fixes) of each clutch within the hen's MCP (Minimum Convex Polygon) range. Each element in the matrix represents the mean differences between usage and availability replaced by its sign. Triple sign indicates significant deviation from random with $P < 0.05$. The rank shows substrate preference, where high values indicate a higher substrate preference.

All substrates (n=22)

Usage/Availability	Cereal	Herbaceous	Other	Rank
Cereal		---	+ + +	1
Herbaceous	+++		+ + +	2
Other	---	---		0

ship was found between food availability around the nest and the home-range of the laying+first week of incubation (80L1_MCP) (Fig. 5c), and between nest attendance and 80L1_MCP (Fig. 5d).

Off-nest habitat use and selection

The spatial distribution of the off-nest fixes, considering laying and incubation stages together, varied in relation to nest substrate (Fisher's exact test: *P* = 0.032) (Fig. 6). In clutches located on fallow or alfalfa, 80% of off-nest fixes were located at ≤ 125 m from the nest centroid, whilst only 57% of fixes were found at this distance for nests occurring in cereal fields.

Compositional analysis showed that habitat used by hens during the laying and incubation period (off-nest fixes) was different from proportional available habitat (n = 22, weighted mean λ = 0.2419, *P* = 0.002). Ranking of habitat preferences from the most to the least selected was: herbaceous >>> cereal >>> other (where >>> denotes a statistically significant difference) (Table 1). We found the same habitat selection pattern considering only clutches in dry farmland (n = 16, weighted mean λ = 0.2695, *P* = 0.006) or considering only those clutches found in cereal (n = 13, we-ighted mean λ = 0.1621, *P* = 0.002).

Nest survival and hatching probability

Only 9 of the 28 clutches hatched (32.1%) and 19 failed (67.9%) (Appendix 2). Among first clutches (n = 16), 7 hatched (43.7%) and 9 failed (56.3%). Among second clutches (n = 8), 1 hatched (12.5%) and 7 failed (87.5%). And among third clutches (n = 4), 1 hatched (25%) and 3 failed (75%). Incubation success was 40% on dry farmland and

Table 1. Absolute and relative frequencies (%) of successfully incubated and failed clutches according to farming system, nest substrate and cause of failure.

Farming system		**Dryland (n=20)**				**Irrigated (n=8)**		**Total (n=28)**
Nest substrate		**Cereal**		**Fallow**		**Alfalfa**		
Succesfully incubated		7	43.75%	1	25.0%	1	12.5%	32.1%
Failed	*Agricultural practices*	1	6.3%	1	25.0%	5	62.5%	25.0%
	Desertion/predation	8	50.0%	2	50.0%	1	12.5%	39.3%
	Unknown	0	0.0%	0	0.0%	1	12.5%	3.6%
		16	57.1%	4	14.3%	8	28.6%	

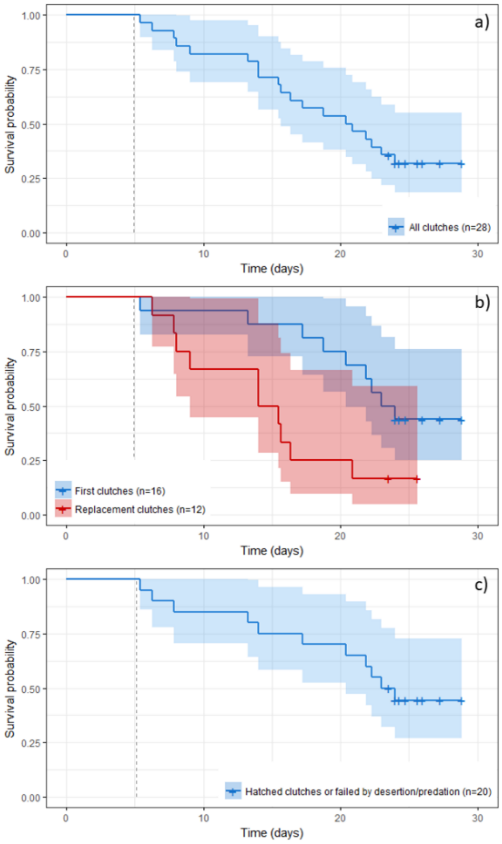


Figure 7. Survival probability of little bustard clutches based on Kaplan-Meier estimates (lines) with 95% confidence bands (shaded): a) Survival probability for all the clutches (n = 28); b) Survival probability for the first clutches (n = 16) and replacement clutches (n = 12); and c) Survival probability of clutches in which failure was not associated with agricultural causes (n = 20). Axis time comprises laying and incubation stages with dashed line indicating the average start time of incubation. The cross marks show hatched clutches or censored observations when a failure event was not detected.

12.5% on irrigated land (Table 2). In dry farmland most of losses were associated to desertion/predation, while on irrigated farmland failures were mostly caused by agricultural practices.

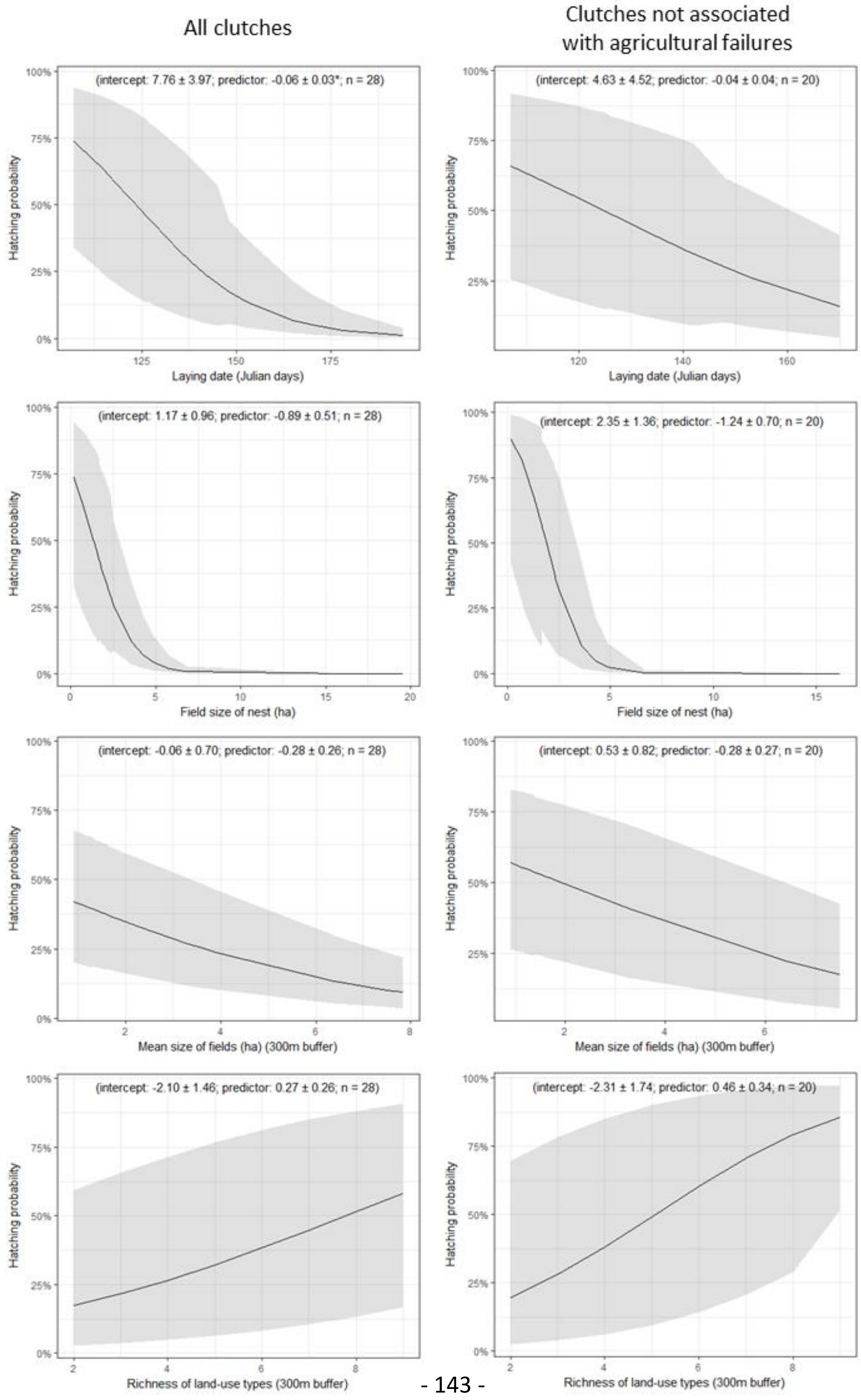
Excluding those clutches which failed as a consequence of farming practices (n = 7) or by unknown causes (n = 1), the Kaplan-Meier survival curves for the laying and incubation period (n = 20) showed a higher failure probability at the end of the incubation stage (Fig. 7c; see Table S5.3 in the Appendix 5 for detailed information on survival probabilities). Considering only the incubation period (n = 19), the risk to fail during the first half and the second half of incubation stage was 0.21 and 0.40, respectively, although this difference was not significant (Gehan's test: 1.249, *P* = 0.212). The risk to fail during the second half of the incubation stage was much higher (0.46) than in the first half (0.07) among first clutches that did not fail by agricultural causes (n = 14) (Gehan's test: 2.330, *P* = 0.020).

Univariate models predicting the hatching probability for the whole set of clutches, indicated that laying date has a negative effect on the hatching probability, whereas the number of fields in a 300 m buffers had a positive effect (Fig.8; see also the Fig. S1.1 in Appendix 1 for a full predictors' responses). Although similar responses were obtained when we excluded from the analyses those clutches that failed as a consequence of farming practices, no factor retained a significant effect. Laying date for hatched clutches was 126.4 ± 14.9 (range: 108–153; n = 9), for naturally failed clutches was 134.4 ± 16.0 (range: 107–170; n = 11) and for clutches failed as a consequence of farming practices was 159.6 ± 13.3 (range: 143–178; n = 7).

Among GLMMs predicting the hatching probability, 11 individual mo-

Table 5 Results of the model averaging explaining the hatching probability of the Little Bustard clutches. The table indicates the estimates ± standard errors and the relative importance of the predictors in both subsets of models, models containing the total set of clutches and models that excluded the clutches failed by agricultural causes. Model averaging was conducted on a subset of the best models (i.e. selection probability in the best set of models based on the < 90% probability of cumulative AICc weight). Coefficients were standardized by the partial sd in model averaging. The predictors are shown by order of predictor importance in the models.

Predictors	Estimate	SE	Predictor importance
All clutches (n=28)			
Intercept	0.00	0.00	
Field size (nest)	−6.41	4.28	1.00
Laying date	−1.76	1.05	0.63
80% MCP (laying + first week of incubation)	1.47	1.16	0.58
Land use richness (300 m buffer)	0.89	0.70	0.31
Field size (300 m buffer)	0.10	1.09	0.15
Excluding agricultural causes (n=20)			
Intercept	0.00	0.00	
Field size (nest)	−4.69	3.03	0.95
80% MCP (laying + first week of incubation)	1.57	1.86	0.36
Laying date	−0.93	0.82	0.19
Land use richness (300 m buffer)	0.76	0.88	0.18
Field size (300 m buffer)	0.07	0.81	0.08


All clutches
Clutches not associated with agricultural failures
(intercept: 7.76 ± 3.97; predictor: -0.06 ± 0.03*; n = 28)
Hatching probability
100%
75%
50%
25%
0%
125
150
175
Laying date (Julian days)
(intercept: 4.63 ± 4.52; predictor: -0.04 ± 0.04; n = 20)
120
140
160
Laying date (Julian days)
(intercept: 1.17 ± 0.96; predictor: -0.89 ± 0.51; n = 28)
0
5
10
15
20
Field size of nest (ha)
(intercept: 2.35 ± 1.36; predictor: -1.24 ± 0.70; n = 20)
Field size of nest (ha)
(intercept: -0.06 ± 0.70; predictor: -0.28 ± 0.26; n = 28)
2
4
6
8
Mean size of fields (ha) (300m buffer)
(intercept: 0.53 ± 0.82; predictor: -0.28 ± 0.27; n = 20)
Mean size of fields (ha) (300m buffer)
(intercept: -2.10 ± 1.46; predictor: 0.27 ± 0.26; n = 28)
Richness of land-use types (300m buffer)
(intercept: -2.31 ± 1.74; predictor: 0.46 ± 0.34; n = 20)
Richness of land-use types (300m buffer)

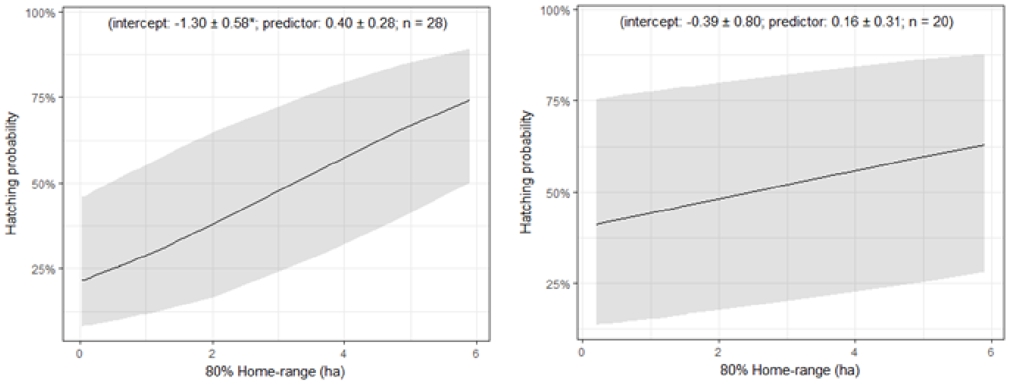


Figure 8. Univariate responses predicting the hatching probability of the Little Bustard clutches in univariate models. At left, univariate responses of selected predictors, predicting the hatching probability for the whole set of clutches (n = 28), and at right, the responses for the clutches failed by agricultural causes (n = 20). Model estimates and significance levels (*** *P* < 0.001; ** *P* < 0.01; * *P* < 0.05) are shown.

dels were selected within 90% probability of cumulative AICc weight, both for models predicting the hatching probability considering all clutches (n = 28) and for models considering only clutches not failed as a consequence of farming practices (n = 20) (see Appendix 6). In both cases, averaged models revealed a negative effect of field size and laying date on the hatching probability, and a positive effect of home-range of the laying+ first week of incubation (80L1_ MCP), land use richness and average field size within a 300 m buffer (Table 5). Field size, laying date and 80L1_MCP were the variables with the highest relative importance to the averaged model built for all clutches. Nevertheless, the relative importance of laying date substantially decreased in the averaged model constructed using clutches not associated with agricultural failures (Table 5).

Among first clutches, model averaging of Cox models with random effects showed the laying date as the main factors explaining clutch survival (0.96 of relative importance). Contribution to models of other predictors was much lower (see Appendix 7 for full model results). The averaged model indicated that the risk to clutch failure increased 18% per day of laying date (coefficient: 0.17, SE = 0.96, *P* = 0.336, hazard ratio: 1.18), but p-value was not significant for the averaged coefficient. An increase of one hectare on the field size caused a risk to fail 1.4-fold higher (coefficient: 0.87, SE = 0.34, *P* = 0.011, hazard ratio: 2.39).

Among cereal clutches, no difference was found on nest distance to the field edge between hatched (10.5 ± 5.5; range: 3.4–18.2; n = 7) and naturally failed clutches (16.5 ± 13.1; range: 1.8–37.7; n = 8) (F = 1.273, *P* = 0.280).

Discussion

We studied the incubating behavior and the hatching success of the Little Bustard in one of the most important areas of the Ebro basin population. Previous research in the area showed that breeding success is limited by low brood survival (Lapiedra et al. 2011) associated to low chick habitat availability. Our research on the incubation behavior adds to our understanding of the factors that compromise the viability of this little bustard population and provide crucial data to develop effective conservation policies.

GPS tracking during laying and incubation was useful to uncover some little known aspects of the little bustard breeding biology in the wild. The fact that 16% of hens did not even start breeding pointed out that there may be reproductive limitations. Since all our hens had experience in reproduction, this makes us to think that other factor such as body-condition could be involved. Having enough accumulated reserves is fundamental for egg production and incubation performance (Ankney et al. 1991, Ankney and Alisauskas 1991). Nevertheless, other factors such as hen senescence or habitat constraints could help to explain it. The obtained rate of hens that did not start breeding was similar to that provided by Lapiedra et al. (2011), suggesting that this parameter is a fairly constant in the population.

Our estimate for incubation length (20.7 ± 1.0 days) was consistent with previous information (Cramp and Simmons 1980, Johnsgard 1991). However, this is the first time that renesting rates are quantified. We found that replacement clutches are more common that it was previously reported (Lapiedra et al. 2011) or assumed (Bretagnolle et al. 2018). Actually, 67% of the females that lost their first nest initiated a replacement clutch, which can be laid as early as 5 days after the loss of the previous one. In that way, hens can lay up to three clutches in a season. Although in our study area the period of first laying extends only for little more than four weeks, the egg-laying period extends for over 12 weeks, as in Western France (Bretagnolle et al. 2018), due to the high frequency of relaying. The period of initiation of second clutches had little overlap with the end of the first laying period, but lasted for more than 8 weeks, until the end of the laying season, and is the main factor responsible for the extension of the laying season as a whole. Curiously, the period for third laying started only a couple of weeks later than the beginning of the second clutch period and lasted for only two weeks. This probably indicates that while laying a second clutch is little constrained by the timing on the season, the laying of a third clutch probably is. However, we should be cautious with this interpretation of results due to our low sample of third clutches.

During the nesting period, female little bustards can make considerable movements between consecutive nests, up to 100 km. This sort of movements can be similar in length to the reproductive dispersal movements between nests in consecutive seasons, which can reach up to 142 km. Both are probably related with the hens trying to find the best conditions to breed, reflecting the ability of this species to track environmental conditions across large expanses of land. Both (intra-season and inter-season) can be relatively long and can contribute to maintain genetic and demographic connection between relatively distant populations. This result is especially relevant, since a weak genetic geographic structure for little bustard populations in Spain has been documented (García et al. 2011).

The bimodal daily pattern of nest-attention was similar to other gyneparental birds ground nesting species (Deeming et al. 2001) or species incubating under high solar radiation conditions (Mougeot et al. 2014). This pattern is probably the best strategy to protect the eggs both from high midday temperatures or from cooling in early morning or late evening (Webb 1987). Nest attention increased as the season progressed, and this may also be related to thermal requirements. We also found that nest attendance increased in the last days of incubation, a trend which has been observed in other species, but which is by no means universal, as different species show different patterns (Skutch 1962). This could be related to the need for further protection of the embryos or hatching chicks. Surprisingly, in spite of this increased nest attentiveness, the risk of failure of our clutches increased during the final days of incubation. Because hatching time was estimated with some error, some of this failure may include also the early death of chicks immediately after hatching, which is a critical time and may explain this increased probability of failure around hatching time.

At the start of the season, clutches were always placed on dry farmland but, after the beginning of June, all of them were laid on irrigated alfalfa fields. Nests were found at variable distances from field edges, depending on nests substrate, being shorter in the cereal crops, where hens have to rely on margins to feed, than in the edible alfalfa or fallow fields, where food is highly available within the field. As field margins are a predation prone habitat (Benson et al. 2010), female little bustards would have to trade-off accessibility to food resources and antipredator behavior, given that predation is a primary cause of nest loss in precocial birds (Martin 1988) and that single-sex incubators are usually constrained in time for foraging (Mertens 1977, Conway and Martin 2000).

In dry farmland, fallows were the prefered substrate for nesting (see also Morales et al. 2013), but most of nests were found on cereal, which was the dominant habitat in the area. Although being preferred, breeding success was low in fallow, because many fallow fields are subject to grazing, tillage, trampling or slurry dumping which can cause nest abandonment. However, hatching success was also low in cereal fields. Contrary to what happens in other farmland areas where little bustards nest mainly on alfalfa (Bretagnolle et al. 2011), nest losses in cereal were mostly associated to desertion/predation rather that to farming practices, that accounted only for 36.8% of failures, a similar value to that reported previously for the same area (43%, Lapiedra et al. 2011). High rates of nest predation are expected in ground nesting species (Martin 1995, Davis 2003) and this might probably be an important cause of nest failure in the Little Bustard as it is also shown in other ground nesting steppe birds. For example, nest predation was the second cause of failure for *Otis tarda* (Ena et al. 1987) and caused

85% of incubation failures in *Anthus campestris* (Calero-Riestra et al. 2013) in Spain. Desertion/predation was reported to cause 85% of incubation failures in *Burhinus oedicnemus* in France (Gaget et al. 2018).

After the beginning of June, no more clutches were laid in dry farmland. The most likely explanation for this is the concomitant deterioration of environmental conditions. By this time, cereal is ripe and field margins and fallow dry, so alfalfa fields offer a more attractive nesting substrate. However, hatching success in alfalfa fields, as it is the case in France, is virtually null, because time between successive farming practices (flooding irrigation or mowing) is shorter than laying plus incubation time (≈25 days). Moreover, little bustard hens require a minimum of vegetation height (~ 40 cm) to nest (Bretagnolle et al. 2018; unpublished data), meaning that when hens start laying in alfalfa fields, mowing time is relatively close.

Most of successful clutches (78%) were first clutches and most of replacement clutches failed (80%). Laying date had a strong impact on hatching success. This is probably caused by a change in nesting substrate as the season progresses. Our results indicate that changes in hatchability throughout breeding season are mainly associated to the differential hatching success in different substrates. However, while substrate change related to farming practices explain the low hatching success of most replacement clutches, a relevant amount of first and second clutches in cereal fields are deserted or predated before any farming practice have destroyed them. Our results do not suggests that low female body condition reduces nests attention and induce desertion or predation, because 1) we did not found differences in female attentiveness between hatched and unhatched nests and 2) most of hens laid a replacement clutch, a situation not compatible with reduced body condition. Alternatively, we found that hatching success is inversely related to some agricultural intensification factors, such as field size or reduced habitat diversity around the nest. This is consistent with our findings that increasing amounts of food resources around the nest reduces home range size and the distance females had to travel out the nest to find food, and increases female attentiveness to the nests, which may reduce the risk of predation and have obvious benefits on hatching success. In that way, reduction of food around the nests produced by intensification would indirectly promote higher predation rates.

Nevertheless, our findings showed how optimal habitats for incubating hens, such as fallows and alfalfa crops, actually are harmful due to the current agricultural management, as suggested by Morales et al. 2013. In that sense the unexpected relation between hatching success and the home-range of little bustard hens, is probably caused by a confounding effect related with nest substrate. Since those clutches situated in cereal fields showed an increased home-range and these were mostly not affected by farming activities.

Finally, our data show that breeding success of Little Bustard is subject to high inter-annual variations. Weather and vegetation conditions could be the main factors explaining this variation, through changes in the timing of crop phenology and farming practices, as well as changes in food availability. Rainfall regime can influence population trends of Little Bustard (Delgado et al. 2009). Rainfalls during the months before spring have a positive effect for Little Bustard, since they contribute to a greater availability of weeds and arthropods during the breeding season (Zaller et al. 2014). In opposite, high temperatures in spring can cause a reduction in the life cycle of primary producers. A study carried out in Spain during 26 six years has shown an advance in spring phenophases and harvest timing of winter cereals (Oteros et al. 2015). Under a global climate change context, warmer temperatures and shorter cereal phenophases are expected, reducing food availability and constraining the time window to nest, especially in cereals and fallows. In addition, high temperatures inhibit little bustard activity during breeding season, limiting the breeding and foraging time (Silva et al. 2015). This could have consequences on hen fitness and reduce, even more, the low productivity of this species. Likewise, it can increase direct nest losses by a heat excess and intense solar radiation. Other factors, such as vegetation structure (height and cover vegetation), could also be involved (Gillis et al. 2012, Capdevila et al. 2016) and further research is needed.

Conclusions and conservation remarks

Incubation behavior of Little Bustards in our study area was consistent with previous information and highlights the outstanding capacity of this species for laying replacement clutches, as an adaptation to cope with high nest predation typical of ground nesting bird. Hatching success in our study area was very low, because clutches in cereal fields were subject to high levels of natural failure and because farming practices reduces hatching success to virtually zero in fallow land and alfalfa fields. The high levels of renesting indicates that failures in cereal fields are more probably associated to predation rather to abandonment, but predation could be associated to low feeding conditions or low habitat quality in a progressively intensified farmland. More detailed research is needed on this topic. Our results also highlight the importance of semipermanent and permanent vegetation for incubating hens, so improving the habitat quality in the cereal pseudo-esteppe, by increasing the amount of field margins and the amount of well managed fallow land could contribute to increase hatching success, and also to provide alternative nesting habitats to the agriculturally unsafe alfalfa fields. The adequation of farming practices in alfalfa cultivations could contribute to increase the extremely low hatchability of replacement clutches. Replacing the widespread flooding irrigation system by aspersion or pivot systems, or increasing the time between successive alfalfa cuts during the critical incubation period could facilitate the hatchability on this substrate.

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Additional files

Appendix 1. Description of predictors and their univariate reponses.

Appendix 2. Summary of incubation descriptors.

Appendix 3. Nest fidelity. Distance between clutches of the same female.

Appendix 4. Habitat nest selection and eigenanalysis of selection ratios based on nest recesses.

Appendix 5. Survival curves of 28 little bustard clutches based on the Kaplan-Meier estimate.

Appendix 6. Model results predicting the hatching probability.

Appendix 7. Model results predicting the hazard to fail of first clutches.

Appendix 1

Table S1 Description of explanatory predictors used in a univariable analysis describing the hatching probability of 28 Little Bustard clutches.

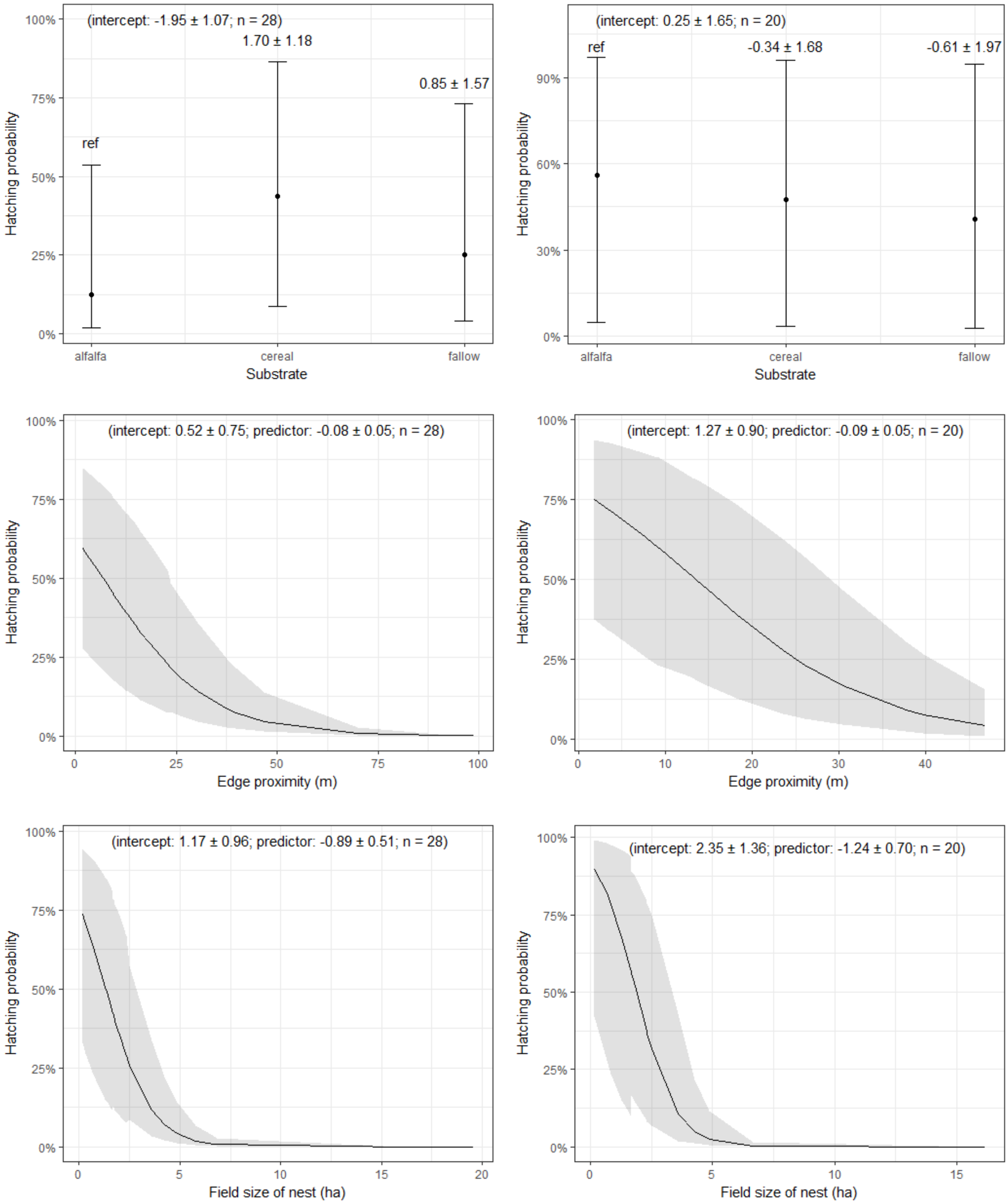
Variable	Description	Units or levels
Nest site		
Nest substrate	*Substrate where the nest was located*	*(cereal, fallow, alfalfa)*
Edge proximity	*Distance from the nest centroid to the field edge*	*(m)*
Field size	*Field size of the nest*	*(ha)*
Timing		
Laying date	*Julian date of laying date*	*(Julian date)*
Laying length	*Length of laying stage*	*(hours)*
Clutch order	*Clutch sequence*	*(first, second, third)*
Nest attendance		
Laying attendance	*Percentage of nest fixes during the laying stage*	*(proportion)*
Food resources		
Food availability	*Proportion of permanent or semi-permanent herbaceous vegetation in a 300m buffer around the nest*	*(proportion in 300 m buffer)*
Habitat heterogeneity		
Number of fields	*Number of plots in a 300m buffer around the nest*	*(N in 300 m buffer)*
Land use richness	*Number of different land use types in a 300m buffer around the nest*	*(N in 300 m buffer)*
Field size mean	*Mean of filed size, occurring in a 300m buffer around the nest*	*(ha, in 300 m buffer)*
Ranging behavior		
80% home-range (laying + first week of incubation)	*80% of home-range size during the laying and the first week of the incubation*	*(ha, 80% MCP)*

Figure S1 Univariate responses predicting the hatching probability of the Little Bustard clutches in univariate models. At right, univariate responses predicting the hatching probability for the whole set of clutches and, at left, responses for failed clutches not associated with agricultural practices.

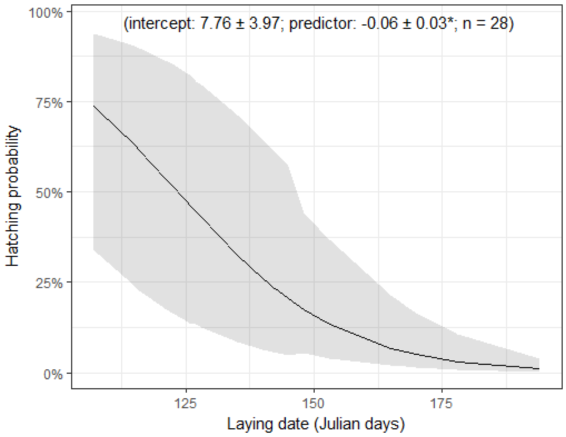
Nest site predictors

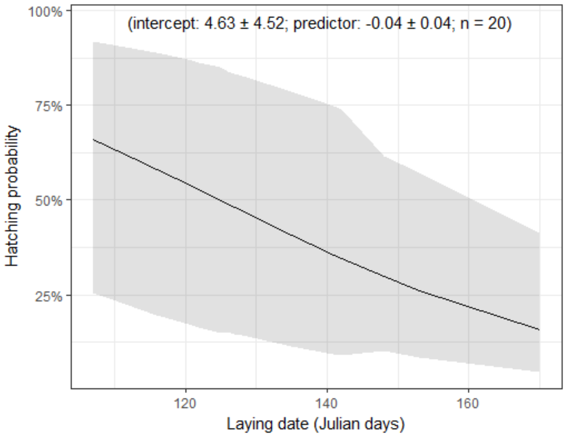
All clutches

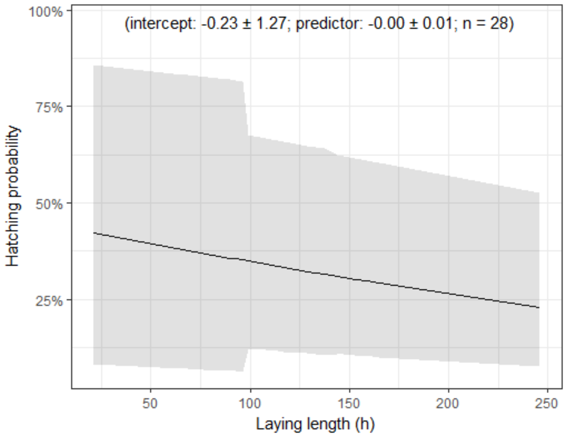
Excluding clutches failed by agricultural practices

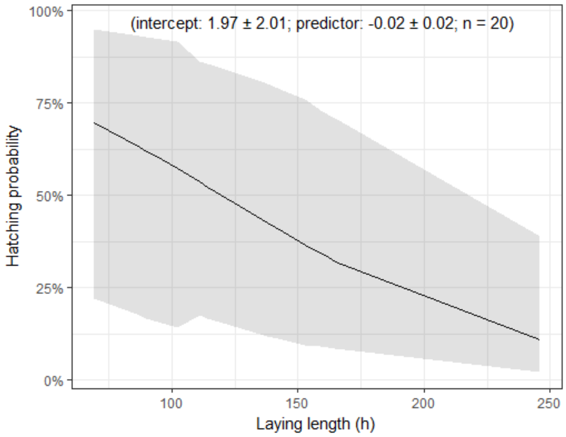


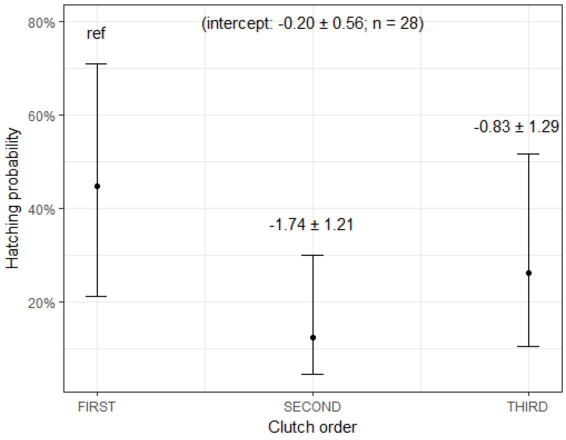
Timing predictors

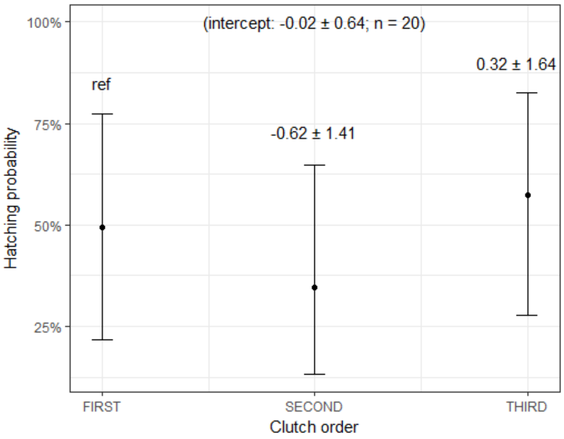




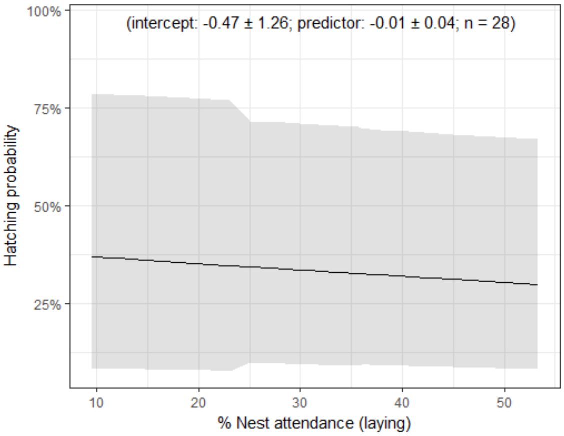


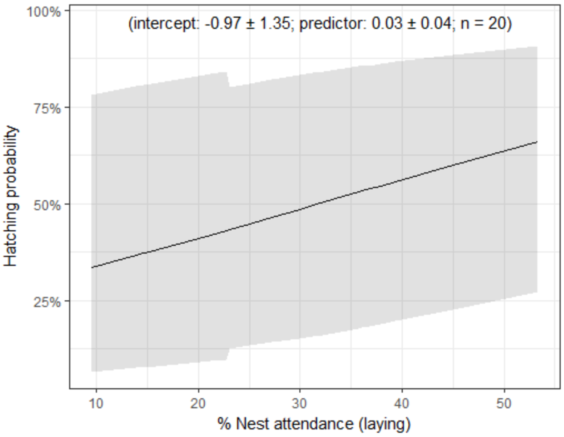




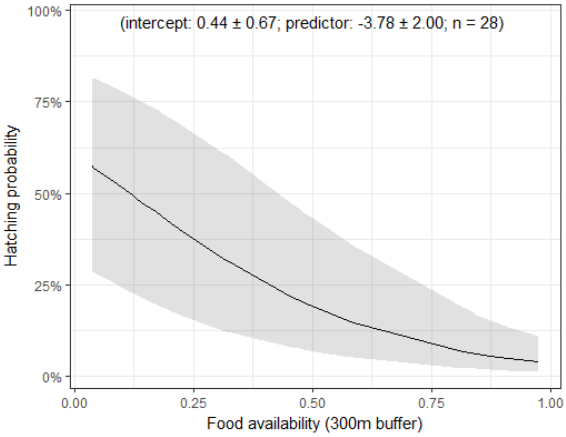


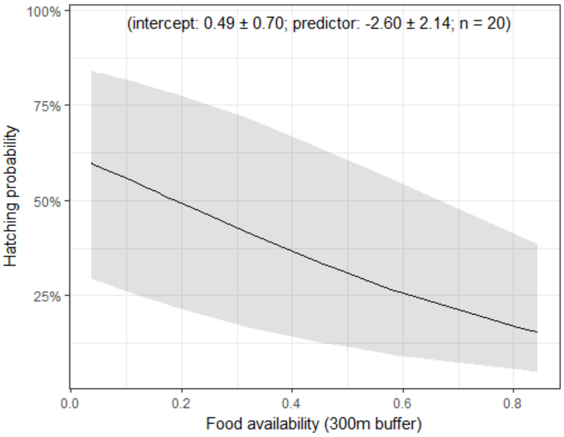
Nest attendance predictors



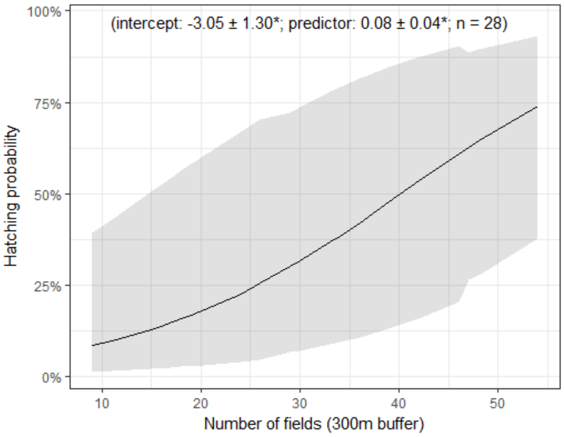


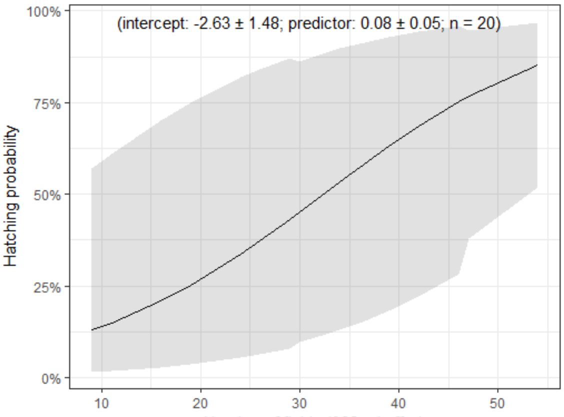
Food availability predictor

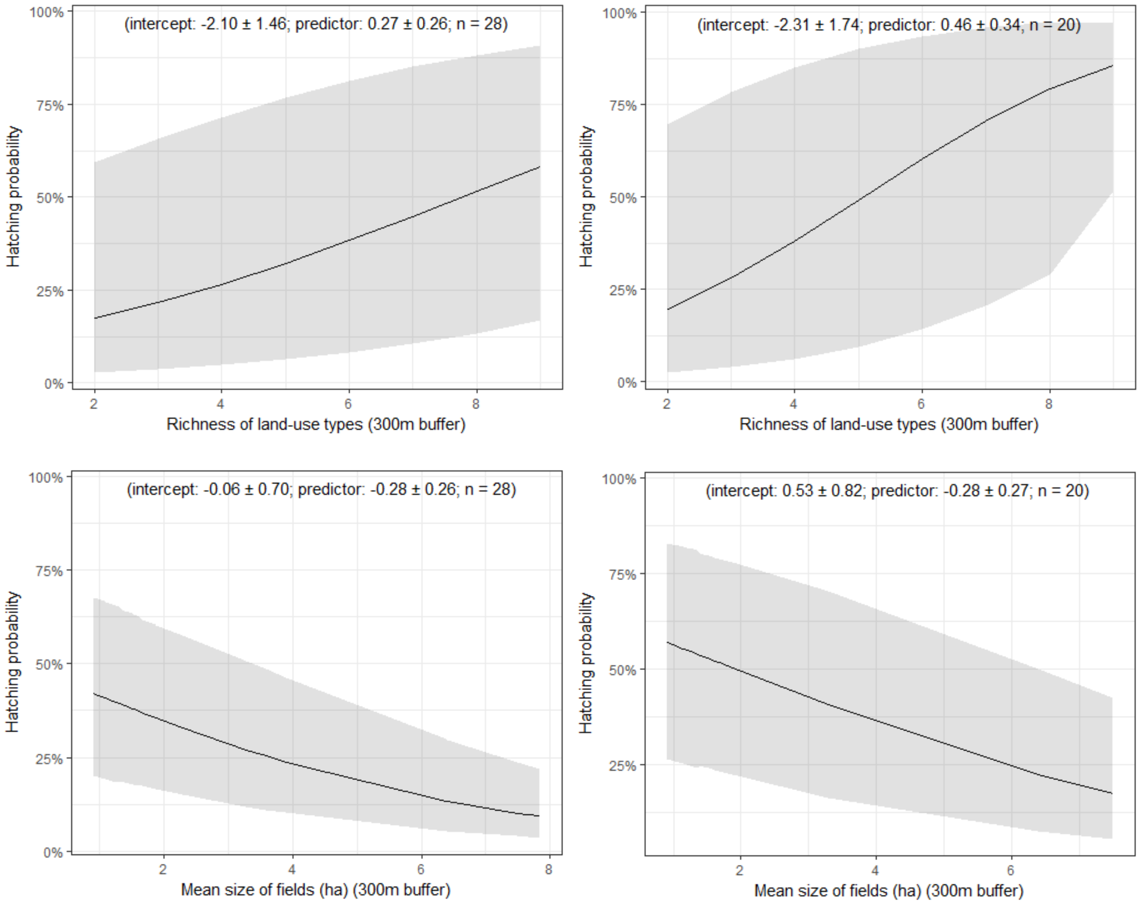




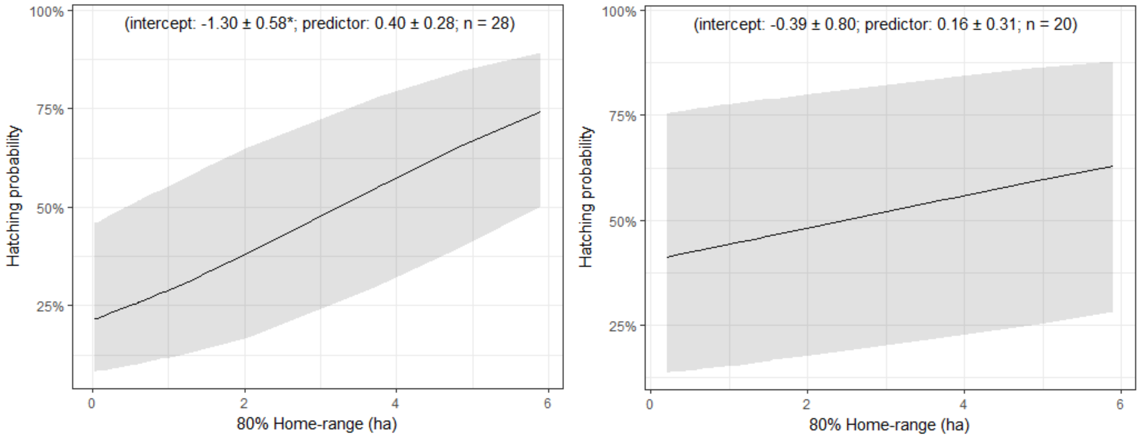
Habitat heterogeneity predictors







Ranging behavior predictor



Appendix 2

Table S2 Laying and incubation descriptors of 28 little bustard clutches in the Ebro Depression. The number of fledglings > 30 days age is indicated if different of 0.

					Laying period				Incubation period					Laying + Incubation			
Id	Female PTT	Clutch order	Farming system	Nest substrate	Start date	Julian date	N of fixes	Duration (days)	Start date	Julian date	Final date	N of fixes	Duration (days)	N of locations	Duration (days)	Hatching success (N fledglings)	Failure cause
1	90594	first	dryland	cereal	07/05/2010	127	27	6.38	13/05/2010	133	19/05/2010	19	5.88	46	12.25	no	non agricultural
2	90594	second	dryland	cereal	28/05/2010	148	19	3.75	01/06/2010	152	23/06/2010	62	21.88	81	25.63	yes	-
3	33139	second	irrigated	alfalfa	13/07/2010	194	5	0.88	14/07/2010	195	21/07/2010	23	6.88	28	7.75	no	?
4	90594	first	dryland	cereal	18/04/2011	108	34	6.63	25/04/2011	115	17/05/2011	65	22.25	99	28.88	yes	non agricultural
5	90594	second	dryland	cereal	25/05/2011	145	10	3.50	29/05/2011	149	03/06/2011	25	5.38	35	8.88	no	agricultural
6	90594	third	irrigated	alfalfa	17/06/2011	168	22	4.50	22/06/2011	173	08/07/2011	57	16.25	79	20.75	no	agricultural
7	33139	first	dryland	cereal	17/04/2011	107	49	10.25	27/04/2011	117	09/05/2011	46	11.50	95	21.75	no	non agricultural
8	33139	second	dryland	cereal	15/05/2011	135	15	2.88	18/05/2011	138	23/05/2011	22	4.88	37	7.75	no	non agricultural
9	33139	third	irrigated	alfalfa	02/06/2011	153	20	4.00	06/06/2011	157	25/06/2011	96	19.50	116	23.50	yes	agricultural
10	33348	first	dryland	fallow	05/05/2011	125	36	6.00	11/05/2011	131	29/05/2011	87	17.88	123	23.88	no	non agricultural
11	34175	first	dryland	cereal	25/04/2011	115	29	4.63	29/04/2011	119	21/05/2011	85	21.38	114	26.00	yes (2)	-
12	35960	first	dryland	cereal	06/05/2011	126	28	4.75	11/05/2011	131	30/05/2011	107	19.50	135	24.25	yes (2)	-
13	37131	first	dryland	cereal	26/04/2011	116	22	4.25	30/04/2011	120	20/05/2011	80	20.00	102	24.25	yes (1)	-
14	33139	first	dryland	cereal	01/05/2012	122	43	3.75	05/05/2012	126	25/05/2012	98	20.25	141	24.00	yes	-
15	34175	first	dryland	cereal	21/05/2012	142	22	4.13	25/05/2012	146	07/06/2012	28	13.00	50	17.13	no	non agricultural
16	34175	second	irrigated	alfalfa	13/06/2012	165	36	6.13	19/06/2012	171	28/06/2012	29	9.25	65	15.38	no	agricultural
17	37131	first	dryland	cereal	04/05/2012	125	32	6.75	11/05/2012	132	31/05/2012	40	20.50	72	27.25	yes	non agricultural
18	37562	first	dryland	cereal	19/05/2012	140	21	3.88	23/05/2012	144	08/06/2012	84	16.38	105	20.25	no	non agricultural
19	37614	first	dryland	fallow	22/05/2012	143	15	2.75	25/05/2012	146	10/06/2012	87	15.88	102	18.63	no	agricultural
20	37562	first	dryland	fallow	21/05/2013	141	26	4.88	26/05/2013	146	12/06/2013	90	17.25	116	22.13	no	non agricultural
21	37562	second	irrigated	alfalfa	27/06/2013	178	35	6.00	03/07/2013	184	13/07/2013	61	10.25	96	16.25	no	agricultural
22	37562	first	dryland	fallow	05/05/2014	125	20	3.75	09/05/2014	129	30/05/2014	101	21.00	121	24.75	yes	-
23	37562	first	dryland	cereal	08/05/2015	128	33	5.38	-	132	-	-	-	33	5.38	no	non agricultural
24	37562	second	dryland	cereal	22/05/2015	142	19	3.63	26/05/2015	146	28/05/2015	17	2.50	36	6.13	no	non agricultural
25	37562	third	irrigated	alfalfa	16/06/2015	167	29	4.88	21/06/2015	172	01/07/2015	49	10.38	78	15.25	no	agricultural
26	37562	first	dryland	cereal	30/04/2016	121	36	6.88	07/05/2016	128	23/05/2016	75	16.13	111	23.00	no	non agricultural
27	37562	second	irrigated	alfalfa	30/05/2016	151	32	6.00	05/06/2016	157	13/06/2016	38	8.00	70	14.00	no	agricultural
28	37562	third	irrigated	alfalfa	18/06/2016	170	33	5.75	24/06/2016	176	02/07/2016	35	8.25	68	14.00	no	non agricultural

Appendix 3

Table S3 Distance between clutches for a hen in a same breeding season and for a hen in consecutive years (time *t* and time *t*–1).

Hen code $_{year/s}$	**Distance between clutches (km)**		
In a same breeding season	1st – 2nd clutches	2nd – 3rd clutches	1st – 3rd clutches
90594 $_{2010}$	0.240 (D-D)	-	-
90594 $_{2011}$	2.080 (D-D)	24.684 (D-I)	22.890 (D-I)
33139 $_{2011}$	0.934 (D-D)	5.354 (D-I)	6.083 (D-I)
34175 $_{2012}$	4.007 (D-I)	-	-
37562 $_{2013}$	18.718 (D-I)	-	-
37562 $_{2015}$	17.583 (D-D)	100.659 (D-I)	90.015 (D-I)
37562 $_{2016}$	45.579 (D-I)	3.073 (I-I)	42.924 (D-I)
In consecutive breeding seasons	1st $_{t-1}$ – 1st $_{t}$ clutches	2nd $_{t-1}$ – 1st $_{t}$ clutches	
90594 $_{2010 – 2011}$	0.216 (D-D)	0.033 (D-D)	
33139 $_{2010 – 2011}$	-	13.896 (I-D)	
33139 $_{2011 – 2012}$	0.936 (D-D)	0.023 (D-D)	
34175 $_{2011 – 2012}$	0.466 (D-D)	-	
37131 $_{2011 – 2012}$	0.403 (D-D)	-	
37562 $_{2012 – 2013}$	48.758 (D-D)	-	
37562 $_{2013 – 2014}$	5.585 (D-D)	24.119 (I-D)	
37562 $_{2014 – 2015}$	92.642 (D-D)	-	
37562 $_{2015 – 2016}$	133.673 (D-D)	142.854 (D-D)	

(D-D): both clutches in dryland; (D-I) or (I-D): one clutch in dryland and other in irrigated land; (I-I): both clutches in irrigated land.

Appendix 4

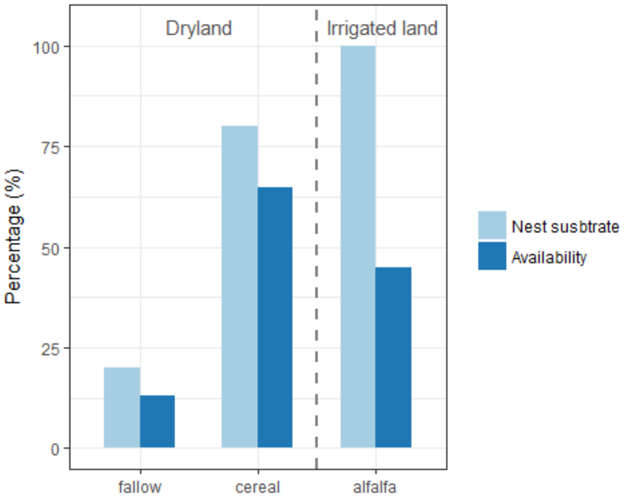


Figure S4.1 Overall percentages of nests (n=28) occurring in different substrates and their availabilities (measured in a 300 m around the nests) in dryland and irrigated areas.

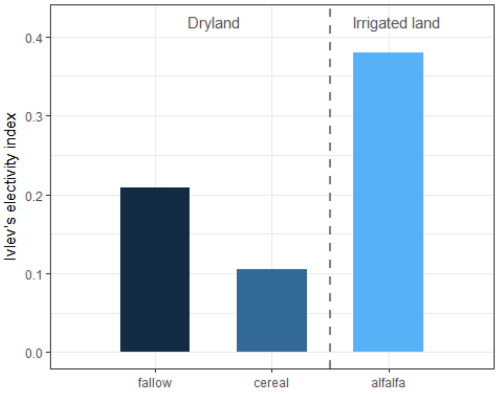
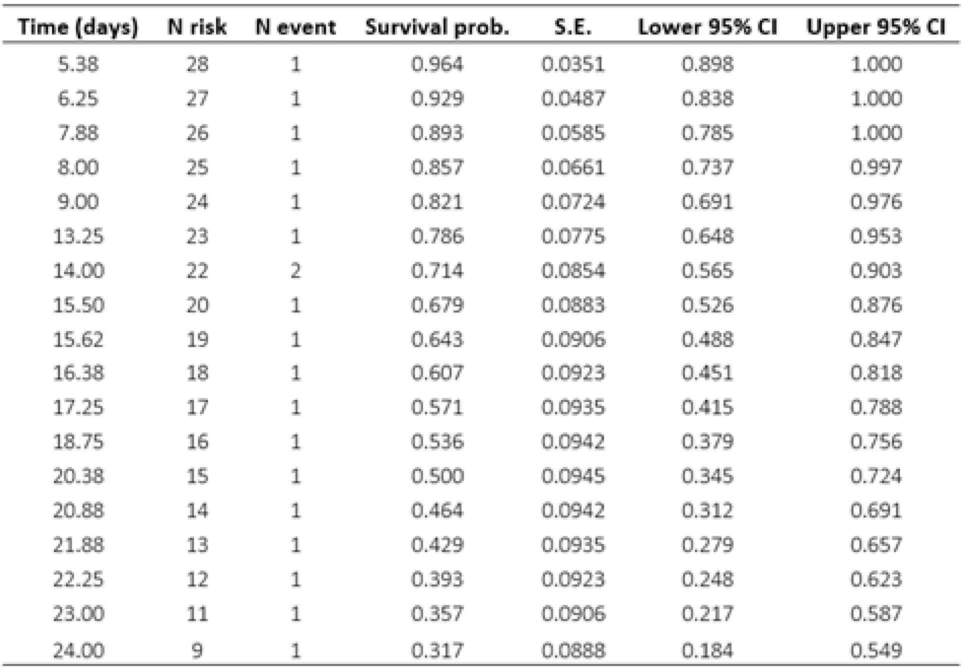


Figure S4.2 Mean Ivle's electivity index for the different habitats used by hen little bustards (r*i* - p*i*) / (r*i* + p*i*). Where r*i* was the % of nests occurred in substrate *i*; and p*i* the % of availability of the substrate *i* measur-ed in a 300 m buffers around the nests (n=28) by both environments, dryland and irrigated land.

Appendix 5

Table S5.1 Survival probabilities by Kaplan-Meier estimate of the 28 little bustard clutches (data associated to Figure 7a in the body text).



Time (days)	N risk	N event	Survival prob.	S.E.	Lower 95% CI	Upper 95% CI
5.38	28	1	0.964	0.0351	0.898	1.000
6.25	27	1	0.929	0.0487	0.838	1.000
7.88	26	1	0.893	0.0585	0.785	1.000
8.00	25	1	0.857	0.0661	0.737	0.997
9.00	24	1	0.821	0.0724	0.691	0.976
13.25	23	1	0.786	0.0775	0.648	0.953
14.00	22	2	0.714	0.0854	0.565	0.903
15.50	20	1	0.679	0.0883	0.526	0.876
15.62	19	1	0.643	0.0906	0.488	0.847
16.38	18	1	0.607	0.0923	0.451	0.818
17.25	17	1	0.571	0.0935	0.415	0.788
18.75	16	1	0.536	0.0942	0.379	0.756
20.38	15	1	0.500	0.0945	0.345	0.724
20.88	14	1	0.464	0.0942	0.312	0.691
21.88	13	1	0.429	0.0935	0.279	0.657
22.25	12	1	0.393	0.0923	0.248	0.623
23.00	11	1	0.357	0.0906	0.217	0.587
24.00	9	1	0.317	0.0888	0.184	0.549

Table S5.2 Survival probabilities by Kaplan-Meier estimate of the first clutches and the replacement clutches of little bustard (data associated to Figure 7b in the body text).

Time (days)	N risk	N event	Survival prob.	S.E.	Lower 95% CI	Upper 95% CI
First clutches (n=16)						
5.38	16	1	0.938	0.0605	0.826	1.000
13.25	15	1	0.875	0.0827	0.727	1.000
17.25	14	1	0.812	0.0976	0.642	1.000
18.75	13	1	0.750	0.1083	0.565	0.995
20.38	12	1	0.688	0.1159	0.494	0.957
21.88	11	1	0.625	0.1210	0.428	0.914
22.25	10	1	0.562	0.1240	0.365	0.867
23.00	9	1	0.500	0.1250	0.306	0.816
24.00	8	1	0.438	0.1240	0.251	0.763
Replacement clutches (n=12)						
6.25	12	1	0.917	0.0798	0.7729	1.000
7.88	11	1	0.833	0.1076	0.6470	1.000
8.00	10	1	0.750	0.1250	0.5410	1.000
9.00	9	1	0.667	0.1361	0.4468	0.995
14.00	8	2	0.500	0.1443	0.2840	0.880
15.50	6	1	0.417	0.1423	0.2133	0.814
15.62	5	1	0.333	0.1361	0.1498	0.742
16.38	4	1	0.250	0.1250	0.0938	0.666
20.88	3	1	0.167	0.1076	0.0470	0.591

Table S5.3 Survival probabilities by Kaplan-Meier estimate of the 20 clutches not associated with agricultural causes (data associated to Figure 7c in the body text).

Time (days)	N risk	N event	Survival prob.	S.E.	Lower 95% CI	Upper 95% CI
5.38	20	1	0.950	0.0487	0.859	1.000
6.25	19	1	0.900	0.0671	0.778	1.000
7.88	18	1	0.850	0.0798	0.707	1.000
13.25	17	1	0.800	0.0894	0.643	0.996
14.00	16	1	0.750	0.0968	0.582	0.966
17.25	15	1	0.700	0.1025	0.525	0.933
20.38	14	1	0.650	0.1067	0.471	0.897
21.88	13	1	0.600	0.1095	0.420	0.858
22.25	12	1	0.550	0.1112	0.370	0.818
23.00	11	1	0.500	0.1118	0.323	0.775
24.00	9	1	0.444	0.1123	0.271	0.729

Figure S5.1 Survival probabilities of 28 little bustard clutches by clutch order (first, second and third clutches). The graph shows Kaplan-Meier estimates (lines) and 95% confidence bands (shaded). Axis time comprises laying and incubation stages. The cross marks show hatching time of successfully incubated clutches.

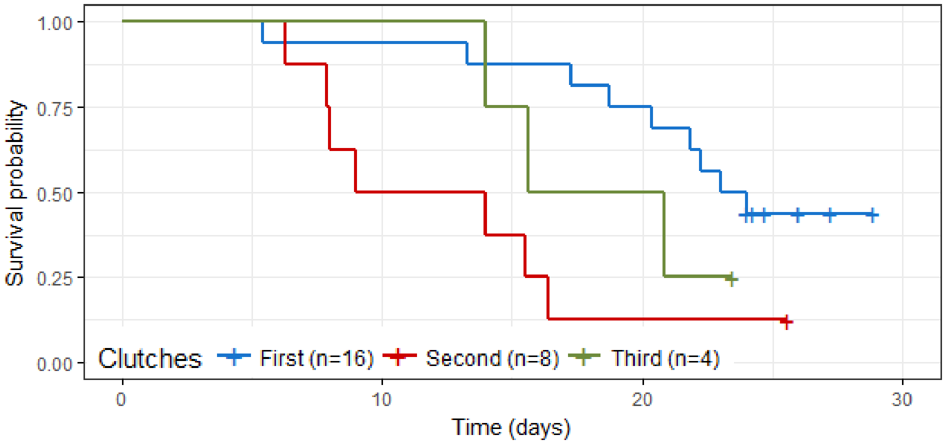


Table S5.4 Survival probabilities by Kaplan-Meier estimate of the first, second, and third clutches of little bustard.

Time (days)	N risk	N event	Survival prob.	S.E.	Lower 95% CI	Upper 95% CI
First clutches (n=16)						
5.38	16	1	0.938	0.0605	0.826	1.000
13.25	15	1	0.875	0.0827	0.727	1.000
17.25	14	1	0.812	0.0976	0.642	1.000
18.75	13	1	0.750	0.1083	0.565	0.995
20.38	12	1	0.688	0.1159	0.494	0.957
21.88	11	1	0.625	0.1210	0.428	0.914
22.25	10	1	0.562	0.1240	0.365	0.867
23.00	9	1	0.500	0.1250	0.306	0.816
24.00	8	1	0.438	0.1240	0.251	0.763
Second clutches (n=8)						
6.25	8	1	0.875	0.117	0.6734	1.000
7.88	7	1	0.750	0.153	0.5027	1.000
8.00	6	1	0.625	0.171	0.3654	1.000
9.00	5	1	0.500	0.177	0.2500	1.000
14.00	4	1	0.375	0.171	0.1533	0.917
15.50	3	1	0.250	0.153	0.0753	0.830
16.38	2	1	0.125	0.117	0.0200	0.782
Third clutches (n=4)						
14.0	4	1	0.75	0.217	0.4259	1.000
15.6	3	1	0.50	0.250	0.1877	1.000
20.9	2	1	0.25	0.217	0.0458	1.000

Figure S5.2 Survival probabilities of 28 little bustard clutches by nest substrate (cereal, fallow and alfalfa). The graph shows Kaplan-Meier estimates (lines) and 95% confidence bands (shaded). Axis time comprises laying and incubation stages. The cross marks show hatching time of successfully incubated clutches.

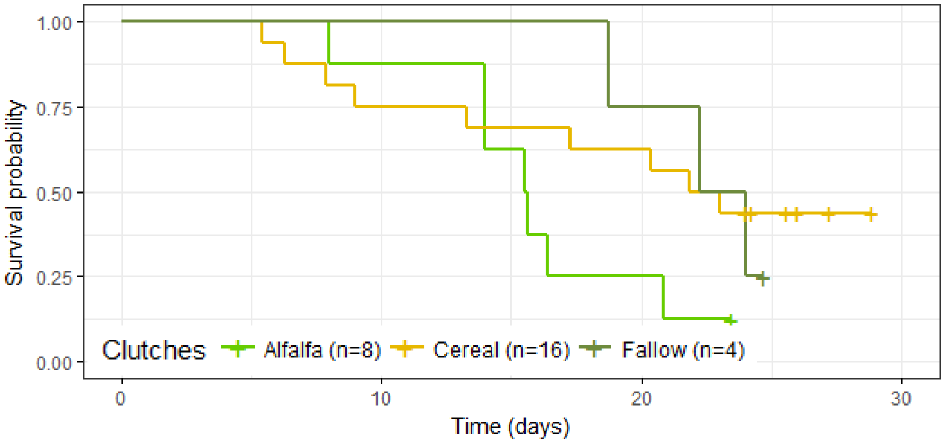


Table S5.5 Survival probabilities by Kaplan-Meier estimate of little bustard clutches in relation to the nest substrate.

Time (days)	N risk	N event	Survival prob.	S.E.	Lower 95% CI	Upper 95% CI
Cereal (n=16)						
5.38	16	1	0.938	0.0605	0.826	1.000
6.25	15	1	0.875	0.0827	0.727	1.000
7.88	14	1	0.812	0.0976	0.642	1.000
9.00	13	1	0.750	0.1083	0.565	0.995
13.25	12	1	0.688	0.1159	0.494	0.957
17.25	11	1	0.625	0.1210	0.428	0.914
20.38	10	1	0.562	0.1240	0.365	0.867
21.88	9	1	0.500	0.1250	0.306	0.816
23.00	8	1	0.438	0.1240	0.251	0.763
Fallow (n=4)						
18.8	4	1	0.75	0.217	0.4259	1.000
22.2	3	1	0.50	0.250	0.1877	1.000
24.0	2	1	0.25	0.217	0.0458	1.000
Alfalfa (n=8)						
8.0	8	1	0.875	0.117	0.6734	1.000
14.0	7	2	0.625	0.171	0.3654	1.000
15.5	5	1	0.500	0.177	0.2500	1.000
15.6	4	1	0.375	0.171	0.1533	0.917
16.4	3	1	0.250	0.153	0.0753	0.830
20.9	2	1	0.125	0.117	0.0200	0.782

Appendix 6

Table S6.1 Results for the best models (i.e., models within the 0.9 of the cumulative AICc weight) predicting the hathing probability of the Little Bustard. Models were based on 28 clutches in the Ebro Basin. The table shows estimates and standar error of the predictors included in the models. The R^2, the number of fixed effects (k), AICc, ΔAICc, AICc weight and the cumulative AICc weight are also shown.

Model	Intercept	Field size (nest)	Laying date	MCP 80% (laying + first inc. week)	Crop richness (300 m buffer)	Field size (300 m buffer)	R^2	k	AICc	ΔAICc	weight	cumulative weight
	β ± se	β ± se	β ± se	β ± se	β ± se	β ± se						
1	−3.33 ± 1.96	−6.47 ± 3.77		1.60 ± 1.21			0.401	2	33.526	0.000	0.173	0.173
2	−3.85 ± 2.22	−6.27 ± 4.14	−1.99 ± 1.03				0.401	2	33.532	0.007	0.172	0.345
3	−4.29 ± 2.53	−7.57 ± 4.70	−1.53 ± 1.09	1.12 ± 0.81			0.455	3	34.175	0.650	0.125	0.469
4	−4.27 ± 3.13	−6.84 ± 5.68	−2.51 ± 1.45		0.88 ± 0.74		0.440	3	34.917	1.391	0.086	0.556
5	−5.64 ± 3.43	−9.80 ± 6.24	−2.16 ± 1.36	1.41 ± 0.90	1.19 ± 0.81		0.506	4	35.034	1.508	0.081	0.637
6	−3.58 ± 2.21	−6.73 ± 4.20		2.03 ± 1.48	0.79 ± 0.72		0.434	3	35.249	1.723	0.073	0.710
7	−2.49 ± 1.34	−4.73 ± 2.71					0.264	1	36.319	2.793	0.043	0.752
8	−3.09 ± 2.02	−5.23 ± 4.07		2.24 ± 2.10		−0.84 ± 1.49	0.410	3	36.392	2.867	0.041	0.794
9	−4.30 ± 2.62	−7.34 ± 5.17	−2.04 ± 1.06			0.31 ± 0.79	0.405	3	36.651	3.125	0.036	0.830
10	−5.83 ± 3.38	−10.77 ± 6.70	−2.79 ± 1.37*		1.31 ± 0.78	1.35 ± 1.17	0.471	4	36.916	3.390	0.032	0.862
11	−4.14 ± 2.60	−7.12 ± 5.10	−1.49 ± 1.09	1.19 ± 0.88		−0.25 ± 1.19	0.456	4	37.729	4.203	0.021	0.883

Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Table S6.1 Results for the best models (i.e., models within the 0.9 of the cumulative AICc weight) predicting the hathing probability of the Little Bustard. Models were based on 28 clutches in the Ebro Basin. The table shows estimates and standar error of the predictors included in the models. The R^2, the number of fixed effects (k), AICc, ΔAICc, AICc weight and the cumulative AICc weight are also shown.

Model	**Intercept**	**Field size (nest)**	**Laying date**	**MCP 80% (laying + first inc. week)**	**Crop richness (300 m buffer)**	**Field size (300 m buffer)**	**R^2**	**k**	**AICc**	**ΔAICc**	**weight**	**cumulative weight**
	$\beta \pm$ se	$\beta \pm$ se	$\beta \pm$ se	$\beta \pm$ se	$\beta \pm$ se	$\beta \pm$ se						
1	−3.33 ± 1.96	−6.47 ± 3.77		1.60 ± 1.21			0.401	2	33.526	0.000	0.173	0.173
2	−3.85 ± 2.22	−6.27 ± 4.14	−1.99 ± 1.03				0.401	2	33.532	0.007	0.172	0.345
3	−4.29 ± 2.53	−7.57 ± 4.70	−1.53 ± 1.09	1.12 ± 0.81			0.455	3	34.175	0.650	0.125	0.469
4	−4.27 ± 3.13	−6.84 ± 5.68	−2.51 ± 1.45		0.88 ± 0.74		0.440	3	34.917	1.391	0.086	0.556
5	−5.64 ± 3.43	−9.80 ± 6.24	−2.16 ± 1.36	1.41 ± 0.90	1.19 ± 0.81		0.506	4	35.034	1.508	0.081	0.637
6	−3.58 ± 2.21	−6.73 ± 4.20		2.03 ± 1.48	0.79 ± 0.72		0.434	3	35.249	1.723	0.073	0.710
7	−2.49 ± 1.34	−4.73 ± 2.71					0.264	1	36.319	2.793	0.043	0.752
8	−3.09 ± 2.02	−5.23 ± 4.07		2.24 ± 2.10		−0.84 ± 1.49	0.410	3	36.392	2.867	0.041	0.794
9	−4.30 ± 2.62	−7.34 ± 5.17	−2.04 ± 1.06			0.31 ± 0.79	0.405	3	36.651	3.125	0.036	0.830
10	−5.83 ± 3.38	−10.77 ± 6.70	−2.79 ± 1.37*		1.31 ± 0.78	1.35 ± 1.17	0.471	4	36.916	3.390	0.032	0.862
11	−4.14 ± 2.60	−7.12 ± 5.10	−1.49 ± 1.09	1.19 ± 0.88		−0.25 ± 1.19	0.456	4	37.729	4.203	0.021	0.883

Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Appendix 7

Table S7.1 Results of the model averaging explaining the risk to fail for first clutches of the Little Bustard. The table indicates the estimates ± standard errors, the hazard ratio and the relative importance of predictors. Model averaging was conducted on a subset of the best models (i.e. selection probability in the best set of models based on the < 90% probability of cumulative weight) based on Cox models with female and year factors as random effects.

Predictors	Estimate	se	Hazard ratio exp(coef)	Predictor importance
First clutches (n=16)				
Laying date	0.17	0.17	1.18	0.96
Field size (nest)	0.87	0.34	2.39	0.22
Field size (300 m buffer)	0.18	0.23	1.19	0.18
Crop richness (300 m buffer)	–0.08	0.29	0.92	0.13
MCP 80% (laying + first week of incubation)	–0.02	0.27	0.98	0.13

Table S7.2 Results for the best Cox models with random effects (i.e., models within the 0.9 of the cumulative AICc weight) predicting the hazard to fail for first clutches of the Little Bustard. Female factor and year factor were included as random effects in the models based on 16 first clutches in the Ebro Basin. The table shows estimates and standar error of the predictors included in the models. The R^2, the number of fixed effects (k), AICc, ΔAICc, AICc weight and the cumulative AICc weight are also shown.

Model	Laying date	Field size (nest)	MCP 80% (laying + first inc. week)	Field size (300 m buffer)	Crop richness (300 m buffer)	R^2	k	logLik	AICc	ΔAICc	weight	cumulative weight
	β ± se	β ± se	β ± se	β ± se	β ± se							
1	0.08 ± 0.04*					0.284	1	–19.469	41.236	0.000	0.319	0.319
2	0.44 ± 0.17**	0.87 ± 0.34*				0.856	2	–6.631	42.201	0.965	0.197	0.516
3	0.09 ± 0.04*			0.16 ± 0.21		0.307	2	–19.211	43.355	2.120	0.110	0.626
4	0.08 ± 0.04*				–0.09 ± 0.29	0.289	2	–19.422	43.778	2.543	0.089	0.716
5	0.08 ± 0.04*		0.02 ± 0.25			0.285	2	–19.467	43.868	2.633	0.086	0.801
6						0.105	0	–21.256	45.430	4.194	0.039	0.840
7	0.08 ± 0.04*		–0.14 ± 0.32	0.25 ± 0.29		0.316	3	–19.104	46.220	4.984	0.026	0.867
8	0.09 ± 0.04*			0.15 ± 0.22	–0.04 ± 0.31	0.308	3	–19.201	46.414	5.178	0.024	0.891

Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

DISCUSSIÓ GENERAL

Les activitats antropogèniques han estat identificades com un dels principals factors responsables del declivi dels ocells esteparis, influenciant la seva distribució, l'ecologia tròfica, la supervivència i el seu èxit reproductor (Onrubia i Andrés 2005). Paradoxalment, les transformacions humanes són les que van permetre l'expansió territorial i poblacional de moltes d'aquestes espècies en el passat. Fa entre 7500 i 4500 anys l'esclarissada i l'eliminació de boscos per a l'agricultura i la ramaderia va oferir a moltes espècies d'ocells uns nous hàbitats que els hi proporcionaven totes les necessitats d'alimentació i nidificació que aquestes espècies requerien (Onrubia i Andrés 2005). En contrast, en les últimes dècades, el desenvolupament d'una agricultura cada cop més intensificada ha provocat que moltes d'aquestes espècies és trobin actualment en un estat de conservació preocupant (BirdLife International 2004, Burfield 2005).

El sisó comú a Europa depèn quasi exclusivament dels sistemes agrícoles i pastorals (Martínez 1994, Salamolard i Moreau 1999, Wolff et al. 2001, Silva et al. 2004, 2014a, Morales et al. 2005b, 2013, Delgado i Moreira 2010, Faria i Silva 2010, Santangeli i Dolman 2011, Lapiedra et al. 2011, Faria et al. 2012, Moreira et al. 2012, Ponjoan et al. 2012, Tarjuelo et al. 2013, Cuscó et al. 2018). De fet, podríem dir que aquesta dependència és extrapolable al conjunt de la seva població global. Ja que inclús en les àrees de distribució on l'hàbitat es podria considerar com més "natural", com per exemple, les estepes euroasiàtiques, s'hi produeixen sovint activitats agrícoles i ramaderes.

Ja en el passat, en algunes àrees orientals de la seva distribució, l'espècie va arribar a ser considerada com extingida en algunes zones de les estepes transurals i l'oest siberià, on als anys 70s i 80s l'espècie era quasi completament absent degut al desenvolupament agrícola en zones de l'estepa eurosiberiana. Durant el mateix període, una situació similar es va observar a les zones veïnes del Nord del Kazakhstan, on després d'una forta regressió, l'espècie ha començat a recuperar, gradualment, la seva distribució i nombre d'efectius poblacionals. Aquesta recuperació s'ha atribuït parcialment a l'abandonament de cultius després del col·lapse de la Unió Soviètica a l'any 1991 (Shlyakhtin et al. 2004, Kamp et al. 2011). En contrast, l'espècie actualment es considera extingida regionalment a Algèria, Àustria, Bielorússia, Bulgària, República Txeca, Alemanya, Grècia, Hongria, Moldàvia, Montenegro, Polònia, Sèrbia i Eslovàquia (BirdLife International 2017).

Normalment, els animals no es distribueixen en l'espai de manera aleatòria. Sinó que la seva distribució espacial és el resultat de la suma d'efectes de molts factors que, sovint, són difícils de separar els uns dels altres. Entre els factors ambientals, les característiques de l'hàbitat i la disponibilitat de recursos han sigut identificats com a factors principals en determinar el comportament espacial dels ocells (p.e., Newton 1998, Cardador i Mañosa 2011, Tarjuelo et al. 2013). En ambients creats per l'home, com els paisatges agrícoles, la distribució de les espècies depèn en gran mesura dels canvis o alteracions antropogèniques que en aquestes ambients s'hi produeixen (Brotons et al. 2004, Sirami et al. 2008, Regos et al. 2018).

En el **capítol 1**, hem pogut demostrar com el comportament espacial de les femelles de sisó durant el període no reproductor està influenciat per l'efecte independent de les variables d'hàbitat i per les limitacions espacials, així com pel seu efecte conjunt. Aproximadament un terç de l'agregació espacial observada en la distribució de les femelles de sisó estava relacionada amb les respostes a un entorn amb característiques adequades i agregat espacialment. Els patrons d'agregació observats suggereixen que la heterogeneïtat de la configuració del paisatge, és a dir com els diferents cultius es troben distribuïts en espai, està involucrada en el comportament espacial de les femelles de sisó. Majoritàriament, els patrons espacials de gran escala (~18 km) explicaven en major mesura la distribució de les femelles durant el període no reproductor, encara que altres patrons d'agregació que actuen a un nivell més local també hi estarien involucrats. Segons els nostres resultats, aquests patrons més locals (~3-5 km) estarien vinculats a l'activitat diària de les femelles.

Basant-nos en els nostres models, els hàbitats seleccionats per a les femelles de sisó durant el període no reproductor a la plana de Lleida serien terrenys plans amb presència de cultius herbacis de regadiu. Els models d'hàbitat van predir un efecte positiu en la probabilitat d'ocurrència en llocs heterogenis, amb disponibilitats intermèdies de cultius d'alfals i rostolls de blat de moro en regadiu, així com també en àrees dominades per rostolls de cereals en regadiu.

En referència a l'efecte de les infraestructures d'origen antròpic, els nostres resultats suggereixen que el sisó és una espècie flexible, en la que alguns individus poden exhibir habituació a les pertorbacions antropogèniques en paisatges altament humanitzats (veure també Martínez-Marivela et al. 2018). En el nostre estudi realitzat a la plana de Lleida, les femelles seleccionaven les zones pròximes a les carreteres. Desconeixem si la selecció d'aquestes zones té algun benefici per aquests individus, tot i que podria estar relacionat amb el fet que aquestes zones podrien presentar un menor grau de molèsties humanes o de depredadors naturals (Forman et al. 2003, Jaeger i Fahrig 2004). No obstant això, altres individus podrien ser sensibles als nivells d'estrès produïts per les molèsties d'origen antròpic (Casas et al. 2009, Tarjuelo et al. 2015).

Com hem mencionat anteriorment, les característiques de l'hàbitat i la disponibilitat de recursos determinen el comportament espacial i, conseqüentment, la distribució dels individus d'una població. Addicionalment, altres factors ambientals com el risc de depredació o les condicions antropogèniques poden afectar al comportament espacial dels individus (Le Cuziat et al. 2005, Alonso et al. 2012). Durant el període no reproductor, l'ús de l'hàbitat s'explica, per una banda, en la utilització de recursos tròfics en zones tranquil·les i segures que els hi ofereix una determinada estructura de la vegetació i, de l'altra, en l'agregació conespecífica (Martínez 1994, Gauger 2007, García de la Morena 2016).

En el **capítol 2** hem comprovat que els sisons presenten una elevada plasticitat tròfica, essent capaços de variar el seu comportament d'alimentació en funció de les condicions presents en diferents sistemes agrícoles. Els recursos tròfics que constitueixen la dieta hivernal del sisó comú a Espanya consistien fonamentalment en plantes lleguminoses cultivades (46.7%) i plantes arvenses de fulla ampla (45.6 %). Per altra banda, les espècies monocotiledònies eren consumides escassament (< 8%), tot i la seva elevada disponibilitat en les diferents àrees d'estudi. En concordança amb el que ja s'havia descrit en espècies properes com el pioc salvatge (Lane et al. 1999, Bravo et al. 2016).

En el nostre estudi, les lleguminoses cultivades van ser una important font d'aliment a l'hivern per al sisó, tant en regadiu (67% d'alfals) com en secà (26%, principalment veces *Vicia sativa*). Això no era sorprenent en les zones de regadiu, on l'alfals ocupava un 19% de la superfície, però va ser d'alguna manera inesperat a les terres de secà, amb només un escàs 1% de disponibilitat de cultius de lleguminoses. Aquest fet indica una forta preferència alimentària per les lleguminoses, tal i com ja s'havia reportat la selecció de les àrees amb cultius de lleguminoses exhibida per els sisons (Martínez 1994, Salamolard i Moreau 1999, Bretagnolle et al. 2011, Cuscó et al. 2018). Tot i aquesta aparent preferència per les plantes lleguminoses cultivades, les plantes no cultivades també van ser molt importants en la dieta hivernal de sisó. El domini de les plantes arvenses va ser notable a les terres de secà, on *Anacyclus clavatus*, *Papaver rhoeas*, *Diplotaxis erucoides* i *Capsella bursa-pastoris* van conformar la major part de la seva dieta. Aquestes plantes arvenses són abundants a la zona d'estudi (dades no publicades) i de gran importància per als sisons, ja que també s'han descrit com a les principals espècies que, juntament amb l'alfals, constitueixen la major part de la dieta primaveral a la plana de Lleida (Cuscó et al. 2013).

En canvi, als hàbitats de regadiu, on els alfalsars semblaven proporcionar un subministrament d'aliment pràcticament il·limitat, els sisons consumien un gens menyspreable 32% de plantes no cultivades. Hipotèticament, els sisons intentarien incorporar una major varietat d'espècies en al seva dieta hivernal per tal d'assolir una gamma completa de nutrients, ja que probablement els requeriments nutricionals de l'espècie no es poden satisfer en base a una sola espècie vegetal (Stephens i Krebs 1986, Raubenheimer i Simpson 1997).

Com ja hem mencionat anteriorment, les diferències a la dieta eren conseqüència de la disponibilitat dels diferents usos del sòl entre agrosistemes. A les zones de secà, la composició de la dieta era molt més diversa, composta principalment per plantes arvenses i lleguminoses. Aquestes plantes probablement van ser proporcionades per rostolls de cereals, que tenen una major disponibilitat de plantes (Ponce et al. 2014, observació personal). En alguns ambients de secà amb cultius de *V. Sativa* proporcionats pels programes d'esquemes agroambientals (Ponce et al. 2014), les lleguminoses conreades eren dominants en la dieta del sisó, tot i que aquestes tan sols ocupaven un 2% de la superfície ocupada per conreus. En altres zones de secà, on conreus de lleguminoses encara eren menys disponibles, la dieta era més diversa, basada en una barreja de lleguminoses i plantes arvenses, o bé composta principalment per plantes arvenses, probablement depenent de la composició dels usos del sòl de cada localitat. Per tant, els sisons segueixen la predicció de la teoria òptima d'alimentació, que proposa que la diversitat alimentària disminueix a mesura que augmenta l'abundància del recurs preferit (Stephens i Krebs 1986). Així, en àrees de regadiu on les lleguminoses són el conreu herbaci dominant, els sisons presenten un espectre tròfic reduït, basat fonamentalment en alfals, malgrat disposar en alguns casos d'una bona densitat de marges i diversitat d'hàbitats, que podria completar una dieta potencialment pobre o poc diversa (Ottens et al. 2014). De tota manera, tampoc podem obviar la possibilitat que la baixa diversitat de la dieta del sisó al regadiu reflecteixi la reduïda disponibilitat de recursos alternatius com a conseqüència de la intensificació agrícola tal com s'ha informat en altres espècies (Britschgi et al. 2006, Moorcroft et al. 2006, Cardador et al. 2012b), i si l'alt consum d'alfals té implicacions en la supervivència i reproducció de l'espècie, donat que és un cultiu gestionat de manera intensiva on s'hi apliquen grans quantitats de pesticides (Barker et al. 1980, Almacelles i Perdiguer 2007, Cantero-Martínez i Moncunill 2012).

Encara que en la present tesi no s'han analitzat els efectes nutricionals i toxicològics sobre la supervivència dels individus i la seva reproducció, s'han analitzat les principals causes que determinen la mortalitat adulta (**capítol 3**) i la productivitat (**capítol 4**), com un primer pas imprescindible per comprendre els impactes antropogènics sobre la dinàmica poblacional de l'espècie.

Així, en el **capítol 3** s'han estimat per primera vegada les taxes de mortalitat adulta del sisó a partir d'una mostra relativament gran d'ocells i en un rang geogràfic extens, de Catalunya a Portugal. Aquest treball és especialment important ja que posa xifres a l'impacte directe d'origen antròpic sobre la supervivència adulta en el baluard poblacional de l'espècie a Europa, contribuint a l'avaluació de les seves necessitats de conservació a escala global. El seguiment d'animals no només ens va permetre estimar les taxes de mortalitat, sinó que també es va obtenir informació sobre les principals causes de mort.

El percentatge de supervivència adulta anual estimada va ser de només el 67%, similar al 68–72% estimat per a la part occidental de França quan la població estava en declivi entre 1998 i 2003 (Inchausti i Bretagnolle 2005). Cal destacar, que aquestes xifres són més baixes que les trobades en altres otídides paleàrtiques vulnerables, com és el cas del pioc salvatge *Otis tarda* (82–93%, Palacín et al. 2017) o l'hubara africana *Chlamydotis undulata* (72–79%, Hardouin et al. 2015).

En referència a les causes de mort, la mortalitat antropogènica sorprenentment va ser gairebé tant elevada com la mortalitat anual registrada per depredació. Aquestes elevades taxes de mortalitat estimades són coherents amb la tendència global de disminució de l'espècie (Morales et al. 2015). La primera causa de mortalitat antropogènica identificada en els nostres models va ser la mortalitat per col·lisió amb línia elèctrica. Aquesta, s'ha estimat que causa la mort anualment del 3.4% o del 3.8% , en funció dels models, de la població adulta. Aquests valors podrien arribar fins al 11.4% o el 13.1% si considerem els intervals de confiança superiors dels nostres models. Realitzant una comparació amb estudis previs es constata que la taxa anual de mortalitat per col·lisió amb línia elèctrica és una de les més elevades registrades per a una espècie en particular (Infante et al. 2005, Jenkins et al. 2010, Silva et al. 2010b). A més a més, el fet que els nostres resultats es basin en dades de seguiment d'ocells amb emissors proporciona estimacions robustes de les taxes de mortalitat ja que aquestes són menys susceptibles als possibles biaixos d'altres mètodes (p.e. Naef-Daenzer et al. 2017).

La segona principal amenaça per a la supervivència adulta del sisó va ser la mort il·legal per tret amb una taxa de mort anual estimada del 2.4% i del 3%, segons el model. Encara que podria arribar fins al 8.7%, tal i com indicava l'interval superior del model més conservador. Aquestes dades són molt importants des d'un punt de vista de la conservació de l'espècie. Tot i que sabem que en el passat el sisó era una espècie objecte de caça a Espanya i Portugal, existeixen poques referències de tradició de caça del sisó a la península Ibèrica (veure Smith 1868). No obstant això, l'amenaça de la caça ja s'havia identificat com a important per Iñigo i Barov 2010, encara que la seva importància mai abans s'havia quantificat.

En referència a la depredació, tot i que les aus rapinyaires eren responsables de la majoria dels casos identificats, no va ser possible determinar estadísticament si eren depredadors més importants que els mamífers. No obstant això, cal assenyalar que el sisó a la península depèn dels paisatges creats per l'home i de les pràctiques agrícoles. Els canvis en els paisatges agrícoles o com aquests es gestionen poden tenir un paper decisiu en la taxa de depredació (Whittingham i Evans 2004). Per exemple, les pastures sobrepasturades podrien provocar que els ocells estiguessin més exposats a la depredació a causa de la reducció de la vegetació. A més, els cultius de regadiu més intensificats poden conduir a taxes de molèsties més altes i l'augment de la urbanització del paisatges rurals pot afavorir un nombre creixent de depredadors associats als humans. Per tant, la nostra mortalitat designada com a "natural" pot dependre molt de com es transformi i/o gestioni l'hàbitat. El nostre treball mostra com les amenaces poc conegudes i fins i tot desconegudes anteriorment estan afectant la supervivència de la població de sisó més important de l'Europa occidental. Addicionalment, altres causes de mort podrien entrar en joc, com és el cas de la intoxicació per aliments contaminats amb plaguicides (veure **capítol 2**), i que a falta de necròpsia no es va poder avaluar i, en cas d'haver-n'hi, s'haurien classificat com a casos de mort per causes naturals.

Així doncs, les morts per causes antropogèniques semblen tenir una major importància del que inicialment es preveia per aquesta espècie. La reducció de la mortalitat antropogènica pot tenir un impacte positiu important en la viabilitat de l'espècie, especialment per a poblacions que mostren una baixa productivitat reproductiva (Bretagnolle et al. 2011, 2018, Lapiedra et al. 2011).

En espècies de vida relativament llarga, com és el cas del sisó, la productivitat juntament amb la mortalitat adulta s'han descrit com els dos paràmetres demogràfics més rellevants en la dinàmiques poblacionals (Newton 1998, Morales et al. 2005a). Així, en el **capítol 4** s'ha emfatitzat en els aspectes relacionats amb la reproducció i productivitat de l'espècie. Addicionalment, s'han descrit per primera vegada els patrons d'incubació de les femelles de sisó.

En el nostre estudi la productivitat de les femelles de sisó va ser de 0.25 polls/femella, molt similar al valor que s'havia reportat prèviament per a la plana de Lleida (Lapiedra et al. 2011). Al igual que en aquell estudi, també vàrem detectar que una part de les femelles (16%) no efectuava cap intent de pondre en algunes de les temporades reproductives. En canvi, algunes femelles van presentar fins a 3 postes en una mateixa temporada reproductiva. Aquestes, eren postes de reposició que tenien lloc després de que el niu fracassés o bé per la mort prematura dels polls durant els primers dies de vida. En referència al lloc de nidificació, existia una elevada correspondència entre el substrat del niu i l'ordre de posta (primera, segona o tercera posta) que podria estar relacionada amb la fenologia dels cultius de cereal. Mentre que en les primeres postes, els nius es situaven en major freqüència en el cereal, tal com s'havia observat prèviament a la plana de Lleida (Ponjoan 2012), una vegada té lloc la collita del cereal, es produeix una pèrdua d'hàbitat per a la nidificació a les zones de secà i, aleshores, les postes de reposició es localitzen en alfalsars de regadiu.

La nostra estimació de la durada d'incubació (20.7 ± 1.0 dies) va ser coherent amb la bibliografia publicada (Cramp i Simmons 1980, Johnsgard 1991). No obstant, les femelles començaven a visitar el niu i pondre els ous 4.9 ± 1.8 dies abans de l'inici de la incubació. Per altra banda, aquesta és la primera vegada que es quantifiquen les taxes de reposició per a l'espècie. Els nostres resultats indiquen que les reposicions de les postes fracassades són molt més freqüents del que s'havia descrit anteriorment (Lapiedra et al. 2011, Bretagnolle et al. 2018). De fet, el 67% de les femelles que van perdre el seu primer niu van iniciar una segona posta, que podia ser reemplaçada tan aviat com 5 dies després de la pèrdua de la posta anterior, i el 57% de les que perdien la segona posta en van fer una tercera. Amb tot, el període de posta a la zona d'estudi s'estén durant més de 12 setmanes, al igual que a l'oest de França (Bretagnolle et al. 2018). No obstant, les primeres postes es comprenien en un període de poc més de 4 setmanes, mentre que les segones postes tenien lloc durant més de 8 setmanes i eren les responsables de l’extensió del període de posta global.

Durant el període de nidificació, les femelles, generalment, mostraven fidelitat al lloc de cria d’un any a l’altre. No obstant, algunes femelles es podien desplaçar considerablement, fins a 100 km, per a situar les postes de reposició, o bé utilitzar noves zones de nidificació en anys successius que podien estar tant llunyanes com 142 km. Ambdós casos, probablement, estan relacionats amb el fet que les femelles de sisó intenten trobar les millors condicions per a reproduir-se i que reflecteix la capacitat d’aquesta espècie per a rastrejar les condicions ambientals al llarg de grans extensions de terreny. A més a més, cal destacar que les femelles podrien anar ampliant les seves àrees de cria amb l’edat, tal i com hem observat per a la femella que va ser monitoritzada durant més anys. Tant els desplaçaments per a pondre les postes de reposició com els canvis de zones de cria entre temporades reproductives poden ser relativament grans i podrien contribuir a la connectivitat genètica entre nuclis poblacionals relativament distants. Aquest resultat és especialment rellevant, degut a la baixa diversitat genètica per a la majoria de les poblacions de sisó a Espanya (García et al. 2011).

L’atenció al niu es veu afectada per una varietat de factors que influencien la reproducció dels ocells. Aquests inclouen la participació d’un o dels dos progenitors, requeriments nutricionals, l’estadi d’incubació i les condicions climàtiques (Skutch 1962). Tal i com s’ha vist en el **capítol 4**, les femelles van mostrar valors intermedis d’atenció al niu durant la posta, mostrant una major assistència al niu durant el migdia. En el moment d’incubar, el percentatge d’atenció al niu va augmentar fins al 86.8% de mitjana. Tanmateix, aquesta és una estima a la baixa, donat que les nostres dades no comprenien el període nocturn, en el que cal suposar una atenció al niu més elevada. D’altra banda, el patró bimodal en les sortides diàries del niu observades durant el període d’incubació, amb una menor freqüència de sortides durant al migdia i al vespre, mostra que no només les baixes temperatures poden afectar als patrons en el comportament d’incubació de les femelles de sisó, sinó que també una forta radiació solar. De la mateixa manera, aquest patró és coherent amb altres estudis centrats en espècies relacionades o que habiten ambients similars (Deeming et al. 2001, Mougeot et al. 2014). Aquest patró podria haver evolucionat ja que la hipertèrmia és clarament més perjudicial per al desenvolupament de l'embrió que la hipotèrmia (Webb 1987). No obstant això, altres factors no exclusius entre ells podrien explicar aquest patró, com per exemple, els requeriments energètics de les femelles. Per un altre costat, l'atenció al niu augmentava al llarg de la temporada reproductiva, fet que podria estar relacionat amb els requisits tèrmics, però parcialment també relacionat amb la disponibilitat de recursos tròfics propers al niu.

Tanmateix, l'assistència al niu incrementava en els últims dies d'incubació, tendència que s'ha observat en altres espècies, però que no és de cap manera un patró universal, ja que les diferents espècies presenten estratègies diverses (Skutch 1962). Aquest fet podria estar relacionat amb la necessitat de protecció dels embrions o dels polls després d'eclosionar. Sorprenentment, tot i que l'atenció al niu augmentava, el risc de fracassar s'incrementava també durant els últims dies d'incubació. No obstant això, ja que el moment d'eclosió era estimat i s'assumeix algun petit error (p.e., no disposàvem de dades d'activitat nocturna), alguns d'aquests fracassos podrien incloure la mort prematura dels polls poc després de l'eclosió, ja que és un moment crític i que podria explicar aquesta probabilitat incrementada de fracassar en les hores pròximes al moment d'eclosió.

Al començament de la temporada reproductora les postes tenien lloc en els secans, però després de l'inici del mes de juny aquestes es situaven en camps d'alfals al regadiu. Els nius eren situats a distàncies variables dels marges del camp, depenent del substrat del niu. En postes localitzades en cereal, els nius es trobaven més pròxims als marges, ja que les femelles depenien dels marges per alimentar-se, mentre que en les postes situades en guarets o camps d'alfals, les femelles disposaven d'aliment en grans quantitats dins del mateix camp (**capítol 2**). La importància de la vegetació herbàcia permanent o semipermanent ha estat destacada per aquesta espècie en nombrosos treballs (Martínez 1994, Salamolard i Moreau 1999, Silva 2010, Lapiedra 2011 et al., Morales et al. 2013, Tarjuelo et al. 2013), ja que aquests recursos proporcionen plantes verdes per als sisons reproductors (Jiguet et al. 2002, Cuscó et al. 2013) i també podrien oferir refugi en cas de presència de depredadors (Martínez 1994, Morales et al. 2008). Aquest punt és especialment important durant les etapes de posta i incubació. Durant la posta, les femelles han d'acumular reserves per a la incubació i tenir fonts d'aliment properes al niu afavoreix un menor temps en els torns de sortida per la cerca d'aliments durant la incubació, que les femelles podrien invertir en altres activitats com ara activitats de manteniment propi (Londoño et al. 2008).

Donat a que els marges dels camps són un hàbitat propens a la depredació (Benson et al. 2010), les femelles de sisó podrien haver de fer front a un compromís entre l'accessibilitat als recursos tròfics i al comportament antidepredador, donat que la depredació és una causa principal de la pèrdua de nius en ocells (Martin 2004) i al fet que en les espècies en les quals cova tan sols un dels progenitors el temps destinat a l'alimentació sol ser restringit (Mertens 1977, Conway i Martin 2000).

Als paisatges agrícoles de secà, els guarets eren el substrat preferit per a la nidificació, encara que la majoria dels nius van tenir lloc en cereal, que era l'hàbitat dominant d'aquests paisatges. Tot i que eren preferits, en els guarets l'èxit d'eclosió va ser baix (25.0%), degut a que molts es troben subjectes a la pastura, al llaurat, al trepig o fins i tot a l'abocament de purins, els quals poden causar danys a la posta o bé l'abandonament del niu. Als cultius de cereal, l'èxit d'eclosió era també baix (43.8%), valor similar al que prèviament s'havia informat per a la mateixa zona (47%, Lapiedra et al. 2011). Mentre que en els camps d'alfals, l'èxit d'incubació es va situar en un ínfim 12.5%, donant un èxit d'eclosió global de tan sols el 32.1%. Aquest és un valor extremadament baix, fins i tot si el comparem amb l'èxit d'eclosió descrit per a la fràgil població de l'oest de França (41.6%, Bretagnolle et al. 2018). Contràriament al que succeeix a altres zones agrícoles on les femelles de sisó nidifiquen principalment en alfals (Bretagnolle et al. 2011), les pèrdues al cereal s'associaven majoritàriament a la deserció/depredació més que no pas a les pràctiques agrícoles, que tan sols representaven un baix 11.1% dels fracassos. I és que en les espècies d'ocells que nidifiquen a terra es preveuen altes taxes de depredació dels nius (Martin 1995, Davis 2003) i això, probablement, podria ser una causa important de fracàs en les postes de sisó, com s'ha mostrat en altres ocells esteparis que nidifiquen a terra (Ena et al. 1987, Yanes i Suárez 1995, Calero-Riestra et al. 2013, Gaget et al. 2018).

Basant-nos en els nostres models, la data de posta va tenir un fort impacte en l'èxit d'eclosió. Aquest fet es deu principalment al canvi de substrat de nidificació a mesura que avança la temporada reproductora i a l'èxit d'eclosió diferencial entre els diferents substrats. No obstant, mentre que el canvi de substrat i les pràctiques agrícoles associades a aquests expliquen el baix èxit d'eclosió de les postes de reposició, una proporció rellevant de primeres i segones postes situades en cereal eren abandonades o depredades abans que ninguna pràctica agrícola les destruís.

Tot i això, els nostres resultats no suggereixen que estiguem davant d'un problema de baixa condició física de les femelles que modifiqui el comportament d'incubació de les femelles i que indueixi a l'abandonament o depredació del niu. Els arguments que ens fan creure això són que no vam detectar diferències en els patrons d'atenció al niu entre les postes eclosionades i les postes fracassades per causes naturals i que la majoria de les femelles que perdien la posta eren capaces de fer una posta de reposició, unes condicions que no semblen compatibles amb una baixa condició corporal. Alternativament, els nostres resultats indiquen que l'èxit d'eclosió està inversament relacionat amb alguns factors d'intensificació agrícola, com ara la mida del camp on està situat el niu i la diversitat d'hàbitat al voltant d'aquest. Això, és conseqüent amb les nostres troballes que mostren que incrementant la disponibilitat de recursos tròfics al voltant del niu és redueix el rang de moviment de les femelles, ja que la distancia que les femelles han de recórrer en la recerca d'aliment és més petita i l'atenció al niu augmenta.

Entrat el mes de juny, cap de les postes va tenir lloc a les zones agrícoles de secà. L'explicació més raonable d'aquest fet seria que es produeix un deteriorament de les condicions ambientals al llarg del període reproductor. Per aquesta època, el cereal ha madurat i els marges i guarets s'han assecat, per tant els camps d'alfals ofereixen un substrat de nidificació més atractiu. No obstant això, a causa de les pràctiques agrícoles, l'èxit d'eclosió en aquest substrat, com en el cas de França, és baix. Això es degut a que el temps entre les activitats agrícoles en els cultius d'alfals (reg per inundació o sega) és més curt que la suma de la durada de la posta i la incubació (≈ 25 dies). A més a més, les femelles de sisó necessiten per niar un mínim d'alçada de la vegetació (~ 40 cm) (Bretagnolle et al. 2018, dades no publicades), cosa que suposa que quan les femelles comencen a covar en els camps d'alfals el moment de la sega del cultiu es troba relativament a prop. Així doncs, les pràctiques agrícoles vinculades al maneig d'aquests cultius els podrien convertir en una trampa ecològica en les zones on la majoria de postes ocorren en aquests cultius (Bretagnolle et al. 2018).

Així, els nostres resultats indiquen que els cultius d'alfals podrien actuar com un embornal atractiu per la majoria de postes de reposició, ja que el 67% d'aquestes tenen lloc en alfals, però només el 17% d'elles arribaven a eclosionar. El fet que les femelles que covaven en alfals presentaven menors distàncies en les sortides al niu, una major atenció al niu, àrees vitals més petites i una major disponibilitat de recursos tròfics dóna suport a la idea que els alfalsos proporcionen un hàbitat d'alta qualitat en quan a la disponibilitat de recursos tròfics, però si no s'adapten les actuals pràctiques de maneig d'aquests cultius, com són el reg per inundació o els intervals entre segues, aquesta situació podria conduir a l'extinció local dels sisons a la plana de Lleida.

Implicacions de l'alta dependència als cultius d'alfals intensificats

Tant en el **capítol 1** com en el **capítol 2**, hem comprovat com els sisons fora del període de reproducció presenten una forta preferència per als cultius d'alfals, ja que la seva distribució espacial i la seva dieta depenien en gran mesura de la disponibilitat d'aquests cultius. Més enllà de que els alfalsars semblen proporcionar un recurs tròfic adient durant l'hivern, aquesta alta dependència cap a aquest recurs, sovint tractat de manera intensiva, podria tenir certes conseqüències negatives sobre la condició física dels individus que podrien repercutir en la reproducció i supervivència dels individus.

Des d'un punt de vista de la ecologia de l'espècie, la forta dependència a les lleguminoses podria donar lloc a un sistema vulnerable, on els sisons podrien ser molt sensibles als canvis en els usos del sòl. Els cultius d'alfals semblen actuar com illes d’hàbitat envoltades d’un entorn inadequat, com per exemple cultius llenyosos de fruita dolça i llaurats (Silva et al. 2004, Cuscó et al. 2018), de manera que la disminució de la superfície d’alfals o l’aïllament entre aquestes illes podria comportar l’abandonament d’aquestes zones per part dels sisons (Saunders et al. 1991, Brotons et al. 2004), tal i com ha estat recentment descrit per Morales et al. (2015) a la vall del Tajo.

Addicionalment, els beneficis d’una dieta diversa sobre la condició física, el creixement o la supervivència, han estat comunicats per a diverses espècies, particularment herbívores (Lefcheck et al. 2013), per la qual cosa és probable que una dieta reduïda basada principalment en l’alfals no compleixi amb el rang complet de nutrients que són requerits pels sisons. De fet, com s’ha mencionat anteriorment, els nostres resultats indiquen que, fins i tot en àrees dominades per alfals, s’inclouen una elevada proporció de plantes arvenses en la dieta, suggerint que el sisó necessita equilibrar la seva dieta hivernal amb varietat d’espècies de plantes.

En el **capítol 1**, també hem pogut observar com algunes femelles presentaven una àrea vital relativament petita durant el període no reproductor, segurament relacionada amb l’explotació de manera intensiva d’unes poques parcel·les d’alfals. Prèviament, s’ha descrit com els bàndols de sisó a la plana de Lleida utilitzen recurrentment els mateixos camps agrícoles (Meca et al. 2013), i aquests poden concentrar centenars d’individus. Aquesta explotació intensiva de l’espai juntament amb l’elevada agregació conespecífica de l’espècie durant el període no reproductor podria tenir certes conseqüències en la condició física dels individus, ja que facilitaria la transmissió de paràsits i malalties (Anderson i May 1978, Mennerat et al. 2010). A més, l’aplicació de fertilitzants d’origen orgànic, tals com els purins i la gallinassa poden contaminar el sòl amb patògens parasitaris i bacterians i afectar les poblacions d’animals salvatges (Olson 2001, Hutchison et al. 2005).

Addicionalment, com ja assenyalàvem anteriorment, els cultius d’alfals al regadiu són gestionats de manera intensiva als quals s’apliquen elevades quantitats de pesticides (Barker et al. 1980, Almacelles and Perdiguer 2007, Cantero-Martínez i Moncunill 2012). És ben conegut que l’ús d’aquests compostos té efectes directes o indirectes sobre la vida silvestre aviària, comprometent la supervivència dels ocells o el seu èxit reproductor a causa de la intoxicació per la ingesta d’aliment, sòls o aigües contaminades (Fry 1995, Lemly et al. 2000). D’aquesta manera, els possibles efectes negatius que pot tenir la gran dependència a l’alfals com a recurs tròfic hivernal sobre les poblacions de sisó i sobre altres ocells d’ambients agrícoles mereixen més atenció des d’un punt de vista ecològic, nutricional i toxicològic.

A més a més, aquesta dependència envers als conreus d’alfals de regadiu no solament es produeix durant l’hivern, sinó que també s’ha fet palesa en el **capítol 4** pel que fa al període reproductor, durant el qual hem observat que l’alfals es converteix en el principal conreu disponible capaç d’acollir les postes de reposició tardanes, amb conseqüències nefastes per a la supervivència d’aquestes postes.

Consideracions demogràfiques

La productivitat i la mortalitat adulta són paràmetres clau per a la viabilitat de les poblacions animals. Aquests paràmetres demogràfics adquireixen una major transcendència en espècies de vida relativament llarga (Begon et al. 2005). La baixa productivitat detectada de tant sols 0.25 polls/femella i any (**capítol 4**) és del tot insuficient per mantenir una població de sisó viable, ja que es considera que perquè una població de sisó persisteixi en el temps s’hauria d’assolir una productivitat mínima d’un poll per femella (Inchausti i Bretagnolle 2005). Els nostres valors de productivitat, han demostrat ser molt consistents amb els resultats trobats anteriorment a la plana de Lleida (Lapiedra et al. 2011), la qual cosa ens fa pensar que no s’han produït canvis significatius que empitjorin la productivitat de l’espècie, però tampoc que en millorin l’alarmant situació actual. Cal destacar però, que existeix un forta variabilitat interanual en la productivitat que, probablement, estaria relacionada amb les condicions meteorològiques anuals i la fenologia de la vegetació (Morales et al. 2002, Delgado et al. 2009, Delgado i Moreira 2010). En el nostre estudi la productivitat va ser nul·la per a la majoria dels anys i només al 2011 es van reclutar polls de >30 dies, essent la productivitat per aquell any de 0.83 polls/femella. Recentment, aquesta variabilitat interanual en la productivitat de les femelles de sisó també ha estat descrita per a les poblacions franceses (Bretagnolle et al. 2018). Però cal advertir que aquestes estimacions es basen en mides mostrals anuals relativament petites i estan subjectes a certs biaixos.

Els estudis basats en models de viabilitat poblacional de les poblacions de sisó han destacat que la productivitat i la supervivència adulta serien els paràmetres més importants per a la preservació de les poblacions de França (Inchausti i Bretagnolle 2005, Morales et al. 2005a) i d'Espanya (Delgado et al. 2009). De fet, Delgado et al. (2009) ressalten que serien la supervivència de les femelles adultes i la seva productivitat els dos paràmetres més importants per a la dinàmica poblacional de l'espècie. Això es deu, principalment, al fet que els sisons presenten un sistema d'aparellament poligínic (veure Legendre 2004) i que en aquest estudi s'estimava una mortalitat diferencial entre mascles i femelles amb un 5% més de supervivència per als mascles dins de la població de més d'un any d'edat. Les diferències en la mortalitat entre sexes es basaven en que la raó de sexes observada per les poblacions estudiades semblava estar força esbiaixada cap als mascles adults (1.39–1.85 mascles per femella). De la mateixa manera que ho estarien altres poblacions europees, com les franceses (1.47±0.12 mascles per femella) (Inchausti i Bretagnolle 2005). Aquest biaix en la raó de sexes s'ha relacionat amb una major mortalitat de les femelles relacionada amb la reproducció i cria dels polls (Bretagnolle et al. 2011, 2018). No obstant això, podria existir cert biaix en aquestes estimes degut a que les femelles de sisó presenten un comportament discret (Cramp i Simmons 1980) i són molt més difícils de detectar que els mascles. A la plana de Lleida, segons dades inèdites basades en un mètode basat en la determinació del sexe mitjançant fotografies de bàndols de sisó en vol i que no està subjecte al biaix de detecció entre mascles i femelles, la raó de sexes no sembla estar tant desequilibrada com en els casos anteriorment mencionats, tot i això hi haurien més mascles que femelles (dades pròpies). Obtenir estimacions fiables de la proporció de sexes és important ja que una raó de sexes esbiaixada envers als mascles podria provocar una disminució de la productivitat deguda a l'escassetat de femelles (Tarjuelo et al. 2013).

Com ja hem avançat, aquest biaix en la raó de sexes s'explicaria per una major mortalitat de les femelles, ja que s'espera que la natalitat d'ambdós sexes estigui relativament equilibrada (Martín et al. 2007, Székely et al. 2014). No obstant, ni en l'estudi sobre mortalitat (**capítol 3**) ni en l'estudi de la incubació (**capítol 4**), no hem detectat cap mort per efecte directe de la sega, com si que han apuntat altres treballs (Bretagnolle et al. 2018), encara que les femelles quedarien molt més exposades als depredadors un cop la sega s'ha produït.

Per altra banda, els valors de supervivència adulta obtinguts en el **capítol 3** propers al 70% no serien suficient per a mantenir les poblacions de sisó d'acord amb les simulacions realitzades per a les poblacions occidentals de França, donant lloc a probabilitats de supervivència de la població del 0.6 (Morales et al. 2005a). Tot i que aquestes prediccions partien de mides poblacionals molt inferiors a les que trobem a la península Ibèrica. En base al mateix estudi, l'increment d'un 10% en la supervivència adulta podria tenir un efecte molt positiu en la viabilitat de les poblacions de sisó a la península (Morales et al. 2005a).

Addicionalment, l'esperança de vida podria ser un paràmetre demogràfic a tenir en compte, ja que aquest determina les vegades que un individu es pot reproduir potencialment al llarg de la seva vida (Lessells 1991). Realment, es desconeix quina és l'esperança de vida mitjana dels sisons adults en condicions de llibertat. L'edat màxima descrita per a l'espècie en condicions de llibertat és de 18 anys, fruit d'una observació al centre-oest de França. Recentment, s'ha reportat l'observació d'un mascle de 14 anys a la plana de Lleida (Mañosa et al. 2018; en premsa).

Tornant a la productivitat, en el **capítol 4** hem pogut observar com a la plana de Lleida la baixa productivitat s'explicava per un baix èxit d'eclosió, però també per una baixa supervivència de les pollicades i al fet que algunes femelles en algunes temporades reproductives no arribaven a pondre. De les 19 oportunitats de reproducció potencials, en 3 casos les femelles no van pondre (16%). De les que si que van pondre, es van obtenir un total de 28 postes de les que els fracassos d'incubació confirmats van ser elevats (67.9%), principalment degut a la ínfima taxa d'eclosió de les postes de reposició (16.7%), ja que aquestes postes tenen lloc, majoritàriament, en camps d'alfals de regadiu on els fracassos s'associen principalment a les activitats agrícoles, mentre que en camps de cereals i guarets aquestes representaven una baixa proporció de fracassos. Tanmateix, pel conjunt de les postes, només un 36.8% de les postes fracassades es podien relacionar amb causes agrícoles.

Excloent les postes de reposició, on l'afectació de les activitats agrícoles era molt elevada, els nostres resultats van mostrar que l'èxit d'eclosió era relativament baix també entre les primeres postes (43.8%). Aquest valor és similar a la taxa d'eclosió trobada anteriorment a la Plana de Lleida (47.1%) (Lapiedra et al. 2011). Aquests valors relativament baixos en l'èxit d'eclosió, probablement, estarien relacionats amb el fet que en les espècies que nidifiquen a terra, es preveuen altes taxes de depredació dels nius (Martin 1995, Davis 2003) i això probablement podria ser una causa important de fracàs en les postes de sisó. No obstant, les diferències trobades en el risc de fracàs, amb un increment substancial de fracassar cap al final de la incubació, ens fa pensar que altres factors poden estar intervenint. El fet que vàrem detectar algunes femelles no arribaven a pondre en alguns anys, probablement es podria atribuir a que aquestes no van assolir una bona condició corporal per a reproduir-se, ja que tenir suficients reserves acumulades és fonamental per a la producció dels ous i l'acte d'incubació (Lack 1968, O'Connor 1984). Hipotèticament, aquest augment del fracàs al llarg de la incubació es podria atribuir a una reducció de la condició corporal causada per l'esgotament físic de les femelles al llarg del procés d'incubació. No obstant això, l'elevada taxa de reposició de le postes fracassades ens fa pensar que no existeix un problema de condició física, almenys per a les femelles que inicien la posta.

Pel que fa a la supervivència de les pollicades, del total de 9 postes eclosionades, tan sols en 3 d'elles algun dels polls de sisó va assolir l'edat de 30 dies, la qual cosa donaria un 66.7% de mortalitat completa de les pollicades que eclosionaven. Aquest valor és pràcticament el doble del trobat prèviament a la zona d'estudi (Lapiedra et al. 2011), on la mortalitat de les pollicades era del 37.5%. No obstant, per a determinar la supervivència dels polls s'hauria de tenir en compte el nombre de polls que arriben a sortir de l'ou, cosa que en el nostre estudi va ser difícil de determinar, ja que no visitàvem els nius fins que les femelles finalitzaven, amb èxit o no, la incubació. Tanmateix, segons Schulz (1987) només el 54% dels polls semblen sobreviure fins esdevenir adults. La baixa supervivència dels polls s'ha atribuït a la disminució de l'abundància d'artròpodes després del període de sega (Inchausti i Bretagnolle 2005, Bretagnolle et al. 2011, Lapiedra et al. 2011) i que es agreujada a causa de la intensificació agrícola. Cal destacar que la dieta dels polls durant les primeres setmanes de vida es basa en el consum d'artròpodes, principalment, coleòpters i ortòpters (Jiguet 2002). A més, l'escassetat de zones de refugi després de la sega podria tenir efectes sobre la mortalitat dels polls (Lapiedra et al. 2011) i que es veuria incrementada per algunes pràctiques agrícoles perjudicials com el llaurat dels rostolls de cereal en només 7-10 dies després de la sega (Lapiedra et al. 2011), pràctica que sembla haver-se accelerat en els últims anys (observació personal). Així que una gran part de l'hàbitat per a les famílies de sisó quedaria llaurat molt ràpidament deixant als sisons sense recursos tròfics ni suficients zones de refugi.

Finalment, tot i que els moviments migratoris no han estat tractats en aquesta tesi, cal mencionar que aquests poden ser importants en les dinàmiques poblacionals dels animals. Els sisons a la península Ibèrica s'han descrit com a sedentaris o migradors parcials (Cramp and Simmons 1980), però veure García de la Morena et al. (2015). Aquests moviments tindrien lloc bàsicament entre les zones de reproducció i els emplaçaments d'hivernada. Degut a la alta fidelitat a les zones de cria (García de la Morena et al. 2015), els sisons tornarien a la primavera següent a les mateixes àrees de reproducció (però veure **capítol 4**). No obstant, s'ha suggerit que els moviments entre poblacions podrien ser importants (Morales et al. 2005a). Basant-nos en les nostres dades de seguiment d'individus, podem dir que els traspassos d'unes poblacions a unes altres no són molt freqüents. Per posar un exemple, de les 18 femelles marcades amb GPS a la plana de Lleida, només s'han detectat moviments puntuals fora de la depressió de l'Ebre en una de les femelles i aquests van tenir una durada de tan sols uns dies (dades no publicades).

Per resumir, des d'un punt de vista demogràfic, la baixa productivitat detectada causada per el baix èxit d'eclosió, especialment de les postes de reposició, però també per l'elevada mortalitat de les pollicades i el fet que un percentatge gens menyspreable de femelles no cova serien els principals factors que explicarien el declivi de les poblacions a la plana de Lleida, així com també l'alta mortalitat dels individus adults observada a nivell peninsular. Finalment, donat que gran part de les morts dels individus adults es deguda a causes antropogèniques, aquestes són evitables i s'hauria de fer un esforç per tal de garantir la supervivència de les poblacions de sisó.

Canviant la percepció respecte al sisó

Recentment, s'ha destacat la necessitat d'abordar la conservació de la biodiversitat des d'una perspectiva socioecològica (Ban et al. 2013, Bennett et al. 2017), donant valor aquells aspectes en que la biodiversitat contribueix al benestar humà a través dels serveis ecosistèmics (Díaz et al. 2015, Morales-Reyes et al. 2018).

En algunes zones agrícoles de secà, la presència del sisó es viu com un impediment al desenvolupament econòmic entre la població agrícola, ja que responsabilitzen a l'espècie del fet que no puguin regar en algunes àrees protegides, causant un greuge comparatiu amb els agricultors de les zones veïnes de regadiu. Aquesta percepció negativa suposa un problema per a la conservació de l'espècie ja que alguns agricultors podrien prendre accions il·legals (Mateo-Tomás et al. 2012) per tal de molestar i foragitar als sisons, destruir els seus nius i, inclús, tirotejar als individus adults (**Capítol 3**; no obstant, cal destacar que desconeixem les motivacions de les persones responsables de les morts per tret detectades). Així que, des de la biologia de la conservació s'hauria de treballar per tal de revertir aquesta percepció perjudicial de l'espècie.

Fruit dels nostres resultats en base a la selecció de zones amb disponibilitat d'alfals (**capítol 1**) i l'elevada utilització d'aquest com a recurs tròfic (**capítol 2**) podríem arribar a pensar que els sisons tenen un impacte negatiu sobre el rendiment d'aquest tipus de cultiu. Lluny de suposar un perjudici per a l'agricultura, creiem que el sisons no tenen un impacte negatiu sobre aquesta i s'hauria de considerar com a una espècie innòcua en la majoria dels casos o, en tot cas, amb certs beneficis ja que es pot alimentar d'espècies perjudicials per als cultius. No obstant això, en determinades zones d'hivernada al centre de la península Ibèrica poden ocasionar danys en cultius, com ara els cultius de melons (communicació personal), ja que tenim constància de que s'utilitzen mecanismes per a foragitar-los i, fins i tot, paranys per a capturar-los. En tot cas, l'hàbitat majoritàriament utilitzat per als sisons són els alfalsars. L'efecte negatiu que podria tenir el consum d'alfals en els camps on es produeixen altes congregacions d'individus seria mínim, donat que aquestes agrupacions es produeixen durant l'hivern, quan l'alfals es troba en un estat vegetatiu inactiu o de creixement reduït (Lloveras 2001). Prèviament, s'ha descrit com la pastura dels camps d'alfals per part de ramats d'oví durant l'hivern té pocs efectes en la producció d'aquests cultius en les primaveres successives (Delgado 1993). A més a més, es d'esperar que l'impacte d'herbivoria per part dels sisons sigui molt menor, donada la seva petita mida corporal i necessitats de consum tròfic molt inferiors.

Addicionalment, el consum d'espècies indesitjables des d'un punt de vista agronòmic podria ser especialment important a l'hivern en els rostolls de cereal i blat de moro (**capítol 1** i **capítol 2**), però també durant la primavera (Cuscó et al. 2013). El consum d'espècies com el panigroc (*Anacyclus clavatus*), la rosella (*Papaver rhoeas*), la campaneta (*Convolvulus arvensis*), la tinya negra (*Lamium amplexicaule*), la ravenissa blanca (*Diplotaxis erucoides*) o els sarronets de pastor (*Capsella bursa-pastoris*) ocasionen pèrdues econòmiques als agricultors. El panigroc, la ravenissa blanca i la rosella han estat identificades com les espècies dicotiledònies no cultivades més abundants en els cereals d'hivern a la Plana de Lleida (Westerman et al. 2012). A banda de ser molt abundant, la rosella es coneguda per la seva capacitat de reduir el rendiment dels cereals d'hivern a les zones del sud d'Europa de clima mediterrani (Wilson et al. 1995, Holm et al. 1997). Encara que altres espècies, com la campaneta, són considerades com a més nocives per part dels agricultors (Giralt et al. 2018). Tot i que creiem que l'efecte d'herbivoria del sisó sobre la propagació de les "males herbes" és limitat, el consum d'espècies considerades com a perjudicials per a l'agricultura pot ser vista com una oportunitat per a canviar la percepció de la pagesia respecte a aquesta espècie.

Finalment, l'atracció que desperta aquesta espècie cap al públic amant de la natura i dels ocells, pot representar una oportunitat per al desenvolupament econòmic de les zones rurals. En l'actualitat, ja existeixen algunes experiències al respecte on els pagesos perceben una quantia econòmica provinent dels visitants que volen observar al sisó i a altres ocells esteparis. Aquesta activitat suposa un complement econòmic a la activitat agrícola i ajuda a canviar la percepció respecte aquesta espècie i dels ocells en general.

Mesures de conservació

En l'actual context de pèrdua de la biodiversitat i abundància de les poblacions d'ocells que habiten els ambients agrícoles a causa de la intensificació agrícola (BirdLife International 2004, Burfield 2005), es fan necessàries mesures de gestió dirigides a mantenir la biodiversitat i efectius poblacionals de les espècies. A continuació, es proposen un seguit de mesures de gestió en base als resultats obtinguts en la present tesi per a una conservació adequada i efectiva de les poblacions de sisó a la península Ibèrica. En zones agrícoles intensificades de regadiu, les mesures dirigides a promoure els paisatges oberts i heterogenis, amb disponibilitat d'alfals i rostolls, en llocs segurs el més a prop possible de les àrees de reproducció, podrien contribuir a beneficiar a les poblacions de sisons residents o escassament migradors en els emplaçaments no reproductors (**capítol 1**). Tot i que l'eficàcia de proveir cultius de lleguminoses com a mesura per incrementar la qualitat de l'hàbitat i la capacitat de càrrega per a les poblacions de sisons en els paisatges agrícoles ha estat ben establerta (Wolff et al. 2001, Ursúa et al. 2005, Bretagnolle et al. 2011, Kovács-Hostyánszki i Báldi 2012, Ponce et al. 2014), suggerim que aquests cultius haurien de ser inclosos dins d'una xarxa en una matriu d'hàbitats diversos que proporcioni diferents hàbitats adequats i complementaris, com per exemple ho serien els guarets (Silva et al. 2004), per tal de proporcionar recursos tròfics variats i alternatius. De fet, tot i que els sisons presenten una alta preferència per a les lleguminoses, tant cultivades com arvenses, la podríem considerar una espècie relativament generalista, ja que consumeix un elevat nombre d'espècies vegetals (**capítol 2**) i l'ús de l'hàbitat varia al llarg del cicle anual en funció de la disponibilitat i fenologia dels diferents tipus de cultius (Mañosa i Cuscó, dades inèdites).

Així, per a una conservació adient de l'espècie cal garantir la diversificació dels usos del sòl en els diferents sistemes agrícoles dominats per cultius herbacis per tal de cobrir els requeriments d'aquesta espècie al llarg del seu cicle anual. A l'hivern, això suposaria proporcionar paisatges diversificats, que continguin grans quantitats de lleguminoses cultivades o silvestres, però també d'altres plantes arvenses per tal de completar la seva dieta. En àrees dominades per cultius de lleguminoses, s'haurien de promoure els guarets. En canvi, en les àrees dominades per cereals amb presència de guarets, s'haurien de proporcionar camps de lleguminoses. Finalment, s'haurien d'evitar les pràctiques associades al tractament intensiu dels guarets, com ara el llaurat recurrent dels guarets tradicionals, o l'herbicidat dels rostolls.

A la primavera, durant el període reproductor, s'hauria de promoure la disponibilitat de vegetació herbàcia permanent o semipermanent per millorar la qualitat de l'hàbitat per a les femelles reproductores (**capítol 4**), però també per als mascles adults (Morales et al. 2005b, 2008, Silva et al. 2014a) i els polls (Lapiedra et al. 2011, Tarjuelo et al. 2013). Aquesta millora de la qualitat de l'hàbitat es podria assolir incrementant la disponibilitat de guarets i augmentant la densitat de marges amb parcel·les de mida relativament petita per tal d'oferir a les femelles reproductores majors fonts d'aliment per a la incubació i, al mateix temps, reduir les possibles pressions sobre les postes localitzades en els escassos guarets existents, que podrien tenir certs beneficis en l'èxit d'incubació. D'altra banda, aquestes mesures podrien afavorir que les femelles decidissin romandre en el secà per a repondre en cas de fracàs i, a més a més, oferirien també recursos tròfics i zones de refugi per als mascles i les famílies de sisó (Morales et al. 2005a, 2008, Lapiedra et al. 2011, Tarjuelo et al. 2013, Silva et al. 2014a).

Addicionalment, mesures dirigides a adequar les actuals pràctiques agrícoles en els cultius d'alfals podrien contribuir a l'increment de l'extremadament baixa taxa d'eclosió de les postes de reposició en aquests cultius (**capítol 4**). La transformació del sistema de reg per gravetat per altres sistemes que no suposin la inundació del camp, com serien el reg per aspersió amb suport fix o el reg mitjançant pivot, i l'ampliació dels intervals entre els talls de l'alfals durant el període en que es produeixen les postes de reposició (del 15 de maig al 15 de juliol) podria facilitar una incubació exitosa en aquest substrat. No obstant, caldria estar atents a les possibles implicacions sobre la configuració de les parcel·les i la heterogeneïtat del paisatge que aquests canvis en el sistemes de reg podrien comportar (**introducció** i **capítol 1**).

Des d'un punt de vista social, cal treballar per a la conscienciació de la societat sobre la situació de vulnerabilitat de les poblacions de sisó a Europa. El desconeixement de l'estat de conservació de les espècies és un problema entre els caçadors i cal comunicar millor la situació real de l'espècie. D'altra banda és necessari revertir l'actual visió negativa que alguns sectors de la pagesia tenen sobre aquesta espècie i s'hauria de promoure una visió de l'espècie amb efectes positius sobre l'agricultura.

L'inesperat alt impacte de les col·lisions amb línies elèctriques (**capítol 3**) posa de relleu la importància d'adaptar les xarxes de línies elèctriques a les necessitats de conservació. Això, pot incloure la senyalització o soterrament de les línies elèctriques existents considerades com a perilloses, així com la minimització o eliminació total del risc de col·lisió en les de nova construcció, ja sigui evitant que el seu traçat discorri per zones de major presència de les espècies afectades (Silva et al. 2014b), o bé considerant el cablejat subterrani (Silva et al. 2010b, 2014b, Barrientos et al. 2012, Raab et al. 2012, Alcazar 2013). Addicionalment, la legislació s'hauria d'elaborar a nivell nacional per tal assegurar la integració d'aquestes mesures preventives en el disseny de les noves línies elèctriques a tot el territori i no restringit a la xarxa Natura 2000.

El conjunt de mesures de gestió que proposem per a la conservació del sisó podrien afavorir la majoria de les espècies d'ocells que habiten els paisatges agrícoles de la península Ibèrica. Tot i que aquestes poden presentar requeriments tròfics diferents al sisó o necessitin d'una estructura de la vegetació diferenciada (Delgado and Moreira 2000, Cardador et al. 2014, Traba et al. 2015, Robleño et al. 2017, Giralt et al. 2018), el foment de les cobertes vegetals, com són els cultius de lleguminoses, els guarets i l'augment de la densitat de marges mantenint una mida de parcel·la relativament petita, es traduirien en una millora de la qualitat de l'hàbitat, oferint una diversitat de recursos per a les diferents espècies (McMahon et al. 2010, Robleño et al. 2017).

CONCLUSIONS

1. El comportament espacial de les femelles de sisó durant el període no reproductor està influenciat per l'efecte independent de l'hàbitat i per limitacions espacials, així com per el seu efecte conjunt.
2. Aproximadament un terç de l'agregació espacial observada en la distribució de les femelles de sisó estava relacionada amb les respostes a un entorn agregat espacialment.
3. Els filtres espacials que representaven patrons d'agregació a ~18 km i 3-5 km tenien una gran importància en l'ocurrència de les femelles. No obstant això, també es van identificar efectes purs de l'hàbitat. El pendent del terreny, la disponibilitat d'alfals i rostolls de blat de moro van ser les variables que més van influir en la selecció de l'hàbitat.
4. En general, els models van revelar un efecte negatiu no lineal del pendent i efectes positius a valors intermitjos en la disponibilitat d'alfals i rostolls de blat de moro. Elevats nivells de rostolls de cereals en regadiu i les carreteres també van tenir un efecte positiu en l'ocurrència a nivell de població.
5. Fins a 62 espècies de plantes van ser identificades en la composició de la dieta del sisó comú a l'hivern mitjançant l'ús de tècniques microhistològiques. Les espècies més consumides eren lleguminoses cultivades (46.7%) i dicotiledònies arvenses (45.6%), mentre que les monotcotiledònies eren escassament consumides (7.7%).
6. La composició en la dieta diferia significativament entre les zones agrícoles de secà i les zones de regadiu. A les zones de regadiu, la dieta es composava principalment per lleguminoses, particularment per alfals (*Medicago sativa*). En constrast, a les zones agrícoles de secà la dieta era més diversa, composada principalment per plantes arvenses (Compositae, Papaveraceae i Cruciferae) i també per lleguminoses cultivades, en particular per veces (*Vicia sativa*).
7. La mortalitat antropogènica anual semblava tenir un impacte crític sobre l'espècie, amb valors quasi tan elevats de mortalitat com els

atribuïts a la depredació. Les col·lisions amb línies elèctriques van ser identificades com la principal amenaça sobre la població adulta (3.4-3.8%/any), seguides de les morts il·legals (2.4-3%/any), les quals tenien un impacte superior al que inicialment s'esperava.

8. La taxa de reposició de les postes fracassades era molt més elevada de l'esperat, essent de 67% per a les primeres postes que fracasades i del 57% per a les segones postes que no arribaven a eclosionar.

9. L'èxit d'eclosió de les postes de reposició va ser molt baix a la zona d'estudi degut a les pràctiques agrícoles perjudicials associades als substrats més utilitzats en les postes de reposició, els cultius d'alfals en regadiu. En conseqüència, l'èxit d'eclosió depenia principalment de les primeres postes situades en sistemes agrícoles de secà, majoritàriament en cereals.

10. El risc de fracassar al final de la incubació va ser molt més alt que a l'inici de la incubació. Tenint en compte que els factors externs haurien de ser relativament constants al llarg de la incubació, podriem hipotetitzar que aquestes diferències es poden atribuir a una reducció en la condició corporal de les femelles deguda a un esgotament físic durant la incubació. No obstant això, l'elevada taxa de reposició de les postes fracassades i al fet que no vam trobar diferències en els patrons d'incubació entre les postes eclosionades i les que fracassaven per causes naturals, ens fa descartar aquesta hipòtesi.

11. El patró diari de sortides del niu durant la incubació era coherent amb els patrons trobats en altres espècies d'ocells d'ambients esteparis i que nidifiquen a terra. Aquest patró va mostrar una distribució bimodal a una freqüència de les sortides del niu més elevades durant al mati i a la tarda.

12. Els nius eren situats pròxims als marges dels camps. La proximitat als marges era més elevada en aquells conreus amb menys disponibilitat de vegetació herbacia permanent o semipermanent. La disponibilitat de vegetació herbàcia permanent o

semipermanent determinava la localització del niu, l'atenció al niu i l'èxit d'eclosió.

13. Mesures destinades a millorar la qualitat de l'hàbitat, com per exemple incrementar la superfície de guarets i la densitat de marges per tal de proporcionar una major font d'aliment per a les femelles durant a la incubació i, al mateix temps, reduir les possibles pressions sobre els nius localitzats en guarets, podria tenir certs beneficis sobre l'èxit d'eclosió.

14. Altres mesures dirigides a adequar les actuals pràctiques agrícoles en els cultius d'alfals podrien millorar la extremadament baixa taxa d'eclosió de les postes de reposició en aquest tipus de cultiu. Per exemple, un canvi en l'estès sistema de reg per inundació a la plana de Lleida per a altres sistemes d'irrigació com podrien ser el reg per aspersió o pivot, i una ampliació dels intervals de sega de l'alfals durant el període reproductor podria facilitar l'èxit d'eclosió en aquest substrat.

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