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Effects of anthropogenic infrastructures on the spatial ecology of raptors and bustards

"Documento Definitivo"

Doutoramento em Biodiversidade, Genética e Evolução

Ana Teresa Dias dos Santos Marques

Tese orientada por:
Professor Doutor Jorge Manuel Mestre Marques Palmeirim
Doutor João Paulo Campbell Alves da Silva
Doutor Francisco Manuel Ribeiro Ferraria Moreira

Documento especialmente elaborado para a obtenção do grau de doutor

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Nota prévia: A presente tese apresenta artigos científicos já publicados ou submetidos para publicação (capítulos 2 a 6), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série — N.º 60 — 26 de março de 2018. Uma vez que estes trabalhos foram realizados em colaboração o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos, com a exceção das bases de dados de seguimento GPS usadas nos capítulos 4, 5 e 6, provenientes de outros projetos.

Lisboa, outubro de 2019

Ana Teresa Marques

"Julgo que aproveitou uma migração de pássaros selvagens para fugir."

Antoine De Saint-Exupéry

O Principezinho

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Abstract

Anthropogenic infrastructures are major drivers of human-related effects in the Anthropocene, and several important negative impacts on different taxa and habitats have been described. In the case of birds these impacts include, for example, habitat loss, mortality and changes in behaviour, which can have major consequences on the viability of populations.

The main objective of this thesis was to study how anthropogenic infrastructures influence the distribution and movements of several bird species, in order to identify management actions and support conservation strategies. The thesis focuses on bustards and raptors species in the Iberian Peninsula, which are known to be vulnerable to human infrastructures such as roads, power lines and wind farms. Census data, mortality events in power lines and GPS tracking databases were used to study the interactions between infrastructures and the little bustard (*Tetrax tetrax*), great bustard (*Otis tarda*), black kite (*Milvus migrans*) and Iberian imperial eagle (*Aquila adalberti*).

In general, this thesis shows that infrastructures, such as roads, power lines and wind turbines, can play an important role in species' distribution (little bustard) and use of space (black kite and little bustard), and may even contribute to accentuate negative population trends (little bustard). Additionally, species features (e.g. morphology or behaviour) and ecology are essential to understand how they are affected and vulnerable to infrastructures. Guidelines for the management of infrastructures and conservation measures targeting vulnerable species are proposed.

Keywords: Iberian Peninsula, mitigation, mortality, movement ecology, wildlife tracking

Resumo

As infraestruturas antropogénicas são atualmente elementos indissociáveis do Antropoceno, sendo responsáveis por vários impactos negativos em diferentes taxa e habitats. A perda de habitat, as mudanças de comportamento e a mortalidade são apontadas como os principais efeitos das infraestruturas nas aves.

O principal objetivo desta tese foi o de estudar como as infraestruturas antropogénicas afetam a distribuição e o uso do espaço pelas aves, com vista à identificação de ações de gestão das infraestruturas, bem como apoiar estratégias de conservação da biodiversidade. A tese foca-se em espécies de abetardas e de aves de rapina da Península Ibérica, conhecidas por serem vulneráveis às infraestruturas humanas, como as estradas, linhas elétricas e parques eólicos. Utilizaram-se dados de recenseamento, dados de eventos de mortalidade e bases de dados de seguimento por GPS para estudar as interações entre as infraestruturas e o sisão (*Tetrax tetrax*), a abetarda (*Otis tarda*), o milhafre preto (*Milvus migrans*) e a águia imperial Ibérica (*Aquila adalberti*).

De uma forma geral, os resultados desta tese mostram que infraestruturas, tais como estradas, linhas elétricas e aerogeradores, podem influenciar de forma importante a distribuição de espécies (sisão) e o uso do espaço (sisão e milhafre preto), podendo até contribuir para acentuar as tendências de declínio das populações (sisão). Por outro lado, tanto as características (e.g. morfológicas e comportamentais) como a ecologia das espécies são essenciais para se compreenderem os efeitos causados pelas infraestruturas. São propostas várias diretrizes para a gestão das infraestruturas e também medidas de conservação direcionadas para as espécies estudadas.

Capítulo 2: A gestão agrícola e as infraestruturas como principais determinantes do declínio populacional do sisão

Neste estudo, analisámos os fatores que contribuíram para o acentuado declínio da população de sisão na Península Ibérica desde o início do século. Com base nos dados dos censos da espécie em Portugal (2003-2006 e 2016), testámos o efeito da disponibilidade de habitats, da densidade de gado, da densidade de infraestruturas lineares e da implementação de medidas agroambientais, na variação espacial e temporal da densidade da espécie. Os nossos resultados mostram que os fatores que influenciam as densidades de sisão mudaram ao longo do tempo. Em 2003-2006, quando a espécie ocorreria em elevadas densidades, a disponibilidade de habitat adequado foi o único preditor que explicava a densidade da espécie. No entanto, em 2016, quando a densidade populacional baixou, outros preditores ganharam importância; nomeadamente áreas com maiores densidades de gado (em

particular gado bovino) e com uma maior extensão de linhas elétricas tinham menores densidades de sisão. Os declínios populacionais durante o período de estudo foram mais acentuados em áreas com densidades mais elevadas, sugerindo que a qualidade dos habitats nestes locais se deteriorou devido a mudanças na gestão do gado e das pastagens. Áreas com maior densidade de linhas elétricas foram também as que perderam mais aves, provavelmente devido ao efeito de exclusão e a maiores níveis de mortalidade por colisão com estas infraestruturas. As medidas agroambientais foram capazes de amortecer o declínio da espécie, dado que as áreas onde estas foram implementadas tiveram menores flutuações populacionais negativas. No geral, os nossos resultados mostraram que atualmente o sisão carece de habitats de qualidade e com baixa densidade de infraestruturas lineares e que a espécie beneficiaria de densidades de gado inferiores e do alargamento geográfico da implementação de medidas agroambientais.

Capítulo 3: Habitat e configuração das linhas elétricas como principais responsáveis pelo risco de colisão de duas espécies de abetarda

Neste trabalho analisámos os padrões espacio-temporais de mortalidade e os fatores de risco de colisão de duas espécies simpátricas, ameaçadas e propensas a colisões: a abetarda e o sisão, com base nos registos de colisão recolhidos ao longo de 280 km de linhas de transmissão no sul de Portugal, entre 2003 e 2015. Os nossos dados mostram que os incidentes em linhas elétricas não são uniformes no espaço e no tempo, e que as variações encontradas estão relacionadas com os requisitos ecológicos, os padrões de distribuição e o comportamento das espécies. Embora ambas as espécies façam voos substanciais entre áreas de habitat adequado, as colisões são mais prováveis em linhas que atravessam pelo menos 20% (para o sisão) ou 50% (para a abetarda) de habitats agrícolas abertos. A configuração das linhas elétricas também é um fator importante, pois postes mais altos e com maior número de níveis verticais de cabos apresentam um maior risco de colisão. Foi igualmente identificado um pequeno, mas significativo, efeito positivo da sinalização dos cabos na redução das colisões de sisão, mas o mesmo não foi identificado para a abetarda, possivelmente devido a limitações da nossa amostra. Devem ser implementadas medidas de mitigação para evitar colisões destas espécies, que incluem o planeamento da localização das linhas, a utilização de configurações de linhas e postes adequados, bem como a sinalização dos cabos, sempre que as linhas elétricas atravessem áreas com mais de 20% de habitats abertos, inclusivamente fora das áreas protegidas.

Capítulo 4: Movimentos pós-reprodutores e seleção de habitat das áreas de paragem migratória de um migrador de curta distância

Neste capítulo, estudámos as paragens durante as viagens migratórias do sisão, uma espécie ameaçada e migradora de curta distância. Utilizando dados espaciais recolhidos por GPS / GSM de alta resolução, seguimos 27 machos reprodutores de sisão no sul de Portugal entre 2009 e 2011. Os movimentos pós-reprodutores foram estudados através de modelos dinâmicos *Brownian Bridges*, de forma a identificar os principais locais de paragem, e modelos lineares mistos generalizados foram usados para estudar a seleção de habitat nesses locais. Durante estes movimentos, os machos fizeram essencialmente voos noturnos, fazendo paragens frequentes e curtas, de forma a alcançar rapidamente as áreas de pós-reprodução. A maioria das aves fez paragens durante a viagem pós-reprodutora (83%), independentemente da distância total percorrida (média de 64,3 km), e a maioria das paragens (84%) durou menos de 24 horas. As aves usavam principalmente áreas agrícolas não irrigadas e irrigadas como locais de paragem, evitando outros usos do solo e topografias acidentadas. Identificou-se um efeito negativo da proximidade a estradas, mas não a linhas elétricas. A elevada frequência de paragem durante os movimentos de pós-reprodução, apesar das curtas distâncias percorridas, juntamente com o comportamento migratório noturno, pode expor esta ave a riscos adicionais de colisão com linhas elétricas. Deduzimos ainda que, mesmo para migrantes de curta distância, a conectividade do habitat entre as áreas de reprodução e pós-reprodução é provavelmente uma questão importante para a conservação.

Capítulo 5: Os aerogeradores causam perda de habitat funcional para aves planadoras migradoras

Neste capítulo modelámos o efeito de exclusão provocado pelos aerogeradores em milhafres-preto. Seguimos 130 aves no estreito de Gibraltar, uma área onde estão instalados vários parques eólicos. Usámos modelos *Brownian bridges* para estimar a utilização do espaço pelas aves e modelos aditivos mistos para analisar o efeito da proximidade dos aerogeradores, bem como da disponibilidade das correntes ascendentes de origem térmica e orográfica, na densidade de utilização da paisagem. Os nossos resultados mostram que áreas até aproximadamente 674 m de distância dos aerogeradores são menos usadas do que o esperado, e este efeito é tão mais acentuado quanto maior a proximidade aos aerogeradores. Estimámos que 3-14% da área adequada para voos planados nesta região esteja afetada por parque eólicos. No geral, apresentamos evidências de que os impactos do setor de energia eólica sobre as aves são maiores do que o anteriormente reconhecido. Além da mortalidade por

colisão, o comportamento de evitamento dos aerogeradores representa uma perda de habitat, em particular nos corredores migratórios.

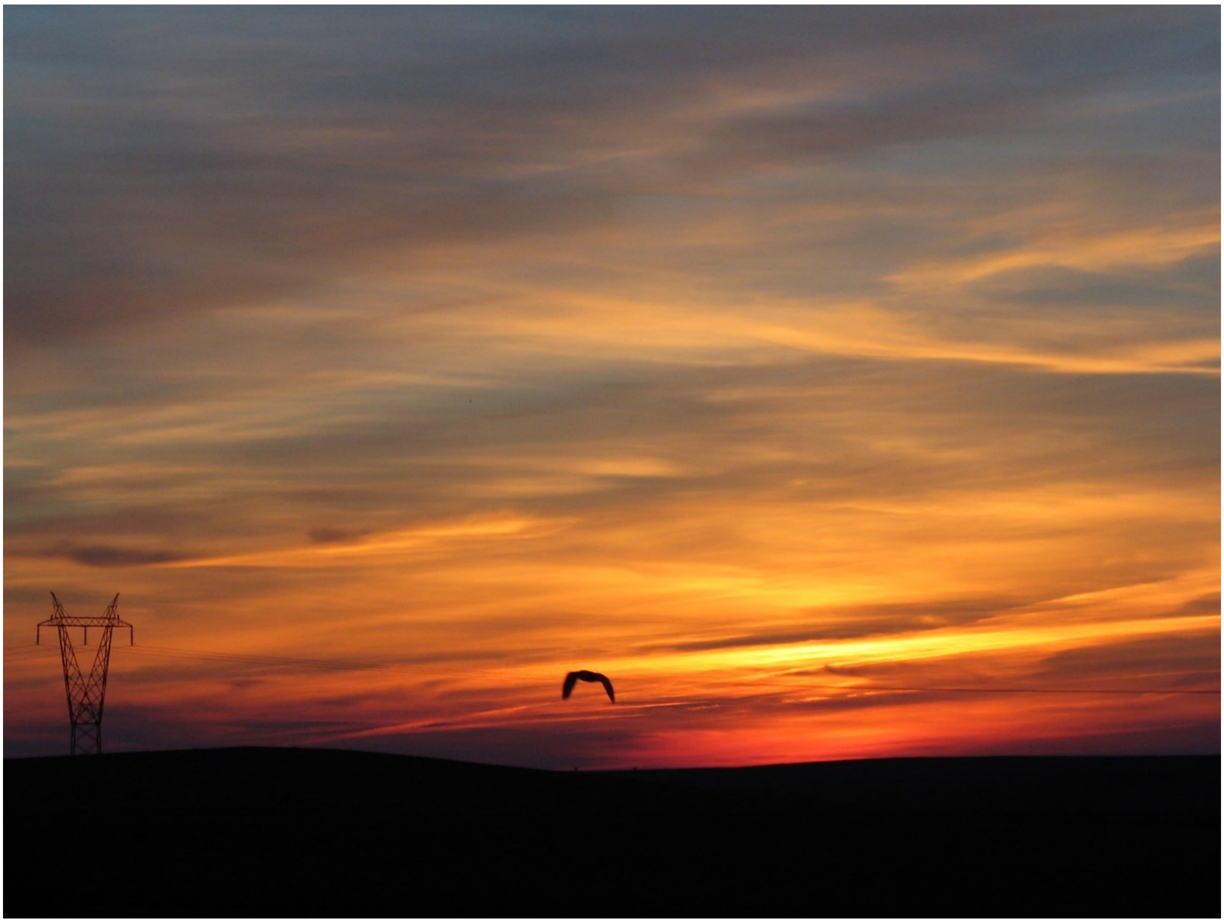
Capítulo 6: Movimentos dispersivos e adequabilidade de habitat para uma ave de rapina globalmente ameaçada, revelados por seguimento remoto de alta resolução

Neste trabalho, usámos equipamentos GPS/GSM para estudar os padrões espácio-temporais de movimentos e a adequação do habitat de águias imperiais ibéricas imaturas. Durante a fase de dispersão, seguimos 12 aves ao longo, em média, de 243 dias e reunimos ca. 38.000 localizações. Utilizamos modelos *Brownian bridges* para identificar áreas de assentamento, e aplicamos modelos *Maxent* para prever áreas adequadas para aves não territoriais na Península Ibérica. As águias viajaram principalmente no centro e no sul da Península Ibérica, onde há habitats mais adequados para a espécie, embora uma ave tenha atravessado o Estreito de Gibraltar até o norte da África. As águias jovens permaneceram nas áreas de assentamento durante a maior parte de sua vida imatura (ca. 90% de tempo), normalmente viajando alternadamente entre diferentes áreas de assentamento. Estas áreas localizam-se, em média, a 208 km do ninho de origem. Durante os meses mais frios, as aves exibiram um comportamento sedentário, realizando menos movimentos do que durante o resto do ano. Os nossos resultados mostram que estas águias preferem paisagens dominadas por sistemas agroflorestais e matagais, com uma topografia suave e aridez elevada. Por outro lado, recolhemos evidências de que as águias imaturas viajam para mais longe do que identificado anteriormente, talvez devido a um aumento da competição intraespecífica. Este fator pode ser responsável pela expansão da área de distribuição da espécie, incluindo da área de reprodução. O nosso modelo preditivo pode ajudar a orientar futuras ações de gestão focadas nesta espécie.

Palavras-chave: ecologia do movimento, mitigação, mortalidade, Península Ibérica, seguimento remoto

Chapter 1

General Introduction



General introduction

1. EFFECTS OF ANTHROPOGENIC INFRASTRUCTURES ON WILDLIFE

Infrastructures are fundamental facilities to human societal living, providing commodities and services, such as the transportation of goods and people or the supply of energy and water (NRC, 2009). Roads, railways, electric grids and telecommunications are some examples.

Roads are the most studied infrastructures regarding their effects on biodiversity and ecology. This is probably because roads are widespread and continuously increasing, but also because the implementation of a road may have major effects on the surrounding landscape in addition to those caused by the structure itself (Ibisch et al., 2016). This is particularly noticeable in pristine areas, like tropical forests, where a new road, by allowing access to previously remote areas, promotes land-use changes and human disturbances to biodiversity (e.g. resource extraction, human settlement, wildfires or hunting), often with irreversible impacts on ecosystems (Ibisch et al., 2016; Laurance et al., 2014, 2009, 2001). Such "contagious" effects, exacerbate the human footprint assigned to roads (Laurance, 2015).

However, due to the increasing human demand for energy, energy infrastructures like power lines, gas pipelines, and wind farms are also expanding and receiving further attention from the scientific and conservation communities. Linear infrastructures are usually long, occur in all types of landscapes and are virtually omnipresent, crossing many natural and semi-natural habitats. Infrastructures also tend to have a clustered spatial pattern, as successive developments tend to occupy existing corridors or nearby areas, contributing to a hyperfragmentation of the landscape (Trombulak and Frissell, 2000). Energy production facilities, like hydropower plants or wind farms, also tends to be located in more remote areas that have to be crossed to supply big consuming areas such as cities. Additionally, new human facilities usually imply multiple infrastructures. For example, the construction of a new railway often requires new train stations, with associated roads that allow the access of passengers and maintenance workers, and new power lines and electrical substations may be also deployed.

The widespread and continuous increase of infrastructures makes them a major driver of human-related effects in the Anthropocene, and several negative impacts have been described to affect different taxa and habitats, including land-use degradation, population fragmentation or animal mortality. Some positive effects, such as the creation of microhabitats or the provisioning of perches and nesting sites have also been described (Berg et al., 2016; Morelli et al., 2014). However, there is a general consensus that the cumulative effects across taxa are very negative (Fahrig and Rytwinski, 2009; van der Ree et al., 2015).

In this chapter I introduce some of the major negative effects of anthropogenic infrastructures on wildlife, focusing on the ones with more impact on birds, in order to contextualize the topics studied in the following chapters of this thesis.

1.1. HABITAT EFFECTS

Habitat loss due to the implementation of the physical components of the structure itself is the first habitat alteration caused by infrastructures. The magnitude of habitat loss depends on the area occupied by the infrastructure and the area used during its construction, so it is expected to be larger in big projects like highways, when compared to power lines, where usually only the base of the power pole occupies ground space. Species with small home ranges in natural areas are the most likely to be affected by habitat loss due to infrastructures (Fahrig and Rytwinski, 2009; Pearce-Higgins et al., 2009). Besides this change to an artificial land-use, several infrastructures imply a permanent vegetation change along their corridors or surroundings, due to safety reasons. One example are power lines installed in forests, whose corridors are permanently managed in order to avoid that trees and tall vegetation reach and interact with the aerial cables, causing power cuts or even fire (Luken et al., 1991).

When an anthropogenic infrastructure is installed it may also contribute to the fragmentation of native ecosystems and the creation of edge effects (Andrews, 1990; Laurance et al., 2009; Sánchez-Zapata et al., 2016; Trombulak and Frissell, 2000), that are widely known for having deleterious effects on wildlife (Ewers and Didham, 2005; Fahrig, 2003). Additionally, land-use degradation is also expected to occur in areas contiguous to anthropogenic infrastructures, and can even exceed the amount of habitat directly cleared by the structure (van der Ree et al., 2015). Road use and maintenance are known to be sources of pollution of heavy metals, salt, dust, ozone, and nutrients, contributing to the degradation of aquatic and terrestrial habitats (Laurance et al., 2009; Trombulak and Frissell, 2000). Anthropogenic infrastructures may also facilitate the spread of exotic species by providing habitat due to vegetation disturbance, stressing or removing native species, and allowing easier access and movement for wild or human dispersion vectors (Laurance et al., 2009; Trombulak and Frissell, 2000).

Several studies have shown that in general the density of birds and mammals is reduced in the vicinity of anthropogenic infrastructures. A meta-analysis on this topic found that the effect of infrastructures can extend for up to 1 km radius for birds, and around 5 km for mammals (Benítez-López et al., 2010).

Such displacement may be related to changes in the habitat (habitat loss, degradation or fragmentation), but is may also result from shifts in animal behaviour, individual mortality or a combination of these effects. In fact, disentangling the mechanisms beyond reduced density in the vicinity of infrastructures is still not fully accomplished, and those mechanisms may vary across taxa (Laurance, 2015).

1.2. BEHAVIOURAL EFFECTS

Infrastructures may change an animal's behaviour through shifts in: home ranges, movement patterns, reproductive success, escape responses, and physiological states (Trombulak and Frissell, 2000).

Changes in space use and movement are probably the most noticeable behavioural effects, and occur because individuals (i) avoid the infrastructure itself, (ii) avoid the disturbance caused by the structure (e.g. traffic, noise, lights, pollution, predators) or (iii) are attracted to the structure (Rytwinski and Fahrig, 2015; Walters et al., 2014). An experiment that applied traffic noise to a roadless area found that bird abundance was highly reduced and some species even disappeared in the periods of noise. This shows that traffic noise can be a major driver of road effects on birds and is independent of changes in habitat, mortality or other disturbance sources (McClure et al., 2013). In fact, noise is known to affect birds through direct stress, as it masks the arrival of a predator or the associated alarm calls, and because it interferes with acoustic communications, mainly during the breeding season (Slabbekoorn and Ripmeester, 2008). Also, the birds that stayed in the noisy roadless area ended having worse body condition and a decreased stopover efficiency (ability to improve their body condition over time) during migration (Ware et al., 2015). The latter result points out that infrastructure effects can extend far beyond the way animals distribute and move through the space occupied by it, and that it can affects animal physiology.

In some cases, anthropogenic infrastructures can even represent a barrier to free movement, mainly to non-flying animals. The barrier effect can be physical, when an individual cannot cross an infrastructure, or behavioural, when an individual may be physically able to do it but does not do so, due to unfavourable environmental conditions or perceived risk (Barrientos and Borda-de-Água, 2017). Ultimately, barrier effects can contribute to a decrease in the functional connectivity and increase the genetic differentiation of populations or the genetic distance among individuals (Holderegger and Di Giulio, 2010).

In contrast, there are some species that are even attracted to infrastructures. An example are the power line poles, frequently used by raptors as perches for hunting and roosting, or used as a support for nesting sites for multiple species (Benítez-López et al., 2010; Mainwaring, 2015). However, such an attraction may, for example, increase the risk of predation of species that are prey for these raptors and may thus contribute to their decline (Walters et al., 2014). Such a mechanism has been proposed to explain, at least partially, the reduced density of grouse species near oil and gas structures (Dinkins et al., 2014) or bustards species near power lines (Silva et al., 2010).

1.3. MORTALITY

Mortality of animals occurs at all types of infrastructures and it is probably the most well documented effect of anthropogenic infrastructures on wildlife. Virtually all terrestrial animals, from insects to large mammals, risk colliding with vehicles travelling on roads (Forman et al., 2003). Flying birds can collide with the overhead power lines or those of the telephone network (Bevanger, 1998, 1994; Janss, 2000), and even with wind turbines (Drewitt and Langston, 2008, 2006). Also, birds that perch on power line poles may be electrocuted, if their body simultaneously contacts with exposed energized wires or components with different electrical potentials (Bevanger, 1998, 1994).

Species-specific features, like morphology, sensorial perception, flock and flight behaviour, and individual conditions may influence the mortality risk due to an infrastructure, and explain why not all animal groups or species are equally prone to this type of mortality (Bernardino et al., 2018; Marques et al., 2014; Sánchez-Zapata et al., 2016). Regarding birds, Strigiformes (nocturnal raptors) are particularly vulnerable to colliding with vehicles (Guinard et al., 2012), while poor fliers like bustards are at higher risk of colliding with power lines (Janss, 2000), and raptors are particularly vulnerable to being caught by rotating wind turbines (Beston et al., 2016) or to be electrocuted on power lines (Janss, 2000).

Mortality levels also depend on site-specific features, like habitat, topography, food-abundance or weather conditions (Bernardino et al., 2018; Marques et al., 2014; Sánchez-Zapata et al., 2016). For example, power lines in open areas like bogs or pastures, in areas with high bird abundance (e.g. wetlands) or crossing migration corridors or daily routes between foraging and roosting grounds, usually have higher bird collision rates (Bernardino et al., 2018; Sánchez-Zapata et al., 2016). There are also some project-specific features that can increase the mortality risk, like road size and traffic intensity (Forman et al., 2003), the number of vertical wire levels of power lines and wire height (Bernardino et al., 2018), the power line pole configuration (Janss and Ferrer, 2001) or the wind turbine height (Marques et al., 2014).

In the United States, the estimates of bird mortality from anthropogenic causes ranges from hundreds of millions for vehicle collisions, tens of millions for power line collisions, millions of power line electrocutions, and hundreds of thousands for wind turbine collisions (Loss et al., 2015). Such high numbers suggest that anthropogenic mortality is widespread and may have demographic consequences. This has indeed been demonstrated to occur for some species of several groups (Boves and Belthoff, 2012; Jones, 2000; Mumme et al., 2000; Sergio et al., 2004; Shaw et al., 2010). In addition to removing individuals from the populations, anthropogenic mortality can be biased towards a certain age, sex or even behaviour (Boves and Belthoff, 2012; Ferrer and Hiraldo, 1992; Morinha et al., 2014; Palacín et al., 2017; Sergio et al., 2004), what can introduce extra unbalance to population dynamics.

1.4. MITIGATION STRATEGIES

There is a general consensus that a multistep approach is necessary to mitigate the effects of infrastructures on wildlife. This involves first acting with a strategic scope and then moving to a local scale. The mitigation hierarchy is the rule beyond the Environmental Impact Assessment (EIA) framework and has the following sequential steps: (i) avoidance – impacts should be avoided wherever possible; (ii) minimisation – the effects should be minimised; (iii) remediation – the area affected during the construction phase or after the project decommissioning should be restored or rehabilitated; and (iv) compensation – the residual impacts that could not be avoided, minimised or remediated should be compensated during the operation (Arlidge et al., 2018; Phalan et al., 2018).

The avoidance phase is the most critical, as it is the most certain and effective way to reduce the impacts on biodiversity, and could also avoid the need for costly minimization and compensatory measures (Bernardino et al., 2018; Laurance et al., 2014; Marques et al., 2014; Phalan et al., 2018; Sánchez-Zapata et al., 2016; Weller, 2015). This can be achieved with a careful spatial planning that selects the location of the new infrastructure that has the least impact on biodiversity. This can be done, for example, by selecting locations away from protected areas or other important sites for nature conservation, avoiding key areas for species particularly vulnerable to the impacts caused by the infrastructure, promoting a spatial aggregation of human structures, avoiding the creation of new vegetation clearings, and minimizing habitat fragmentation.

Minimization is still necessary for most infrastructures, even if the avoidance phase was correctly implemented. At this stage the project management should engage in finding the best technical options to reduce impacts. For example, animal mortality is almost certain in some infrastructure types, even in areas with low ecological value, and can be reduced if roads are fenced and wildlife crossing structures are built (Weller, 2015). Regarding power lines, it is possible to implement pole designs that prevent birds from being electrocuted (López-López et al., 2011; Tintó et al., 2010). Still, wind turbine operation can be interrupted in periods of high bird or bat activity, significantly reducing mortality (Tomé et al., 2017; Weller and Baldwin, 2012).

The third step should be to aim to remediate the biodiversity loss within the footprint of the infrastructure project (Arlidge et al., 2018). This may happen: in areas temporarily used during the project construction, but that are not needed after the project is completed; at the margins of the infrastructure, where exotic vegetation can be managed or vegetation can be planted in bare soil; or at the end of the life-cycle of the project, when management actions are undertaken to recreate the initial habitat conditions.

Compensation, the final step, should be a last resort and only considered if the previous steps do not reduce adverse impacts to an acceptable level. It assumes that negative effects on biodiversity can be quantified and balanced elsewhere, through positive management interventions such as the restoration of degraded habitat, the protection of areas where there is an imminent or a projected loss, or the improvement of biological parameters (e.g. promoting an increase in birth rate or a decrease in mortality rate) of the species affected by the project. This is a controversial stage of the mitigation hierarchy, mainly because there are limits to what is possible to compensate and because this mechanism is often used to legitimise developments which would not otherwise have been permitted (Phalan et al., 2018; Walker et al., 2009).

2. BIRD TRACKING AND MOVEMENT ECOLOGY

The movement of an individual, defined as a change in spatial location across time, is a fundamental characteristic of life and plays a major role in most ecological and evolutionary processes (Nathan et al., 2008). Animal movement plays a central role in several questions of animal ecology. Understanding how and why animals move and how this process is linked to external factors is central to understand, for example, (i) how and why animal use resources, (ii) how and why animals interact among themselves or (iii) how and why they compete and reproduce (Cagnacci et al., 2010; Demšar et al., 2015). Movement is, therefore, directly linked to spatial ecology and species distributions, and is essential to forecast the impact of anthropogenic actions, like habitat fragmentation, climate change or the introduction of exotic species (Demšar et al., 2015; Nathan et al., 2008).

The analysis of animal movement currently adopts a Lagrangian approach which quantifies movement based on tracks of individuals rather than whole populations (Nathan et al., 2008). This is possible due to recent advances in tracking technologies, where miniaturized radio transmitters, global positioning system (GPS) or cellular and satellite networks are now available, leading to increased autonomy and data collection capacity. But mainly to the possibility of tracking more individuals, which enables developing powerful models that can then be inferred for the whole population. This has in turn permitted a growth in knowledge about animal movements and spatial ecology (Bridge et al., 2011; Giuggioli and Bartumeus, 2010). These technologies have also changed the way ecologists collect data by moving the point of observation from the observer to the observed animal (Cagnacci et al., 2010; Demšar et al., 2015), and overcoming human biases during data collection, which can occur, for example, when studying long-distance migrations or deep-ocean movements, or when observations are done during harsh climacteric conditions (e.g. fog or snow) or during the night (Hebblewhite and Haydon, 2010).

Research in movement ecology was boosted by the development and widespread use of GPS telemetry (Figure 1), which has allowed the collection of data about animal location with unprecedented temporal and spatial resolution (Cagnacci et al., 2010; Tomkiewicz et al., 2010). These technologies started to be deployed on large-bodied animals, but advances in miniature devices (smaller and lighter weight) are widening the range of species on which they can be used (Tomkiewicz et al., 2010).

Figure 1 - Attachment of a solar GPS/GSM tracking device on a little bustard (left) and release of the tagged bird (right).

GPS telemetry-based research has brought major benefits to nature conservation and management, not only by allowing the modelling of the importance of habitats to animals with an unprecedented rigour but also to increase our knowledge about human impacts on animals (Hebblewhite and Haydon, 2010). However, it also brings new challenges to biodiversity conservation, particularly of nomadic or migratory species, which have large and/or seasonal home ranges (Runge et al., 2014), and where maintaining connectivity is key (Allen and Singh, 2016). It is now clear that traditional approaches to conservation, such as the creation of protected areas, need to be complemented with strategies that are flexible in time and/or space, accounting for particularities in the life cycle of all the species (Allen and Singh, 2016; Runge et al., 2014).

Movement ecology has been widely used to study the effects of anthropogenic infrastructures on wildlife. It was used to identify large scale phenomena occurring across species (Tucker et al., 2018), to understand how animals use the landscape when a new structure is developed (Dahl et al., 2013; Grilo et al., 2012; Polfus et al., 2011; Pruett et al., 2009; Roeleke et al., 2016; Whittington et al., 2005), to identify barrier effects (Rondinini and Doncaster, 2002; Shepard et al., 2008), to quantify mortality rates (González et al., 2007; Marcelino et al., 2017; Schaub et al., 2010; Schaub and Pradel, 2004; Väli and Bergmanis, 2017), and to help design mitigation techniques (Bastille-Rousseau et al., 2018; Colchero et al., 2011; Katzner et al., 2012; Miller et al., 2014).

3. GENERAL INTRODUCTION TO THE STUDIED SPECIES

3.1. LITTLE BUSTARD

The little bustard *Tetrax tetrax* (Linnaeus, 1758) is a medium sized bird from the Order Otidiformes and Family Otididae, with a fragmented Palaearctic distribution (Birdlife International, 2018). Currently, it has two widely separated breeding populations, one in Western Europe, mainly in the Iberian Peninsula and France, and the other in Southern Eurasia, mainly in Russia and Kazakhstan (Iñigo and Barov, 2010).

The species is a steppe bird, which has adapted to dry grasslands and extensive arable and pastoral lands, and in the western range it is highly dependent on farming habitats and management (Iñigo and Barov, 2010). It is a polygynous species with an exploded lekking mating system, where territorial males gather in key locations during the breeding season that are then visited by females with the single purpose of mating (Jiguet et al., 2000; Morales et al., 2001; Ponjoan et al., 2012). The little bustard is considered a migratory or partially migratory species, with most of the individuals showing a migratory behaviour. In the eastern range the species has an obligatory migratory population undertaking long migratory journeys, while in Iberia short- or medium-distance movements to post-breeding or wintering grounds are the norm (García de la Morena et al., 2015).

Globally, the species is classified as Near Threatened (Birdlife International, 2018), while in Europe its status is Vulnerable (Birdlife International, 2004). Iberia is considered key for the Little Bustard, as by the end of the XX century this area was considered a stronghold for the species, despite declining in Spain since the 1990s' (Iñigo and Barov, 2010). In recent years, the species numbers have dropped dramatically in Iberia: a mean population decline of 49% was recorded in Portugal from 2003-2006 to 2016 (Silva et al., 2018) and an equivalent decline of 48% was recorded in Spain from 2005 to 2016 (García de la Morena et al., 2018). Changes in farming practices have modified the agricultural landscape and, hence, the loss of little bustard habitat has been indicated as the main reason for its decline (Silva et al., 2018; Traba and Morales, 2019). Additionally, adult birds have shown an annual survival rate of 67%, the lowest number known for bustard species, and there is a high anthropogenic mortality rate (Marcelino et al., 2017).

Collision with power lines is the main anthropogenic cause of mortality of the little bustard, affecting 3.4 - 3.8% of adult birds per year (Marcelino et al., 2017). This is the highest mortality rate per collision with power lines ever recorded for a species. Morphological characteristics and bird sensorial perception are key species-specific features that explain such a high mortality rate (Bevanger, 1998; Janss, 2000; Martin, 2011; Martin and Shaw, 2010), but behavioural changes across seasons were also considered relevant (Silva et al., 2014). In addition to mortality, little bustards also avoid the vicinity of anthropogenic infrastructures, mainly to roads and power lines. The proximity of roads was found to have a negative effect on little bustard space use during the breeding season (García et al., 2007; Osborne and Suárez-Seoane, 2007; Santangeli and Dolman, 2011; Santos et al., 2016; Suárez-Seoane et al., 2002), and a similar pattern has been described for power lines (Lourie, 2016; Santos et al., 2016; Silva et al., 2010).

3.2. GREAT BUSTARD

The great bustard *Otis tarda* (Linnaeus, 1758) is also a steppe bird of the Order Otidiformes and Family Otididae, with highly fragmented populations across the Euro-Asiatic range, from Portugal to China (Birdlife International, 2018). The Iberian Peninsula harbours a large majority (>60%) of the great bustards worldwide and is thus a key for the conservation of the species (Palacín and Alonso, 2008).

It occurs in lowlands and undulating open countryside with relatively low levels of annual rainfall, and is well adapted to agricultural landscapes presenting high crops diversity with low intensity cultivation and disturbance (Morales and Martín, 2002; Nagy, 2009). Great bustards exhibit a lek-like mating system, similar to the little bustard, and have an accentuated sexual dimorphism, with big and heavy males that are among the heaviest living flying birds (Morales and Martín, 2002). The western population (including Iberia) is partially migratory, and some birds make seasonal short distance movements (Palacín et al., 2009).

Population numbers have declined throughout the 19th and 20th century and the species is classified as Vulnerable, both at European and global levels (Birdlife International, 2018; Nagy, 2009). Currently, the great bustard is particularly vulnerable to the loss and degradation of its habitat through agricultural intensification, land-use changes, increased mortality caused mainly by power lines, and low reproductive success (Birdlife International, 2018; Nagy, 2009).

Like the little bustards and other Otididae species, great bustards are highly vulnerable to colliding with overhead wires. The species is considered a "poor flier" with a reduced manoeuvrable flight capacity caused by their heavy body and relatively small wings (Rayner, 1988). Moreover, their eye morphology makes them blind in the direction of travel (Martin and Shaw, 2010), failing to see ahead. Finally, they also gather in large flocks during a large part of the year. All these characteristics increase their collision risk with power lines (Bernardino et al., 2018) making power lines the main source of anthropogenic mortality for the species. Moreover, collision with power lines has been described to induce changes in the migratory patterns of great bustards; migrant birds have a higher mortality rate due to collisions than sedentary ones (21.3% vs. 6.3%), so the proportion of resident birds has greatly increased during a 15-year period (Palacín et al., 2017). Eliminating or reducing the mortality rate due to collisions with power lines has been the target of several conservation projects focusing on the species (Barrientos et al., 2012; Janss and Ferrer, 1998; Marques et al., 2007; Raab et al., 2012, 2011).

3.3. BLACK KITE

The black kite *Milvus migrans* (Boddaert, 1783) is a medium-size diurnal raptor, from the Order Accipitriformes and Family Accipitridae. It is widely distributed and can be found in Europe, Asia, Africa and Australia. It is presumably the raptor species with the largest range and also the most abundant one and, although there is evidence indicating that some populations are declining, it is classified as Least Concern at a global level (Birdlife International, 2018).

This raptor is a generalist species and can occupy a large variety of habitats, but it shows a preference for locations near water bodies like rivers, lakes and other wetlands. Black kites are food opportunists, and can either hunt live preys or scavenge, spending long periods soaring and gliding in search of food resources (Cramp and Simmons, 1980). They can also feed on the litter of landfills (Martín et al., 2016). Black kite flight is highly dependent of uplift availability, as their circular soaring flight occurs in areas of high thermal uplift potential and linear soaring is associated with locations with higher orographic uplift (Santos et al., 2017).

Populations from the Palearctic have a migratory behaviour, wintering in sub-Saharan Africa. During the migratory journey birds gather in large flocks (Agostini and Duchi, 1994) and the species is the most common soaring species crossing Spain and the Strait of Gibraltar (100,000 - 150,000 birds annually) during the post-breeding migration (Martín et al., 2016). In this region, black kites are likely to frequently interact with wind farms, as ca. a thousand wind turbines are displaced in the southern part of Cádiz, Spain, towards the Strait of Gibraltar (IECA, 2015), and collisions with wind turbines have already been reported for the species (Ferrer et al., 2012).

3.4. IBERIAN IMPERIAL EAGLE

The Iberian imperial eagle *Aquila adalberti* (Brehm, 1861) is a large raptor (Order Accipitriformes and Family Accipitridae), endemic to the western Mediterranean region, that currently breeds exclusively in the Iberian Peninsula (Birdlife International, 2018). The species uses a great variety of landscapes, but the majority of breeding couples are located on plains and in mountain ranges with patches of Mediterranean forest as well as in agroforestry systems (*montados* or *dehesas*) (González et al., 2008). However, the Iberian imperial eagle is a super-specialist predator, and its occurrence is highly associated with a large abundance of the wild rabbit *Oryctolagus cuniculus* (Linnaeus, 1758), the species' main prey (Ferrer and Negro, 2004; González and Oria, 2004; R. Sánchez et al., 2008).

It is a long-lived species and wild birds can reach 23 years of age (González et al., 2006). Breeding birds are territorial, monogamous and sedentary, and occupy their territories year-round, defending them from the intrusion of other raptors (Sánchez et al., 2008). Like other long-lived raptors, the juveniles of this species have a transient period during which they undergo long-distance trips away from their birth area and use different temporary settlement areas that are usually revisited (Ferrer, 1993; González et al., 1989). They usually start exhibiting territorial behaviour when they are 4.5 years old (González et al., 2006).

The species is classified as Vulnerable globally and is considered one of the rarest raptors in the world (Birdlife International, 2017; Sánchez et al., 2008). Currently, the breeding population includes less than 500 pairs, and is increasing and recovering from a major decline which peaked during the 1970s' with only 38 breeding pairs in Spain (Ortega et al., 2009). Human persecution (for predator control and museum collections) and the decline of the rabbit populations due to viral diseases are indicated as the main drivers of the crash of the species. National and regional plans as well as several conservation projects targeting the Iberian imperial eagle were undertaken in Spain since the end of the 20th century and more recently in Portugal, which has contributed to the recovery of the species (González et al., 2008).

Nowadays, the major treats to the species include the lack of food resources, i.e. rabbits, and the high anthropogenic mortality due to electrocution on power line poles and illegal poisoning (González and Oria, 2004). Electrocution on power lines has been reported as the main known cause of death for the species (mainly affecting non-adult eagles), accounting for ca. 60% of mortality (González et al., 2007). Across Iberia efforts have been made to correct hazardous electric pylons and most of the new power lines use safer designs that prevent the electrocution of large raptors (López-López et al., 2011). Hence, the implementation of anti-electrocution devices in highly risky locations has been one of the main actions of plans and projects promoting the conservation of the Iberian imperial eagle.

4. THESIS AIMS AND OUTLINE

The main objective of this thesis is to study how anthropogenic infrastructures affect and shape the distribution and movement of bird species in order to identify management actions and support conservation strategies. It focuses on four species, two bustards and two raptors, due to their vulnerability to infrastructures and conservation interest of the species itself or of the geographic areas studied.

After this general introduction, the dissertation includes five chapters, each one corresponding to a research manuscript, followed by a general discussion of the overall findings. In **Chapter 2** we analyse the main drivers behind the population decline of the little bustard since the beginning of the millennium, and test the effects of habitats alterations, as well as roads and power line networks. The species has suffered a major decline in a decade both in Portugal and Spain, and previous studies are not fully conclusive on the factors leading to such a step decline. In **Chapter 3** we focus on the drivers of collision with power lines of the two most vulnerable species to such mortality source in Iberia. We pooled data on bustards' collision with power lines collected during 13 years in Portugal to understand the drivers responsible for the collision risk. We describe the spatial and temporal patterns of collision and determine the relative importance of habitat, power line technical features, and wire marking, which allowed us to propose improvements to current mitigation measures targeting these species.

In **Chapters 4, 5 and 6** we took advantage of three pre-existing GPS tracking databases to deepen our insight on the interactions between birds and anthropogenic infrastructures, and to contribute to the mitigation of impacts. In **Chapter 4** GPS-tracking data was used to study the stopover ecology and habitat selection of the little bustard during the post-breeding movements, a period with high mortality due to collision with overhead cables, focusing on the effects of linear infrastructures on the species habitat selection. In **Chapter 5** we modelled the displacement effect of wind turbines on migrant black kites tracked by GPS, while accounting for habitat suitability for soaring flights. This analysis was performed in a migratory bottleneck from the Western European–West African Flyway, used by thousands of soaring birds each year, and where a high number of wind farms are operating. Finally, in **Chapter 6** GPS-tracking data was used to describe the movements and the use of settlement areas by immature Iberian imperial eagles, and to identify areas potentially suitable for the species during the non-territorial phase of their life-cycle. Such data can be used to identify priority areas for the implementation of management actions focusing on this species.

The individual chapters of this dissertation are:

- **Chapter 2:** Grassland management and infrastructures as major drivers of the population decline of an endangered grassland bird
- **Chapter 3:** Habitat and power line configuration as major drivers of collision risk in two bustard species
- **Chapter 4:** Male post-breeding movements and stopover habitat selection of an endangered short-distance migrant, the Little Bustard *Tetrax tetrax*
- **Chapter 5:** Wind turbines cause functional habitat loss for migratory soaring birds
- **Chapter 6:** Dispersal movements and habitat suitability of a globally threatened raptor revealed by high resolution tracking

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Chapter 2

Grassland management and infrastructures as major drivers of the population decline of an endangered grassland bird

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Grassland management and infrastructures as major drivers of the population decline of an endangered grassland bird

ABSTRACT

European grassland birds have been facing major global population declines, mainly due to changes in agricultural policies and practices associated with livestock production. In this study we analyzed the factors related to the steep population decline of the little bustard in Iberia since the beginning of the 21st century. We used the data from the species census in Portugal (2003-2006 and 2016) and tested the effect of habitat availability, grazing management, linear infrastructures density and implementation of agri-environmental measures, on the spatial and temporal variation of the species density across its distribution area. Our results showed that the drivers explaining spatial variations in little bustard density changed across time. In 2003-2006, when the species occurred in high densities, habitat availability was the only predictor affecting little bustard density. However, in 2016, when the population density was lower, other predictors gained importance, with the species abundance having stronger declines in areas with higher stocking rates and proportion of cattle, and with higher power line density. Population declines across the study period were larger in areas that held higher densities, suggesting that the quality of these grasslands deteriorated due to changes in livestock management. Areas with higher densities of power lines also lost more birds, probably due to avoidance behavior and higher mortality levels. Agri-environmental measures were able to buffer the species decline. Overall, our results show that the little bustard is currently lacking high quality grassland habitat with reduced levels of linear infrastructures. The species would benefit from a reduction of the cattle density and with further implementation of agri-environmental measures.

Keywords: agriculture, Common Agricultural Policy, conservation, grazing, habitat degradation, farmland management, population tendency, *Tetrax tetrax*

1. INTRODUCTION

Natural and semi-natural grasslands across the world are known for their high biodiversity value (Dengler et al., 2014; Tilman and Downing, 1994; Watkinson and Ormerod, 2001). However, they are highly prone to changes in management with negative impacts on biodiversity, including conversion to arable land, intensification or abandonment (Dengler et al., 2014). Intensification in persisting grasslands is often expressed in an increased use of fertilizers and pesticides, or increases in livestock density (Donald et al., 2002, 2001). In Europe, changes in livestock management have been pushed by the Common Agricultural Policy, and coupled payments (per livestock head) have been promoting increased livestock numbers, mainly cattle (Fragoso et al., 2011; Ribeiro et al., 2014).

Semi-natural grasslands or pseudosteppes in the south-western Iberia peninsula are recognized as key farmlands for biodiversity in Europe, mainly due to their importance for threatened grassland bird species (Hoogeveen et al., 2004; Lomba et al., 2014; Moreira et al., 2005; Suárez et al., 1997). The extensive traditional management of such systems creates a quite heterogeneous and diverse landscape throughout the year, due to the extensive cultivation of cereals and legume crops on a rotational basis to support sheep raising. However, such systems are being rapidly replaced by highly specialized cattle livestock systems for beef production and a consequent increase of permanent pastures (Fragoso et al., 2011; Ribeiro et al., 2014). Although, such changes maintain grasslands they potentially reduce the quality of the habitat, by promoting land-use homogeneity, changing the harvest dates or altering the structure of the vegetation (Faria et al., 2016; Santana et al., 2017; Stoate et al., 2009). Additionally, other sources of disturbance and mortality, as roads and power lines, are increasingly affecting bird populations depending on grasslands (Hagen et al., 2011; Lee and Power, 2013; Marques et al., *in press*; Reijnen et al., 1996, 1995; Silva et al., 2010b).

The little-bustard (*Tetrax tetrax*) is a Near Threatened grassland bird (Birdlife International, 2018). In Iberia, which holds the majority of the population of the species in the Western Europe (Iñigo and Barov, 2010), the species is classified as Vulnerable (both in Spain and Portugal; Madroño et al. 2004; Cabral et al. 2005), but the species status has been proposed to change to Endangered due to recent population declines (García de la Morena et al., 2018). Here, the species depends on grasslands mainly during the breeding season (Morales et al., 2005; Moreira et al., 2012; Silva et al., 2010a), and several conservation areas (Special Protection Areas; SPA) have been created in core distribution areas for the species. Also, agri-environment schemes promoted by the Common Agricultural Policy (CAP) have been targeting this species inside SPA (Stoate et al., 2009), which farmers can voluntarily embrace, receiving a compensatory payment for management options benefiting this species and other grassland birds. In spite of this, the species numbers dropped dramatically since the beginning of the 21st century: a mean population decline of 49% was recorded in Portugal from 2003-2006 to 2016 (Silva et al., 2018) and a decline of 48% was recorded in Spain from 2005 to 2016 (García de la Morena et al., 2018). Habitat loss due to agricultural intensification were associated with previous declines and extinctions of the species throughout the Europe (Iñigo and Barov, 2010). However, the evidences collected so far reveal that the declines in the Iberian Peninsula may not be fully explained by such drivers. In Portugal, for example, the decline in absolute male densities was stronger within Special Protected Areas (SPAs) when compared with areas without conservation status, even though the amount of grassland habitat coarsely remained constant (Silva et al., 2018). Also, in Spain, the area of potential habitat has only been reduced by 17%, far below the species population decline (García de la Morena et al., 2018). These indicators suggest that habitat loss is certainly not the only main driver of decline, a deterioration of habitat quality in remaining grasslands, as a consequence of changes in management, may play an important role (García de la Morena et al., 2018; Silva et al., 2018). Additionally, to land use and management changes, the increase of linear infrastructures, such as power lines and roads, known to be a driver of little bustard mortality and habitat selection during the breeding season (García et al., 2007; Osborne and Suárez-Seoane, 2007; Santangeli and Dolman, 2011; Santos et al., 2016; Silva et al., 2010b; Suárez-Seoane et al., 2002) might contribute to explain the observed trends.

In this study, we used the data collected during two little bustards' census in Portugal, where 51 areas spread across the species distribution area were sampled in 2003-2006 and then again in 2016, to access the main drivers affecting spatial and temporal variations in little bustard density. Using such regional scale, we analyzed the effect of four main potential drivers on spatial variations of little bustard densities, for each time period and temporal variations across periods: (i) the availability of the grassland habitat, i.e. habitat quantity; (ii) livestock density as a proxy of habitat quality; (iii) the amount of linear infrastructures, and (iv) the existence of agri-environmental schemes.

2. MATERIAL AND METHODS

2.1. LITTLE BUSTARD DATA

Little bustard male densities were surveyed in two different time periods, 2003-2006 and 2016 (Silva et al., 2018), across 51 areas (totaling ca. 150,000 ha; mean = 2,889 ha; range = 1,657 – 9,997 ha)) located in the Alentejo region, southern Portugal (Figure 1). The region concentrates the large majority of the breeding population of the species (Equipa Atlas, 2008). Bird density was estimated following a standardized protocol targeting male birds, as females have a cryptic behavior and are hard to detect (Delgado and Moreira, 2010; Juana and Martínez, 1996; Morales et al., 2005). A network of point counts defined along non-paved roads, distanced by 600 m from each other and from paved roads or inhabited houses, was used to census birds in each area, covering an average density of approximately 1.0 points/km2 per survey (range 0.47-3.00). In all 51 areas, 1,526 and 1,441 survey points were sampled in 2003-2006 and in 2016, respectively (differences due to changes in road availability). Still, 99% of all sampling points were replicated in the exact same location of the previous survey. At each point location, little bustard males were counted within a 250 m radius during 5 minutes at early morning and late afternoon, during April and May. For further details on little bustard census see Moreira et al. (2012) and Silva et al. (2018).

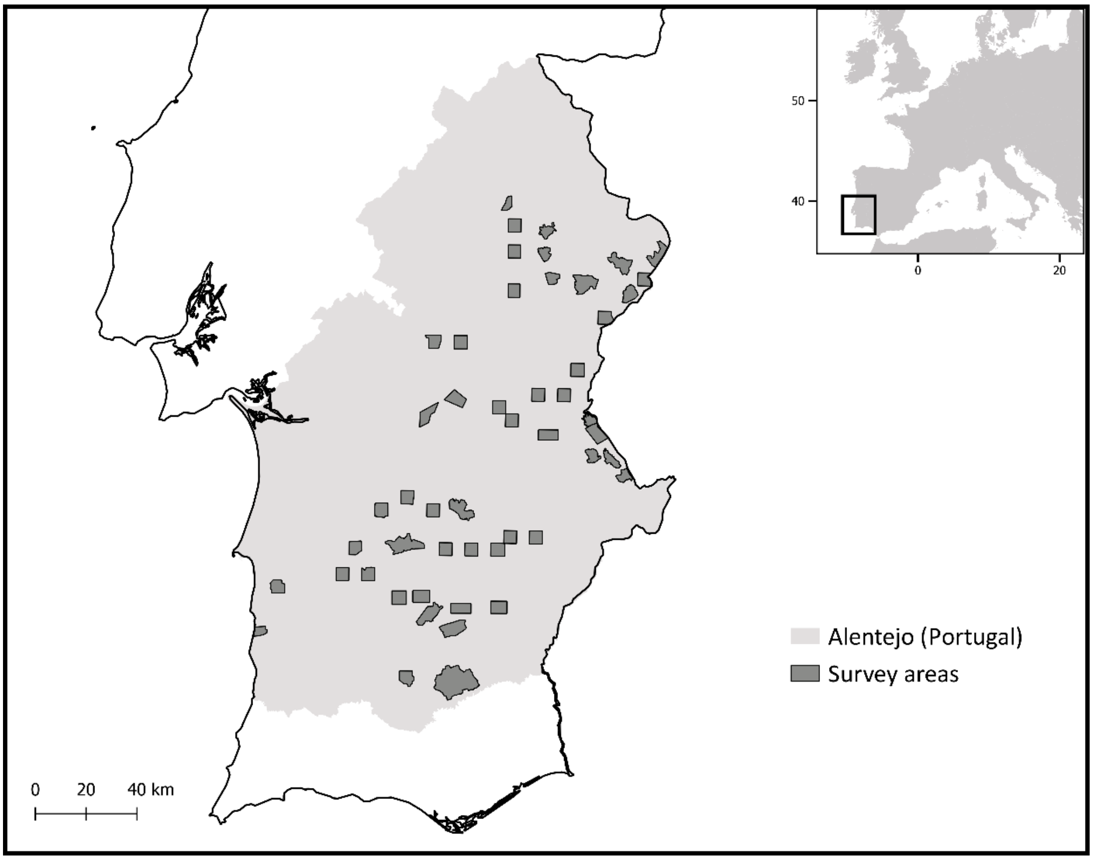

Figure 1 – Location of the 51 survey areas in Alentejo, Portugal.

2.2. POTENTIAL DRIVERS OF BUSTARD POPULATION DENSITY

For each survey period, and for each of the 51 areas, information on four major types of potential drivers of spatial and temporal changes in little bustard densities were gathered (Table 1):

2.2.1 Habitat availability

We quantified the amount of permanent pastures, non-irrigated annual crops and fallow land, the major land use types considered suitable for the species (Moreira et al., 2012; Silva et al., 2014, 2010a), in each area. Land use data was collected from the official land cover maps of Continental Portugal for 2007 and 2015 (DGT, 2018), publicly available on-line at http://mapas.dgterritorio.pt/geoportal/catalogo.html. We used land use classes 2.1.1 and 2.3.1 as our cartographic base for non-irrigated annual crops and permanent pastures, respectively. This information was later refined to match the census years based on (i) Google Earth and Bing images and (ii) field validation. The proportion of the total surface of each area covered by suitable habitat was estimated (Table 1).

Table 1 - Description and summary statistics for the predictor variables used to model little bustard density during the breeding season in Alentejo, Portugal. Means, standard deviation, and range are provided for continuous variables and frequency per classes is presented for the categorical variable.

Variable	**Description**	**Mean (SD)**	**Range**
Habitat	Proportion of the survey area covered with potential breeding habitat: non-irrigated annual crops, permanent pastures and fallow land	0.51 (0.25)	0 - 0.98
Stocking rate	Density of cattle and sheep livestock units per area of pastures and fallow land (LU/ha)	0.89 (0.59)	0.21 – 3.00
Cattle proportion	Proportion of cattle in the stocking rate	0.68 (0.19)	0 – 0.95
Roads	Density of roads in each survey area. The length of the structures at the survey area boundaries was divided in half (km/km2)	0.31 (0.19)	0 – 0.70
Power lines	Density of power lines in each survey area (km/km2)	0.46 (0.28)	0.01 – 1.41
Agri-environmental schemes	Agri-environmental schemes are implemented (Y) or not (N) in the survey area (census 2003-2006/ census 2016)	Y: 5/ 9 N: 46/ 42	-

2.2.2 Grazing management

Agricultural statistics were used to characterize livestock densities in our survey areas, focused on the two main livestock grazers of the region: cattle and sheep. Two variables were estimated: (1) stocking rate, i.e. the number of livestock units (LU) per area of pastures and fallow land (stocking rates were calculated according to the following ratio: bovine = 1 LU; adult sheep = 0.15 LU), and (2) the proportion of cattle in the total (cattle + sheep) stocking rate (Table 1). Both variables were derived from the results of the national agrarian census (RGA – Recenseamento Geral Agrícola) of 1999 and 2009, complemented with information obtained from Instituto Nacional de Estatística regarding the amount of pastures and fallow land (INE, 2011, 2001). We used the smallest administrative region in the country (i.e. Freguesia) as our unit, and applied a weighted mean based on the area occupied by of each Freguesia in our individual survey areas to obtain an estimate for each area. Due to the temporal lag between the little bustards' census and the available data on livestock we used the mean value between 1999 and 2009 data as a proxy of average grazing intensity in our sampled areas. Some obtained values of estimated livestock densities were considered artificially high (in 3 of the sampled areas), as they do not represent the real density of livestock in the field and are probably related to livestock in stables or grazing in other regions. So, we set densities to a maximum of 3 LU/ha, corresponding to the highest values estimated by direct counts in the field.

2.2.3 Linear infrastructures

We gathered data on the distribution of the paved roads and of the power line network during both censuses and calculated their density (km/km2) per study area (Table 1). We used the data from OpenStreetMap contributors, namely the classes: motorway, trunk, primary, and secondary (Haklay and Weber, 2008), to identify the main paved roads. For power lines, we mapped both the transmission (> 110 kV) and the distribution (< 110 kV) networks, based on data provided by the electric companies in Portugal (REN and EDP). Both data were validated for each census period based on Google Earth, Bing images and field checks. The length of the roads at the boundaries of the survey areas was downweighted when calculating its density, by dividing the length in half, as it was considered that only one side of the structure potentially influenced the bustard population within the study area. This prevalence of roads bordering study areas was particularly high in designated areas, whose administrative limits are often delineated using roads.

2.2.4 Agri-environmental measures

To check if agri-environment mechanisms promoted under the CAP contributed to the observed densities and population trends, we included a predictor describing if agri-environmental measures were implemented in each study area, in any of the time periods (Table 1).

2.3. DATA ANALYSIS

First, we used Generalized Linear Mixed Models (GLMM) to test if little bustard density and potential drivers (habitat, stocking rate, cattle proportion, roads and power lines) varied across census, using the census year as a fixed factor and the sampled area as a random effect. These models were fitted in R (R Core Team, 2016) with the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017).

To access the main drivers influencing the density of the little bustard across the study region, in each survey, we first performed two models that assessed the factors influencing spatial variations in bird densities separately for each census date (hereafter referred to as spatial models). These models included the density in each survey area as the response variable, and the predictors included: breeding habitat availability, stocking rate, cattle proportion, road density, power line density and presence/ absence of agri-environmental measures (Table 1). In each spatial model the predictors value corresponded to the one collected for the sampled year, except for the two grazing predictors, where we used the mean value of the available data as described above. A third model, the population variation model, assessed the factors underlying spatial patterns of changes in the little bustard density. In this model the variation in bird density across time (census 2016 – census 2003-2006) was the response variable. As predictors, we included the mean values of breeding habitat availability, stocking rate, cattle proportion, road density, power line density and presence/ absence of agri-environmental measures (Table 1), which aimed to access the main global pressures in each survey area. Additionally, we included the little bustard density in the first census as a predictor, as the magnitude of the absolute variation in density is constrained by the initial value in the area.

We used Spearman correlation coefficient and variance inflation factors to check for collinearity between the explanatory variables (Zuur et al., 2009). Variance inflation factors values (all < 2.0) and pairwise correlation between explanatory variables (all $|r|<0.55$) were low for our dataset, so all variables were used in the analysis.

Generalized Additive Models (GAM) were used to fit the three models, thereby accounting for potential non-linear responses (Wood, 2017; Zuur et al., 2009). The spatial models were fitted using a Gaussian distribution and a logarithmic link function, ensuring that fitted values were positive. To model the variation on the density values across census we used a Gaussian distribution with an identity link function. For the three models the optimal smoothing parameter was estimated by restricted maximum likelihood estimation (REML), and a basis dimension ($k = 3$) was defined to allow some complexity in the functions, while avoiding over-fitting the data. The models were fitted in R (R Core Team, 2016) with the package mgcv (Wood, 2018).

The modelling procedure involved the fitting of the full model, followed by backward elimination of non-significant ($p > 0.05$) variables to find the optimal model. The final model adequacy was evaluated by plotting residuals versus fitted values and explanatory variables, and the model fit was evaluated by the proportion of the null deviance explained (Zuur et al. 2009). Spline correlogram plots with 95% pointwise confidence intervals calculated with 1,000 bootstrap resamples were used to check for spatial autocorrelation in model residuals (Bjørnstad and Falck, 2001). We assumed that variable selection and parameter estimation were unbiased if there was no significant autocorrelation in model residuals (Rhodes et al., 2009). Correlograms were estimated in R with the ncf package (Bjørnstad, 2016).

3. Results

3.1. Major changes between census

The mean little bustard density significantly declined from 2.68 ± 0.38 males / ha in 2003-2006 to 1.44 ± 0.28 males / ha in 2016 (Table S1, Figure 2). Most of the sampled areas (n = 35) showed a negative trend between the two censuses and the species disappeared on 12 of them. In contrast, little bustard density increased in 12 areas.

Habitat availability significantly declined from 0.57 ± 0.03 to 0.45 ± 0.04 (Table S1, Figure 2), with declines in 28 of the sampled areas. Losses of favorable habitat over 5% were recorded in 19 areas and 6 areas had losses greater than 40%, reaching a maximum of 89%.

There was a significant global increase of the estimated stocking rate, although this parameter even reduced in 16 of the areas, and the proportion of cattle in the total stocking rate experienced a major and also significant increase (Table S1, Figure 2), across the whole region. An overall significant increase of the linear infrastructures also occurred across the study periods (Table S1, Figure 2). Roads grown from 0.27 km/km^2 ± 0.03 in 2003-2006 to 0.33 ± 0.03 km/km^2 in 2016, while power lines increased from 0.43 km/km^2 ± 0.04 to 0.49 ± 0.04 km/km^2.

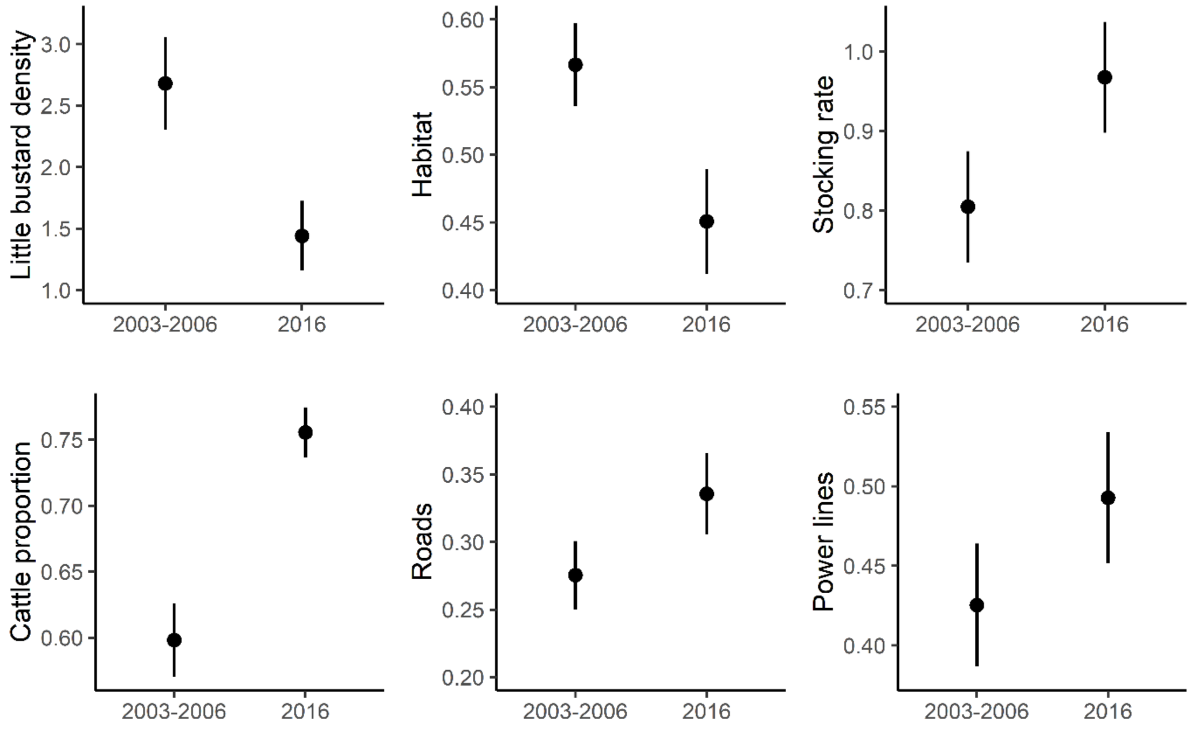

Figure 2 – Variation (mean and standard errors) in the little bustard density and the environmental predictors between the two census periods (2003-2006 and 2016). The grazing regime predictors (stocking rate and cattle proportion) are presented for 1999 and 2009, the only periods with livestock statistics available for the survey areas.

3.2. DRIVERS OF SPATIAL VARIATIONS IN LITTLE BUSTARD DENSITIES FOR EACH PERIOD

In the first census (2003-2006), habitat availability was the only significant predictor of spatial variation in little bustard densities, with higher densities occurring in areas with more habitat. In the 2016 census, habitat availability was also important, but the model also included variables related to grazing management (the species was more abundant in areas with intermediate levels of stocking rate (ca. 1.5 LU/ha) but lower levels of proportion of cattle in the total stocking rate (<60%)), existence of agri-environmental measures (benefiting bird densities) and densities of power lines (negative effect of increasing power line densities) (Table 2 and Figure 3). This latter model had a much higher explanatory power compared to the former one (79.7% vs 24.6%).

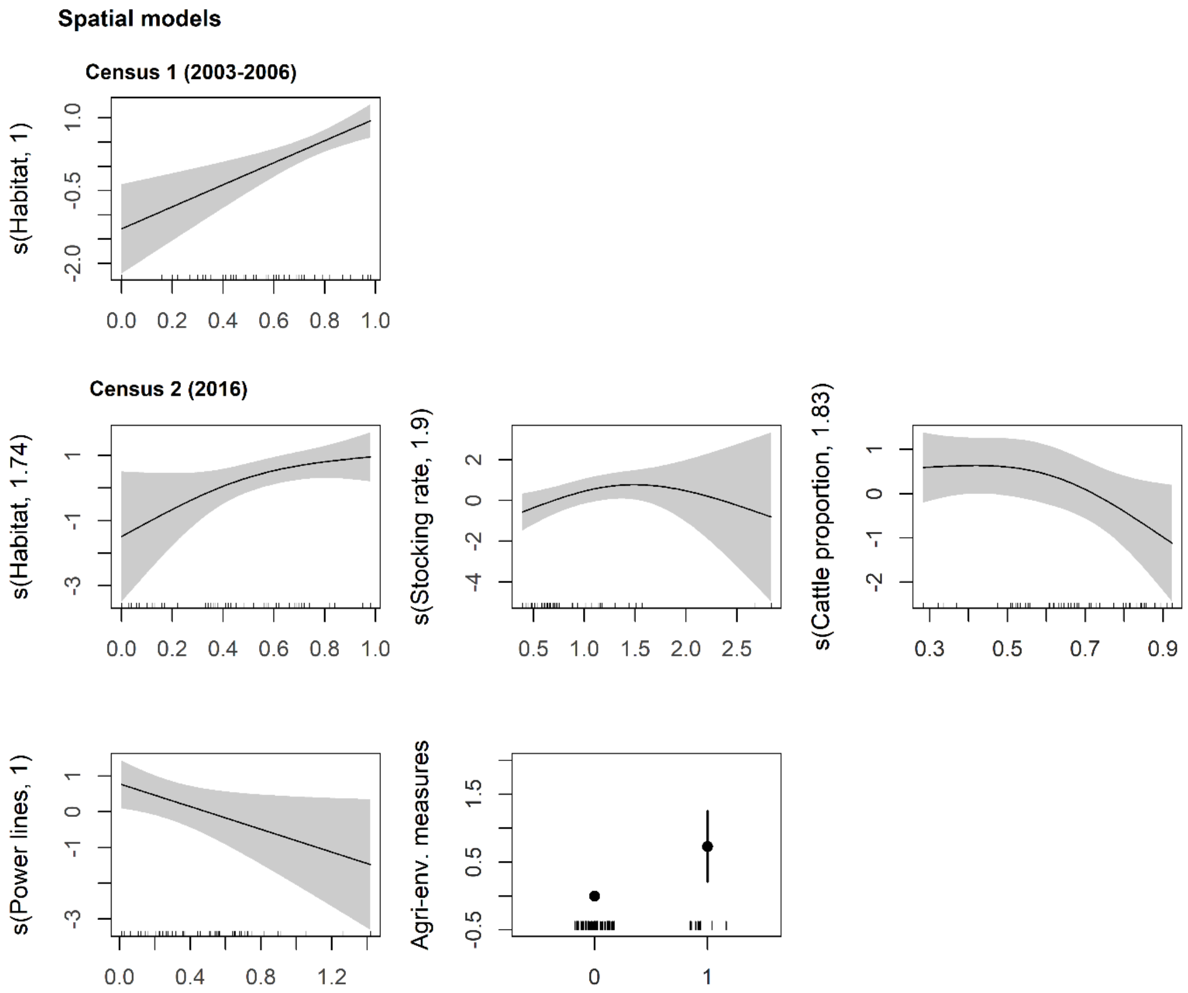

Figure 3 – Generalized additive model partial effects for the two spatial models of the relationship between the little bustard density in each census (2003-2006 and 2016) and the environmental predictors. Shaded areas represent 95% confidence intervals. The y-axis shows the contribution of the fitted centered smooth terms s (names of the predictor, estimated degrees of freedom) to the response variable (little bustard density in each census). Ticks in the x-axis represent the location of observations along the predictor.

Table 2 – Summary statistics for the three GAM models: the two spatial models tested the effect of the environmental predictors on the little bustard density in each census period (2003-2006 and 2016) and the population variation model tested the effect of the environmental predictors on the delta in little bustard density across census (2016 – 2003-2006). SE – Standard error; t – T statistics; edf – Estimated degrees of freedom; F – F statistics.

	Model coeficients	**Estimate**	**SE**	**t**	**edf**	**F**	**p-value**	**Deviance explained**
Spatial models								
Census 1 (2003-2006)	Intercept	0.87	0.16	5.49			0.000	24.6%
Density ~	Habitat				1.00	14.82	0.000	
Census 2 (2016)	Intercept	-0.52	0.28	-1.86			0.011	79.7%
Density ~	Agri-environmental measures	0.73	0.27	2.72			0.009	
	Habitat				1.74	4.06	0.021	
	Stocking rate				1.90	4.31	0.025	
	Cattle proportion				1.83	4.82	0.011	
	Power lines				1.00	5.22	0.027	
Population variation model								
Density variation ~	Intercept	-1.43	0.17	-8.57			0.000	81.7%
	Agri-environmental measures	1.06	0.52	2.05			0.047	
	Density census 2003-2006				1.80	86.11	0.000	
	Habitat_mean				1.70	7.53	0.002	
	Cattle proportion_mean				1.83	7.10	0.004	
	Power lines_mean				1.00	5.19	0.028	

3.3. DRIVERS OF LITTLE BUSTARD DENSITY VARIATIONS

Regarding the population variation model (Table 2 and Figure 4), larger declines in little bustard density occurred in areas with higher densities in the first census, a larger proportion of cattle in the stocking rate, more power lines, and where there were no agri-environmental measures implemented. Areas with a high proportion of available habitat (>40%) were the ones with smaller losses.

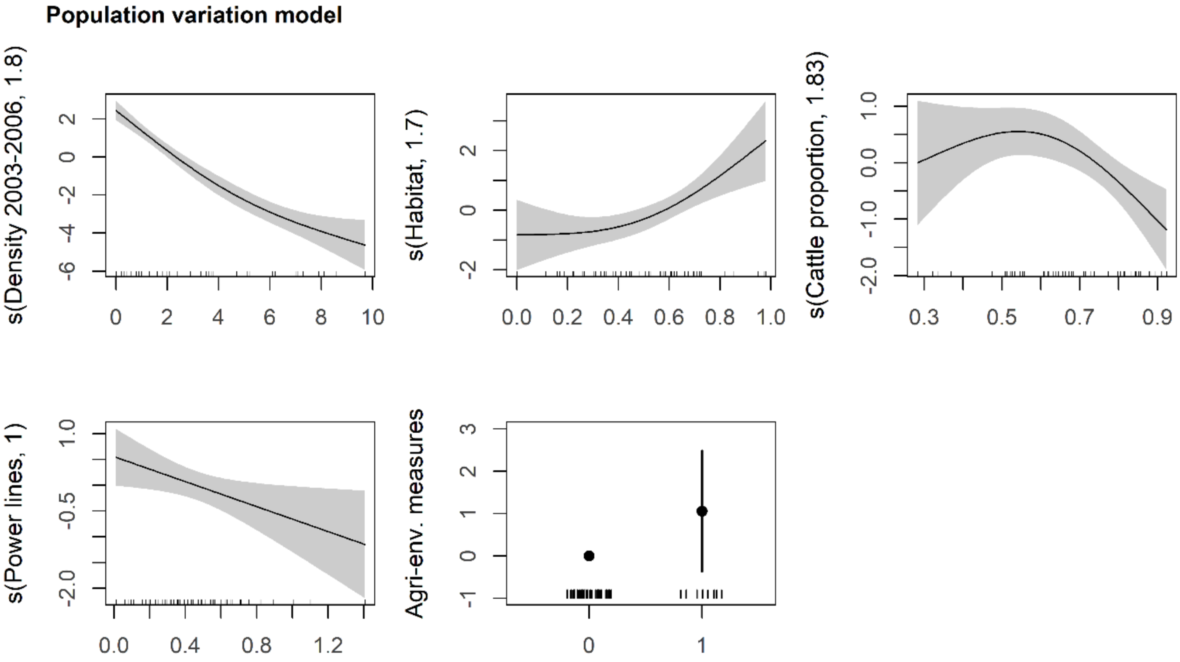

Figure 4 – Generalized additive model partial effects for the population variation model of the relationship between the delta in little bustard density across census (2016 – 2003-2006) and the environmental predictors. Shaded areas represent 95% confidence intervals. The y-axis shows the contribution of the fitted centered smooth terms s (names of the predictor, estimated degrees of freedom) to the response variable (delta in little bustard density between census). Ticks in the x-axis represent the location of observations along the predictor.

4. DISCUSSION

4.1. CHANGES IN BUSTARD DENSITIES AND THEIR DRIVERS ACROSS TIME

- Changes in bustard densities

There was an overall reduction of little bustard density in our study areas, from 2003-2006 to 2016, matching the patterns previously reported for the whole region (Silva et al. 2018).

- Changes in habitat quantity and quality

Global changes in key population drivers likely explain the observed trends. First, there was a reduction of available habitat across time. The major losses were observed in areas allocated to recent irrigation projects, which converted grasslands to permanent crops such as olive groves or vineyards. These were usually located outside SPA. Second, even in the remaining grasslands, habitat degradation likely occurred, due to different reasons: (i) from 2000 to 2016 the number of beef cattle increased 48% in the Alentejo region, while sheep declined 27% (Fig. S4; INE, 2019), what likely led to the observed overall increase of the stocking rate. (ii) Accordingly, the area devoted to hay production has been increasing in the region to ensure the demands of plant biomass for cattle, which causes changes in vegetation structure and directly affects little bustards through adult mortality and nests destruction, as haying produces shorter stubbles and occurs on average 1 month earlier then the harvest of cereal grain crops in our region (Faria et al., 2016). Changes in livestock also iii) represent the loss of the traditional rotation system based on cereal production and its heterogeneous habitat, mainly a significant reduction of fallow land (Fig. S4; INE, 2019). In fact, a recent work linked the loss of fallow lands with the overall decline of farmland birds, including the little bustard, in Spain (Traba and Morales, 2019). All these shifts in land use and livestock management were promoted by the Common Agricultural Policy reform of 2003 (Fragoso et al., 2011; Ribeiro et al., 2014). (iv) Finally, there was an overall increase of anthropogenic infrastructures within the sampled areas. These are known to negatively impact on little bustard populations through direct mortality (Marcelino et al., 2017; Marques et al., *in press*) and habitat degradation (García et al., 2007; Osborne and Suárez-Seoane, 2007; Santangeli and Dolman, 2011; Santos et al., 2016; Silva et al., 2010b; Suárez-Seoane et al., 2002).

4.2. DRIVERS OF SPATIAL VARIATIONS IN LITTLE BUSTARD DENSITIES

- The importance of habitat availability

As expected, habitat availability was a relevant driver of spatial variations in bustard densities in both census, confirming that grasslands are key to the little bustard during the breeding season. However, the remaining predictors where only relevant in the second census, maybe because the species occurred in high densities in 2003-2006 and birds occupied both optimal and suboptimal habitats, whereas when the densities declined, birds redistributed through areas with better habitat characteristics and avoided less suitable areas. Additionally, the species was exposed to higher levels of drivers that did not occur in the first census.

- Grassland habitat quality driven by changes in livestock management

The little bustard response to grazing changed across time. During 2003-2006 the species did not show a response to such predictors, while areas with intermediate levels of stocking rate and with lower proportions of cattle (< 60%) were preferred in 2016 (Figure 3), when there was also an overall increase of livestock intensity. Such variations across census suggests that the changes in grazing management, altered the habitat quality of the grasslands and therefore the response of the birds to our predictors. Similarly to our results for 2016, previous studies found that intermediate levels of cattle grazing were good for the little bustard (Faria et al., 2012; Reino et al., 2010) and the highest densities of the species in Alentejo were even recorded in areas grazed by cattle during 2007-2008 (Silva et al., 2010a). However, the increase of stocking rates with a higher proportion of cattle observed in several areas in 2016 seemed not favorable for the species.

- Power lines effects

Little bustard densities declined with the increase of power line densities during the second census. Power lines are known to affect the spatial distribution of the little bustard, although it is not clear if due to an increased perceived predation risk or neophobia (Silva et al., 2010b; Walters et al., 2014). The effect of power lines was only noticeable when the population was decreasing, probably because birds selected areas of higher habitat suitability, avoiding areas populated by power lines; whilst birds were forced to also occupy less suitable locations (i.e. with higher power lines densities) when the species density was higher, because no additional territories were available in locations of high habitat suitability. Additionally, power lines are a cause of anthropogenic mortality for the little bustard (Marcelino et al., 2017), with high fatalities numbers during the beginning of the breeding season (Marques et al., *in press*), what can also contribute to the reduction of density of the species at breeding areas.

- Agri-environmental measures promote grassland birds' populations

Areas benefiting from agri-environmental schemes had higher densities during the second census. This result confirms that such management measures, including the promotion of the extensive cereal rotation system and the adjustment of agricultural works (e.g. harvest time), can contribute to maintain higher density populations and mitigate the overall population decline.

4.3. DRIVERS OF TEMPORAL CHANGES IN POPULATION DENSITIES

- Largest declines in higher density areas – a reflex of significant loss of habitat quality?

The regional variations in population densities were quite variable across areas (ranging from losses from 6.9 males/ ha to gains of 2.9 males/ ha), suggesting that the driving forces behind such changes vary across the region and with the specificities of each area.

Major density declines occurred in areas highly suitable for the species, i.e. in areas where the species occurred in higher densities during the first census. Areas with higher densities were the ones where the magnitude of the impacts of habitat loss and degradation, as well as the overall population decline, could be more clearly expressed, suggesting the loss of male densities in remaining areas was limited by their already low densities.

- Amount of habitat attenuated the decline

Habitat quantity was also relevant to attenuate the decline of the species between 2003-2006 to 2016, as study areas with the largest expanses of grasslands (> 40% of the study area surface) where the ones with smaller density losses (some even with gains). Large and continuous grasslands are known to host high density values for the species in Portugal (Moreira et al., 2012; Silva et al., 2010a), and our results suggest that such landscapes have more resilient populations, which are able to buffer the general population decline. Little bustards preference for larger landscapes is probably due to their exploded lek mating system, as larger fields allow greater aggregations of males, which are preferred and are more visited by females, and have lower disturbance levels, high proportion of nesting females and lower rates of predation as a result of reduced edge effects (Silva et al., 2010a).

- Effects of livestock (proportion of cattle)

Areas dominated by cattle livestock were the ones with higher reductions of little bustard density across census. Such finding also suggests that the higher cattle densities and the underlying changes in land use management are causing changes in the quality of grasslands habitats (see section 4.1).

- Impact of power lines (and roads)

Areas with a higher density of power lines had major densities losses between census, further suggesting that such infrastructures affect the grassland habitat quality, by promoting fragmentation and avoidance behaviors of little bustards, as well as mortality of the species.

The fact that the road network was not relevant in explaining little bustard spatial variation was unexpected, as roads are responsible for habitat fragmentation and a source of human presence and disturbance (Fahrig and Rytwinski, 2009), and are known to affect the spatial distribution of the little bustard during the breeding season (e.g. Suárez-Seoane et al. 2002; García et al. 2007; Osborne & Suárez-Seoane 2007; Silva et al. 2010b; Santangeli & Dolman 2011). This may happen because the effect of roads was masked by the one from power lines. In fact, both linear structures tend to occur spatially clustered, with power lines and roads running parallel, and we had a moderate positive correlation between these predictors in our dataset (r=0.39, p-value=0.004, Pearson's correlation).

- Agri-environmental measures produce positive outcomes

The density variations across time confirmed that agri-environmental measures attenuate the decline of the little bustard, confirming that such agriculture policies contribute with positive outcomes for the conservation of grasslands species like the little bustard and for High Nature Value Farmlands in general.

4.4. A FUTURE FOR THE LITTLE BUSTARD

Habitat quantity and quality is key to the little bustards' populations. The species needs large expanses of grasslands, with few anthropogenic structures as power lines and roads, that fragment the landscape and cause mortality of the species. The production of livestock in grasslands need to be properly managed, with lower or lower-intermediate levels of grazing and avoiding practices, as earlier mowing, which cause adult mortality and nest losses during the breeding season.

Our study shows that areas with agri-environmental management were able to hold back the decline of the little bustard, revealing that agri-environmental schemes are having successful outcomes regarding the conservation of grassland birds. Therefore, we believe that only changes in the agriculture policies can revert the decline of the little bustard and maintain the population of the species at an adequate conservation status as the EU Bird Directive (2009/147/EC) aims. This can be achieved through a reinforcement of the attractiveness of agri-environment schemes with a support for an extensive livestock production following the traditional low-impact practices.

Authorities should also implement monitoring programs focused on grassland species and their habitats that allows to detect the effect of the agriculture practices and its changes across time. Future studies should address the habitat features that being affected by present livestock management.

Although our population variation model had a good performance in explaining our data (ca. 80% deviance explained), we believe that the decline of the species in Alentejo is not only related to pressures occurring during the breeding season. In fact, multiple threats, as decreased habitat quality in breeding areas, loss of post-breeding and wintering areas and high mortality rates, may be acting in a synergic way, pushing the species to an extinction vortex (Brook et al., 2008). The annual survival rate of little bustards in Iberia is just 67% (Marcelino et al., 2017), similar to the one estimated for western France when the population was declining during the 90s (Inchausti and Bretagnolle, 2005). Anthropogenic mortality, mainly due to collision with power lines and illegal hunting, is quite high in the species (ca. 7-7.4% annually) and has similar levels to the mortality due to predation (ca. 7.7-8.7% annually; Marcelino et al. 2017). On top of lower survival rates, the species may also be losing post-breeding and wintering habitat at a fast rate, as key areas for the non-breeding season lack conservation status (Silva et al., 2007, 2014; Silva and Pinto, 2006). Little bustards are short-distant migrants (Alonso et al., 2019; García de la Morena et al., 2015) that move to more productive agriculture areas during the dry season, in search of green vegetation (Alonso et al., 2019; Silva et al., 2007). However, Alentejo is facing major landscape changes during the 21st century, and large expanses of open agriculture lands have been transformed into permanent crops as olive groves, almond plantations and vines or permanent pastures, in fact, the area devoted to annual crops decrease 58%, while permanent crops increased 11% from 2000 to 2016 (Figure S4; INE, 2019).

Therefore, a successful recovery of little bustards' populations will imply a better management of the grassland habitat but also wide conservation actions that reduce the anthropogenic mortality levels and conserve the non-breeding habitat.

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SUPPLEMENTARY MATERIAL

Table S1 – Summary statistics for the GLMM models analyzing changes in little bustard density and our predictors (breeding habitat availability, stocking rate, cattle proportion, roads, power lines) across the two census (2003-2006 and 2016).

Model coeficients	Estimate	SE	t	p-value
GLMM1: little bustard density				
Intercept	2.680	0.334	8.02	0.000
Census 2016	-1.239	0.301	-4.12	0.000
GLMM2: breeding habitat availability				
Intercept	0.567	0.035	16.23	0.000
Census 2016	-0.116	0.027	-4.25	0.000
GLMM3: stocking rate				
Intercept	0.805	0.083	9.745	0.000
Census 2016	0.163	0.056	2.921	0.005
GLMM4: cattle proportion				
Intercept	0.598	0.024	24.99	0.000
Census 2016	0.157	0.015	10.44	0.000
GLMM5: roads				
Intercept	8.507	1.359	6.258	0.000
Census 2016	1.660	0.458	3.625	0.000
GLMM6: power lines				
Intercept	0.425	0.040	10.632	0.000
Census 2016	0.067	0.013	5.286	0.000

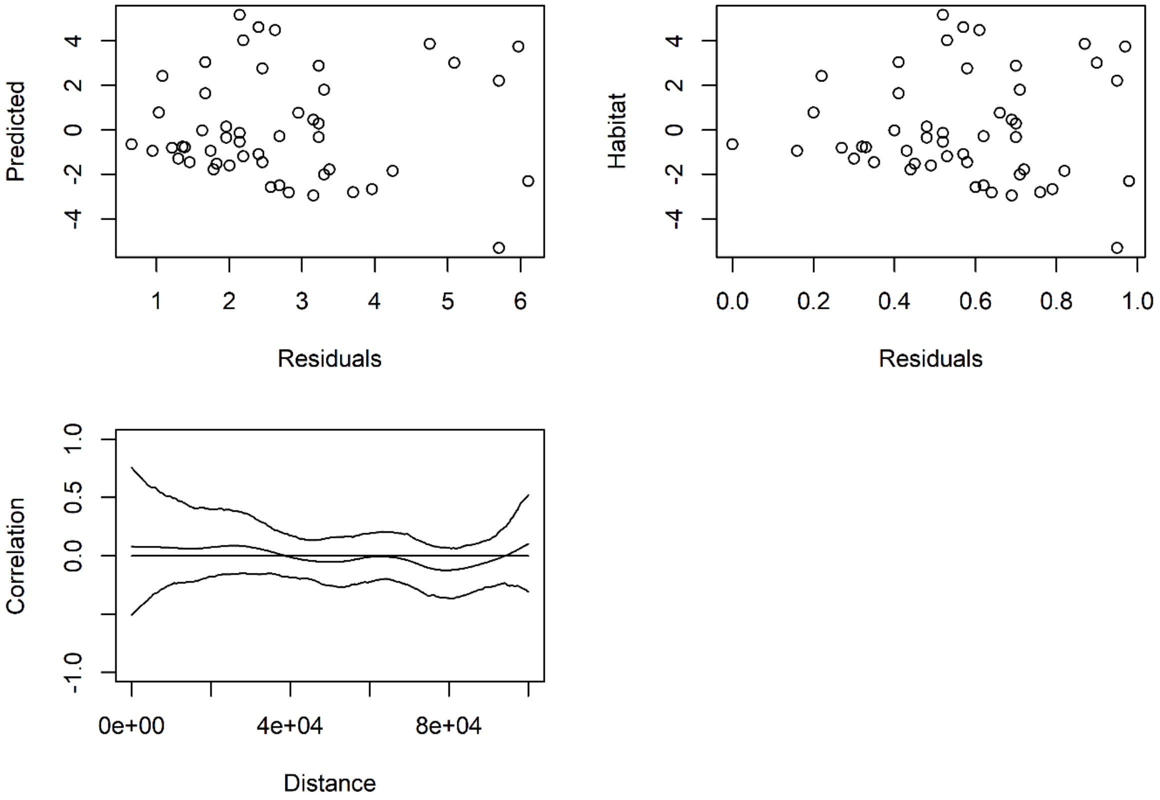


Figure S1 – Validation plots for the spatial model of the census 2003-2006: residuals versus fitted values and residuals versus explanatory variables. A Spline correlogram describing the spatial autocorrelation in the residuals is presented in the bottom right corner. Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad and Falck, 2001).

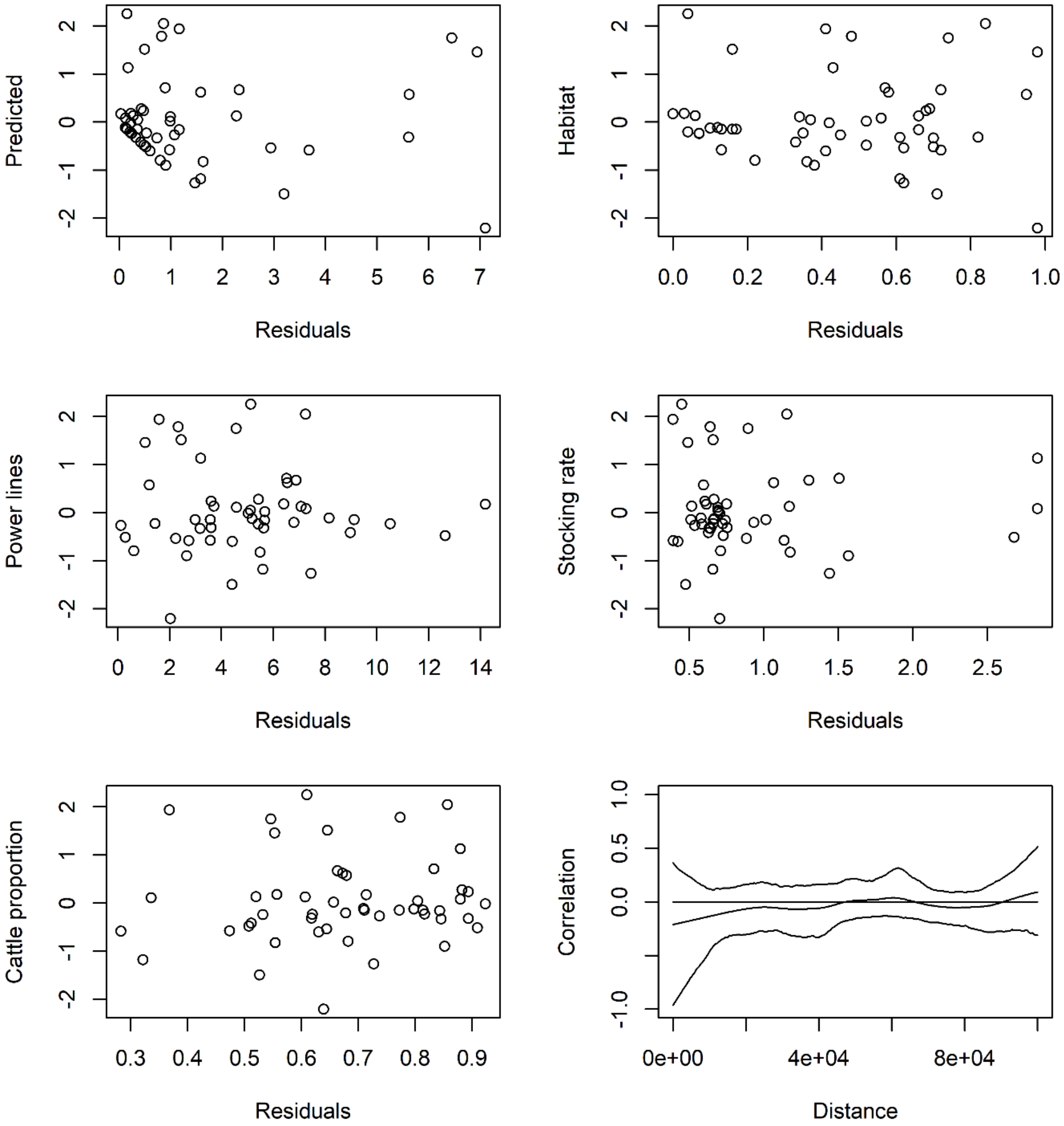


Figure S2 – Validation plots for the spatial model of the census 2016: residuals versus fitted values and residuals versus explanatory variables. A Spline correlogram describing the spatial autocorrelation in the residuals is presented in the bottom right corner. Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad and Falck, 2001).

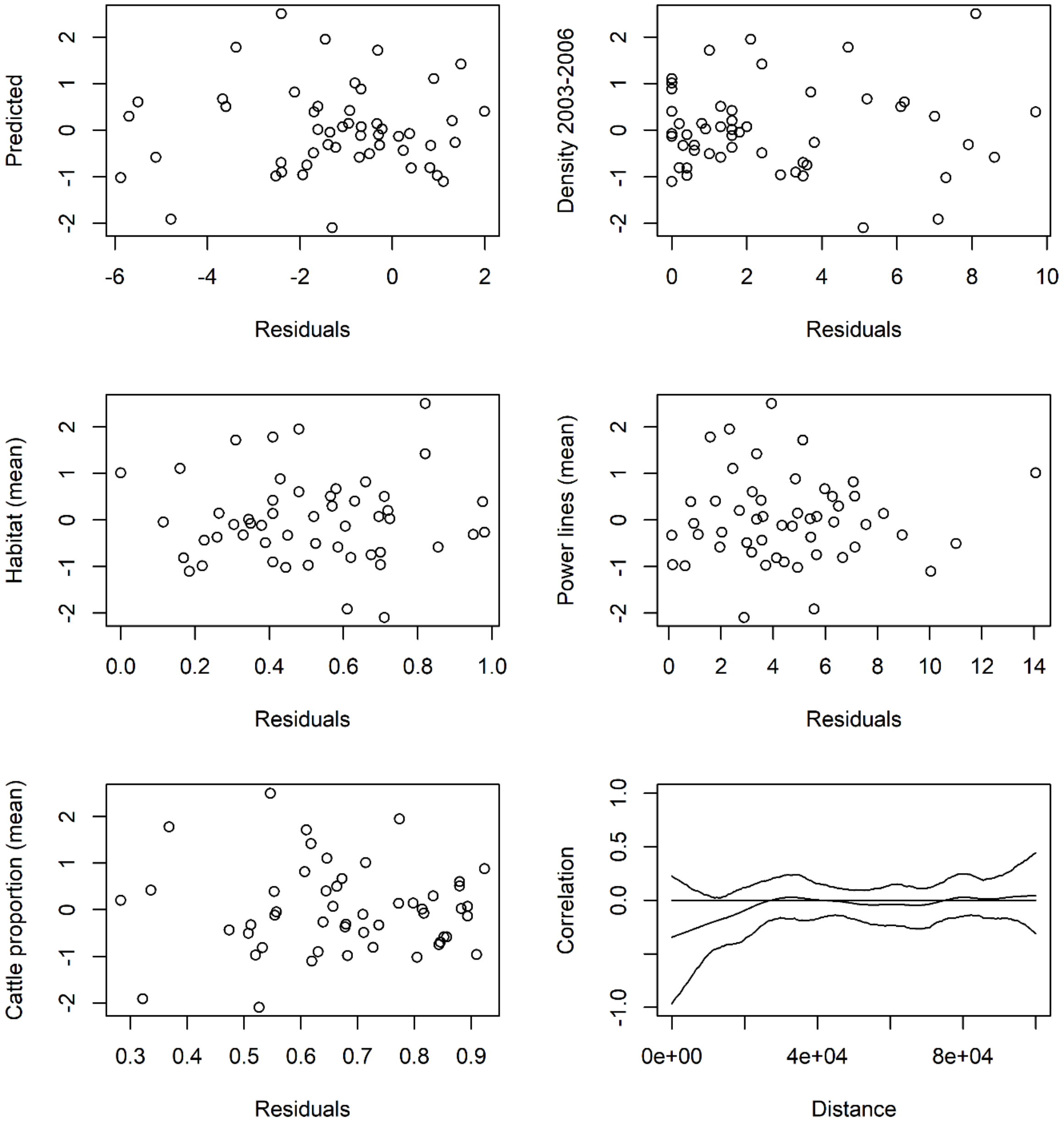
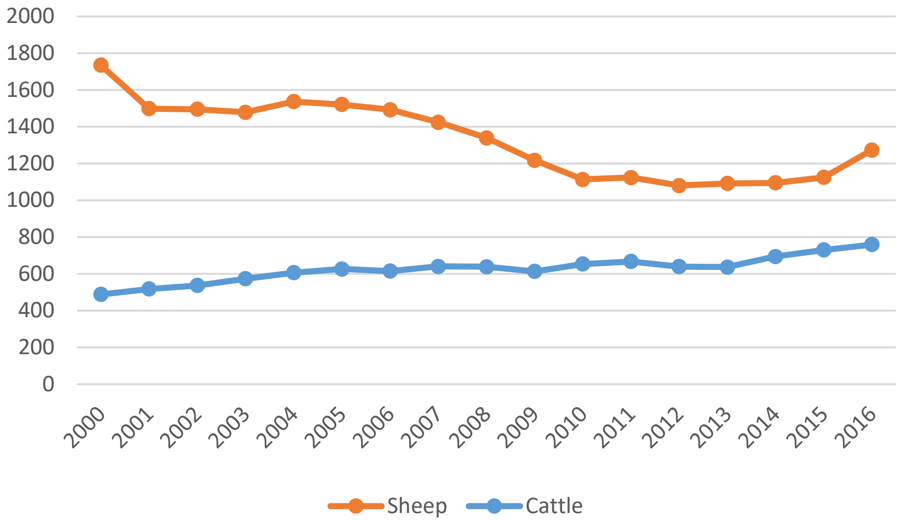


Figure S3 – Validation plots for the population variation model: residuals versus fitted values and residuals versus explanatory variables. A Spline correlogram describing the spatial autocorrelation in the residuals is presented in the bottom right corner. Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad and Falck, 2001).

a)



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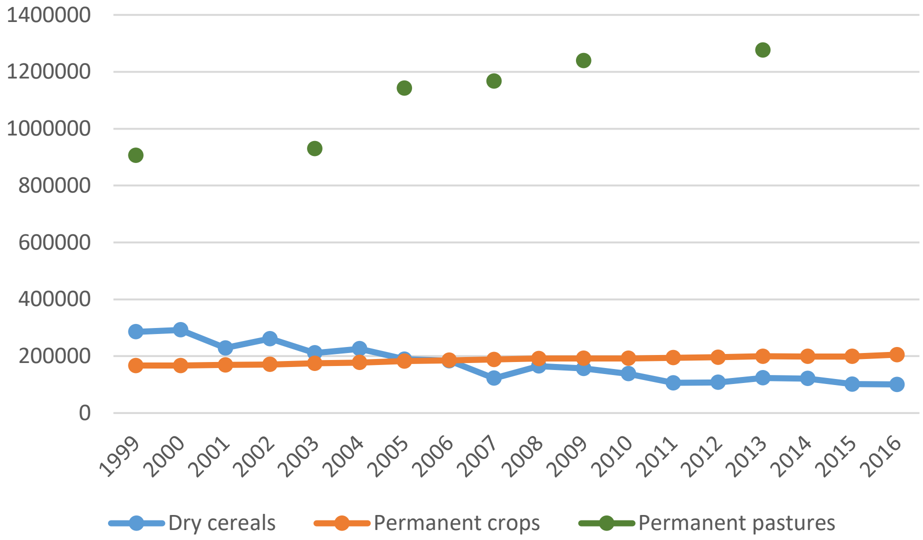

Figure S4 – Agricultural trends in Alentejo from 1999/2000 to 2016: a) sheep and cattle beef (number of animals), and b) dry cereals, permanent crops and permanent pastures (ha) (INE 2019).

References:

Bjørnstad ON, Falck W. 2001. Nonparametric spatial covariance functions: Estimation and testing. Environmental and Ecological Statistics **8**:53–70. Available from http://link.springer.com/10.1023/A:1009601932481.

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Chapter 3

Habitat and power line configuration as major drivers of collision risk in two bustard species

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Habitat and power line configuration as major drivers of collision risk in two bustard species

ABSTRACT

Collision with power lines is a major cause of mortality in many bird species. Understanding the biotic and abiotic factors increasing collision risk is therefore important to minimize mortality by increasing the efficiency of mitigation measures, such as power line re-routing or wire marking. Here, we used collision events registered from 2003 to 2015 along 280 km of transmission power lines in southern Portugal, to analyse spatiotemporal patterns and collision risk factors in two sympatric, threatened, and collision-prone species: the great bustard (*Otis tarda*) and the little bustard (*Tetrax tetrax*). We found that the occurrence of collisions was not uniform across space and time, and variations could be explained by the species' ecological requirements, distribution patterns, and behaviour. Although both species make substantial flights between areas of suitable habitat, collisions were far more likely in power line sections with more than 20% (for the little bustard) or 50% (for the great bustard) of open farmland habitat in the surroundings. Power line configuration was also important, as taller pylons and those with a higher number of wire levels posed a higher risk for both species. We found a small but significant effect of wire marking reducing collisions in the little bustard, but could not confirm a similar effect in the great bustard, possibly due to data constraints. Mitigation measures for preventing bustard collisions, including adequate route planning, line configuration and wire marking, should be implemented whenever power lines cross areas with >20% of open habitat, even outside protected areas.

Keywords: anthropogenic mortality; birds; collision risk; mitigation; *Otis tarda*; *Tetrax tetrax*; transmission lines

1. INTRODUCTION

Collisions with power lines represent an important source of anthropogenic mortality for birds (Bevanger, 1998; Drewitt & Langston, 2008; Loss et al., 2015). In the United States, for example, tens of millions of birds are estimated to die annually due to collision with power lines (Loss et al., 2014). There is evidence of population-level effects on some threatened collision-prone species (e.g. Marcelino et al. 2018; Shaw et al. 2017, 2010).

The main strategies to mitigate bird collision with power lines include (i) power line route planning that avoids important areas of occurrence and flight paths, (ii) choosing power line configurations with lower collision risk, and (iii) increasing wire visibility through the attachment of markers like spirals or flappers (Bernardino et al., 2018). Wire marking is frequently used in areas of conservation importance for birds, although with variable or unknown effectiveness (Jenkins et al., 2010; Barrientos et al., 2012).

The planning and implementation of mitigation actions requires a good understanding of the biotic and abiotic drivers of bird collision with power lines. However, relatively little is known about such drivers (Loss et al., 2015) mainly because collision risk is species-specific and thus hard to model. Moreover, most published studies focus on single sites, and assessments at a large spatial scale are rare (Silva et al., 2014). These reasons may explain why some of the most common recommendations of good practice in the installation of power lines are not supported by scientific evidence (Bernardino et al., 2018). One example is the power line configuration: wire height, the number of levels of wires and the spacing between them are assumed to influence the collision risk, but there is still little scientific evidence to support it (Bernardino et al., 2018).

Gruiformes, including bustards, are highly prone to collisions with power lines due to their morphological features and visual perception (Bevanger, 1998; Janss, 2000; Martin & Shaw, 2010), and there are many studies on interactions between power lines and bustards (e.g. Janss & Ferrer, 2000; Raab et al., 2011; Burnside et al., 2015; Mahood et al., 2016; Shaw et al., 2017). However, few focused the identification of the factors contributing to collision risk for this group. In South Africa, Shaw et al. (2017, 2010) modelled the collision risk of the blue crane (*Anthropoides paradiseus*) and the Ludwig's bustard (*Neotis ludwigii*) using fatality events. Such models revealed some of the factors that put birds at risk but were unable to identify the location or configuration characteristics that make some power lines particularly dangerous. In Europe, Silva et al. (2014) used an alternative approach to assess collision risk without using collision records and developed a spatially-explicit risk model for the little bustard (*Tetrax tetrax*) based on habitat suitability, population densities, and bird flight behaviour.

In the Iberian Peninsula, the sympatric great bustard (*Otis tarda*) and little bustard are known to be highly prone to collision with overhead wires. Both species are considered "poor fliers", having a less manoeuvrable flight due to their heavy body and relatively small wings (Rayner, 1988), and their eye morphology makes them blind in the direction of travel (Martin & Shaw, 2010). These features are known to make species prone to collision (Bernardino et al., 2018). The great bustard is a Globally

Threatened species (Birdlife International, 2017). Collision with power lines is a main source of anthropogenic mortality for the species, and has been described to induce changes in its migratory patterns; migrant birds have a higher mortality rate due to collisions than sedentary ones (21.3% vs. 6.3%), so the proportion of resident birds has largely increased during a 15-year period (Palacín et al., 2017). The little bustard is a Near Threatened species (Birdlife International, 2017) that has experienced large population declines during the last decade (García de la Morena et al., 2017; Silva et al., 2018). A recent study found that the annual survival rate of adult little bustards in Iberia, which hosts the largest population in Western Europe (Iñigo and Barov, 2010) is just 67%, the lowest known value for wild bustard species. Moreover, 3.4 to 3.8% of this population collides annually with power lines, representing the main anthropogenic source of mortality in the species (Marcelino et al., 2017). Therefore, collisions with these structures are likely to have population-level effects on both species.

Great and little bustard use similar habitats and both make regional migrations, but differences in morphology and behaviour may result in distinct collision risk patterns and drivers. In this study, we aimed to identify and contrast the main drivers of collision risk in these two sympatric collision-prone species. We gathered and pooled data collected during 13 years in southern Portugal, along 280 km of transmission power lines, to determine for both species: (i) the spatial and temporal patterns of collision; (ii) and the relative importance of habitat, power line technical features, and wire marking, as determinants of collision risk. Results are discussed to suggest improvements to mitigation measures targeting these species.

2. METHODS

2.1. STUDY AREA

This study was conducted in the Alentejo region (ca. 27,000 km^2), in southern Portugal (Figure 1). The landscape is characterized by plains or low hills (up to 1000 m above sea level) and land-use is dominated by (i) agricultural areas (ca. 40%), mainly permanent crops like olive groves or vineyards and open areas occupied by non-permanent crops and pastures (ca. 47% of the agricultural areas); (ii) forests (ca. 20%), mainly silvo-pastoral sparse woodlands dominated by holm oak (*Quercus rotundifolia*) or cork oak (*Quercus suber*) (INE, 2011; DGT, 2014). The climate is typically Meso-Mediterranean and Thermo-Mediterranean, characterized by hot, dry and long summers and by mild and wet winters (Rivas-Martínex et al., 2002).

Alentejo harbours the whole Portuguese breeding population of great bustard (ca. 1,150 birds; Pinto et al. 2005) and 90-95% of that of little bustard (ca. 8,900 males Silva et al. 2018). The main breeding areas of both species are inside Special Protected Areas (Figure 1), but key areas during post-breeding and winter lack conservation status (Silva & Pinto, 2006; Silva et al., 2007, 2014). The Special Protected Area status requires the implementation of management actions that include the mitigation of bird collision risk, namely through the installation of wire-marking devices in new power lines.

The total length of the transmission power line network in the region is 1,239 km (Figure 1), mainly 150 kV and 400 kV power lines. Wire-marking was implemented in some line sections, mainly those inside Special Protected Areas. In general, wire-marking devices were installed on both earth wires, assembled in an alternated way, to produce a visual spacing effect, in profile, of 1.5 - 5 m. The large majority of such devices were spirals with a diameter of 30 cm (white and red/orange), but small spirals with ~10 cm of diameter (grey or white and red/orange) and rotative flappers (FireFly) were also used.

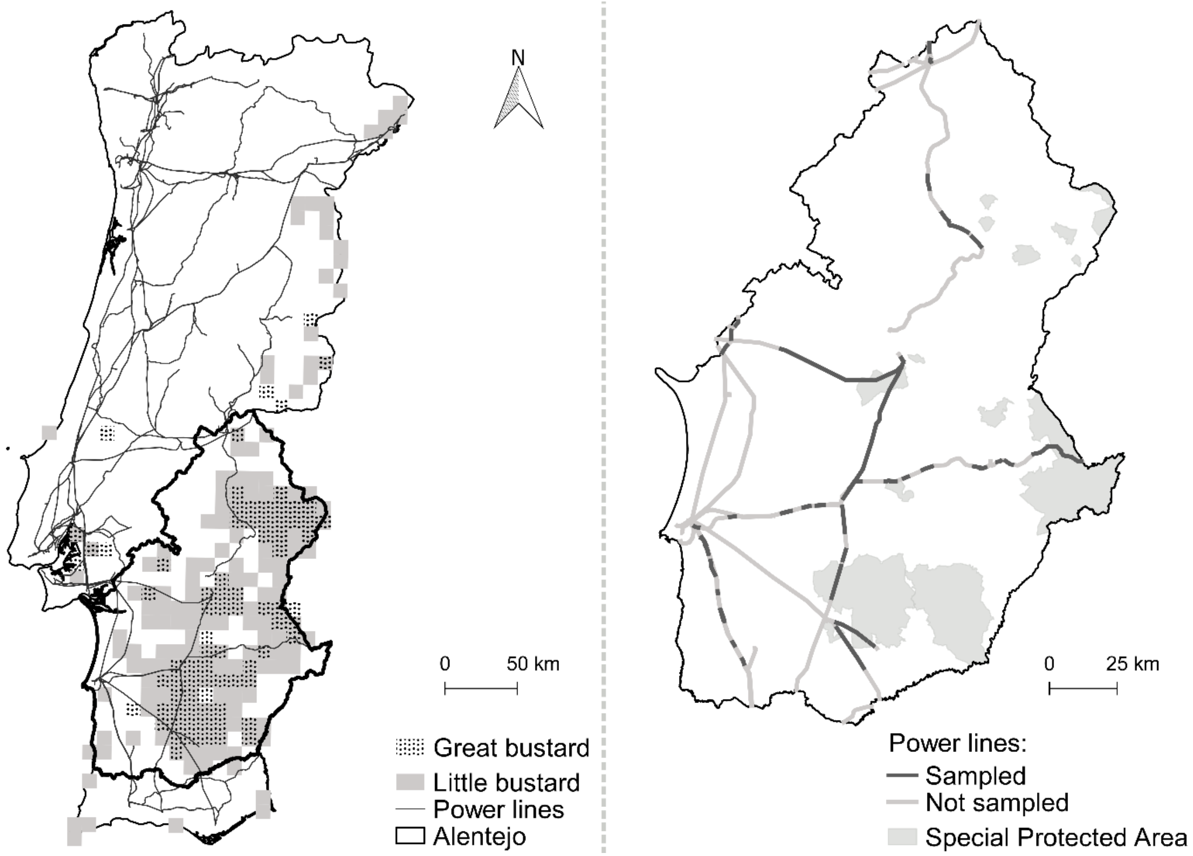


FIGURE 1. Great bustard and little bustard breeding range (Equipa Atlas 2008) and transmission (150-400 kV) power line network in Portugal (left panel). Surveyed sections of the power line network and Special Protected Areas with open habitats in the study area – Alentejo (right panel).

2.2. DATA COMPILATION

We compiled data from the nine studies on bird collision with transmission power lines done in Alentejo from 2003 to 2015, all promoted by the company that manages the Portuguese transmission network (REN – Redes Energéticas Nacionais). These studies included (i) a national assessment of bird mortality at transmission power lines, (b) two studies focusing on wire-marking effectiveness, performed by non-governmental organizations and by the public administration, and (iii) six monitoring programs of single power lines carried out within the scope of Environmental Impact Assessment processes (Supplementary Table 1).

This resulted in a total of 280 km of power lines that were systematically surveyed at least once per season, which represents ca. 23% of the transmission grid in the region. Sampling effort was uneven across studies, e.g. study duration ranged from 12 to 67 months and the survey frequency varied from 15 to 90 days (Supplementary Table 1). Collision data also varied in spatial and temporal detail, with the lower resolution data corresponding to the number of carcasses per 2-km power line section. Due to this distinct sampling effort and data details across studies, we divided the total sampled power line in 144 sections of ca. 2-km each (mean ± SD = 1,946 m ± 319; range: 755 – 2,767 m), and used the presence/absence of mortality of each species per section in our analysis (except for the temporal analysis). None of the studies characterized malfunctioning of the marking devices, as fall from the wire, flapper twist or colour changes.

2.3. SEASONAL AND SPATIAL PATTERNS OF COLLISION

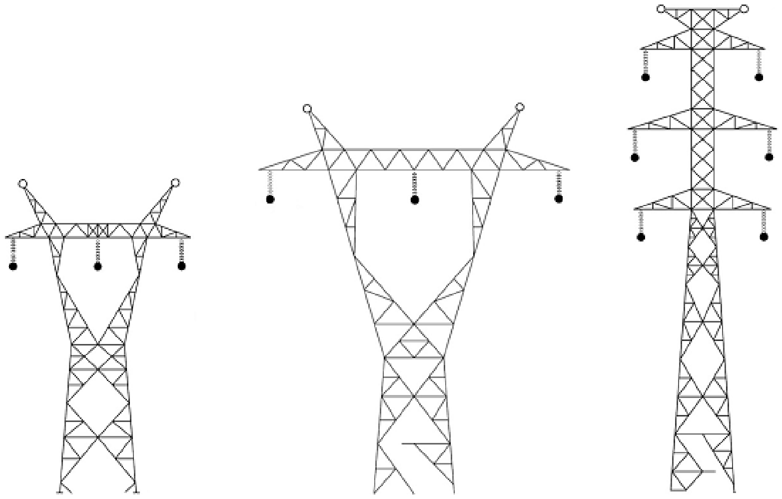
The location of power line sections with bustard mortality events was registered for each species. Seasonal patterns (across the months of the year) of fatality by collision were estimated for each species, separately for power line sections inside and outside the Special Protected Areas network. The protected areas concentrate most of the individuals during the breeding season, so different collision patterns across time could be expected there. Only studies with a regular sampling effort of 15 or 30 days reported bustards' fatalities events with detailed temporal data, therefore the seasonal data presented here results from a constant annual survey effort.

2.4. COLLISION RISK MODELLING

To identify the main drivers of bustard collisions with power lines we selected a group of variables related to habitat availability, power line configuration, wire marking, and survey effort (Table 1). Great bustard and little bustard, both grassland species, have strict habitat requirements and are typical of open and flat or gently undulating landscapes (Birdlife International, 2017). They are both short distance migrants, performing seasonal movements of up to 260 km in the case of great bustard and up to 300 km in the little bustard. A large proportion of birds (65% in the great bustard and 89-96% in the little bustard) move from their breeding grounds to areas with higher food availability during late Spring and Summer (Rocha, 2006; García de la Morena et al., 2015; Palacín et al., 2017; Alonso et al., 2019). Collisions are more frequent during the post-breeding and wintering seasons (Silva et al., 2014; Palacín et al., 2017), when bustards make most migratory movements, so collisions events could be associated to some of the habitat types crossed during these movements, and not just to the habitats they normally use. Land cover information was extracted from COS2007 (DGT, 2007) and different cover categories were merged into three broad classes, which are not likely to have changed much during the study period: open farmland, forest, and agro-forestry (Table 1). We used the dominant land cover type (in terms of total area) in a 1-km buffer adjacent to each power line section, as a surrogate of habitat availability in the close vicinity of the line. Additionally, we measured the proportion of open farmland in a 5-km buffer surrounding each power line section as an indicator of potential suitable habitat availability in the region. To characterize power lines each section was classified according to three main configurations: (i) small configuration (low pylon height), (ii) medium configuration (medium pylon heights), both with conductor wires displaced horizontally and two collision levels, and (iii) large configuration, with conductor wires displaced vertically and four collision levels, higher pylons, and larger distance between top and bottom wires (Figure 2). All three power line configurations have two earth wires above the conductors. A presence/absence variable was used to represent the presence of anti-collision devices (of any type) in each 2-km section. Finally, we included an indicator of survey effort (accumulated surveyed distance in all sampling visits, see Table 1), to account for potential survey bias among power line sections.

Table 1. Description and summary statistics of the predictor variables used to assess the drivers of collision risk of great bustard and little bustard. Means and range are provided for continuous variables and frequency per classes is presented for categorical variables (n=144 sampled transects).

Variable	**Description (units)**	**Mean (SD) / Frequency**	**Range**
Open_Habitat	Proportion of open farmland habitat in a 5 km buffer around the power line section (%): COS 2007 (DGT, 2007)	0.43 (0.19)	0.14 – 0.87
D_Habitat	Dominant habitat in a 1 km buffer from the power line section (COS 2007; DGT 2007): open farmland (COS categories: 2.1.1, 2.1.2, 2.3.1), forest (3.1.1, 3.1.2, 3.1.3, 3.2.4) and agro-forestry (2.4.4)	open: 81 forest: 36 agro-forestry: 27	-
Configuration	Power line configuration (see Figure 2): S – small configuration, horizontal 150 kV; M – medium configuration, horizontal 400 kV; L – large configuration, vertical 150 or 400 kV	S: 77 M: 36 L: 29	-
Marking	Wire markers devices to minimize collision (presence/absence)	0: 90 1: 54	-
Effort	Total (accumulated) surveyed distance in all sampling visits (length of the power line section (km) x minimum number of samples) (km)	48.3 (50.5)	4.6 – 265.5



	Small configuration, horizontal (single circuit) at 150 kV	Medium configuration, horizontal (single circuit) at 400 kV	Large configuration, vertical (double circuit) at 150 or 400 kV
No. of vertical wire levels	2	2	4
Mean pylon height (SD) (m)	30.2 (4.7)	38.0 (7.1)	47.3 (8.1)
Mean distance between top and bottom wires (SD) (m)	5.7 (0.5)	8.3 (0.7)	22.3 (3.2)

Figure 2. Characterization of the three main configurations of transmission power line pylons in Alentejo, Portugal. The solid dots represent the position of the conductor wires, while the open dots represent the earth wires.

We used Spearman correlation coefficient and variance inflation factors to check for collinearity between explanatory variables (Zuur et al., 2009). Variance inflation factors values (all < 1.6) and pairwise correlation between explanatory variables (all |r|<0.60) were low for our dataset, so all variables were used in the analysis.

We assessed the global effect and relative importance of each explanatory variable with Boosted Regression Trees (De'Ath, 2007), using the dismo package (Hijmans et al., 2016) and following Elith et al. (2008) recommendations along the modelling process. Boosted Regression Trees is a non-parametric machine-learning method that fits a large number of a simple classification or regression trees (models that relate a response to their predictors by recursive binary splits), whose predictions are combined to give more robust estimates of the response (De'ath & Fabricius, 2000; Elith et al., 2008). Boosted Regression Trees major advantages include its capability to accommodate both continuous and categorical predictor variables, missing values, immunity to the effects of extreme outliers, and facility for fitting interactions between predictors (Leathwick et al., 2006).

We built one Boosted Regression Trees model for each species, using the presence/absence of mortality on power line sections as the response variable. As input parameters we used the Bernoulli family, a tree complexity of three (i.e. the complexity of variable interactions that may be fitted), a 0.0005 learning rate (the weight applied to individual trees) and 0.8 as the bag fraction (at each iteration, 80% of the data were drawn at random). Each model was built with a default 10-fold cross-validation (using the function 'gbm.step'). When fitting initial models (Supplementary Figure 1), some of the generated fitted functions had varying shapes without underlying ecological meaning. For example, the fitted function for the effects of open habitat on great bustard was quite variable for high proportions of this habitat type. Additionally, it seemed that collision risk for this species was higher in the presence of wire marking. Such patterns often result from combinations/interactions of variables in specific geographical contexts which, in spite of having no ecological meaning, contribute to increased model fit (Leathwick et al., 2006; Elith et al., 2008). For example, the higher likelihood of great bustard collisions in the presence of wire marking is likely to be an artefact resulting from the fact that most power lines that cross important areas for this species during the breeding season have been marked. Therefore, following Leathwick et al. (2006), we refitted the models by imposing monotonically increasing (for the proportion of open habitat and survey effort) or decreasing (for wire marking) constrained functions for some variables. Imposing monotonic trends reduces the total amount of deviance explained by the models, but it also decreases the likelihood of overfitting (Leathwick et al., 2006; Jorda et al., 2015) and avoids falsely attributing explanatory power to some variables (Smith et al., 2013). Model performance was assessed using the explained deviance (as a percentage of the null deviance), correlation and area under the receiver operator characteristic curve (AUC), through cross-validated statistics (Buston & Elith, 2011).

The relative importance of each variable in a model was estimated based on how often the predictor was selected and the improvement to the model as result of the selection (Buston & Elith, 2011). Importance values of variables were expressed as percentages (summing 100%). We used the function 'gbm.plot' to build partial dependence plots and visualize the fitted functions from the Boosted Regression Trees models. Important interactions between predictor variables were visualized using the 'gbm.interaction' function.

Due to its stochasticity component, each Boosted Regression Trees run provides slightly different results. Therefore, we performed 100 runs of 'gbm.step' to estimate the range (minimum and maximum values) for both the fitted functions, importance of variables, and cross-validated measures of model performance (Fernandes et al., 2016).

We used spline correlogram plots with 95% pointwise confidence intervals calculated with 1,000 bootstrap resamples to check for spatial autocorrelation in model residuals (Bjørnstad & Falck, 2001). We assumed that variable selection and parameter estimation were unbiased if there was no significant autocorrelation in model residuals (Rhodes et al., 2009). Correlograms were built with the function 'spline.correlog' from the ncf package (Bjørnstad, 2016).

All analyses were performed in R 3.3.1 (R Core Team, 2016).

3. RESULTS

Bustard mortality with transmission power lines was extensively recorded in studies conducted in Alentejo. A total of 156 fatality events were recorded, 59 of great bustards and 97 of little bustards. Most (75%) of the fatality records resulted from 2 studies, one with a wide geographic range (42% of the total number of power line sections surveyed in the region) corresponding to 35% of the fatality events (Neves et al., 2005), and a local study that applied an intensive survey effort (15-days interval during 29 months) that found 40% of the events (Marques et al., 2007).

3.1. SPATIOTEMPORAL COLLISION PATTERNS

Collision events of both species exhibited a clustered spatial pattern at this regional scale (Figure 3). Great bustard collisions were concentrated in just 15 (10.4%) of the 2-km power line sections, 12 of which also had little bustard fatalities. Little bustard collisions were more spread across the study area, occurring in a total of 42 sections (29.2%).

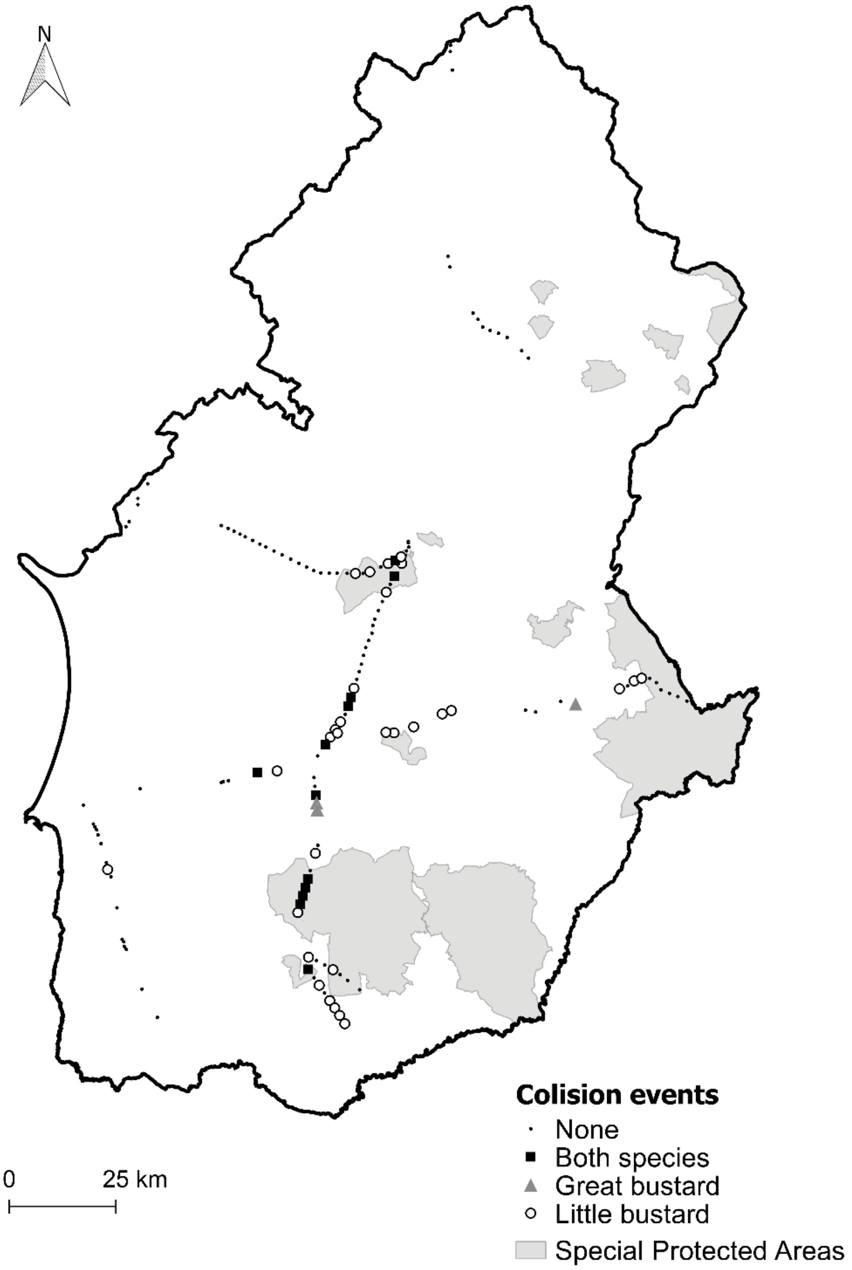


Figure 3. Presence-absence of mortality events of great bustard and little bustard in each sampled power line section in Alentejo, Portugal. For visualization purposes, power lines sections are represented by its central point.

The number of collision events varied along the year (Supplementary Figure 2). Most of the carcasses of great bustards were found inside Special Protected Areas (73%), while little bustards were more frequently found outside (55%). Inside Special Protected Areas, 65% of the collision records of great bustard occurred during the autumn (September to November), with a second peak in spring (18%, in

April-May). Outside Special Protected Areas fatalities were concentrated between August and October (50%). Little bustard collision events were registered all year around. Inside Special Protected Areas fatality peaks were recorded during the breeding season (ca. 37% from March to May) and during the post-breading period (12% in July, and 39% from October to December). However, outside Special Protected Areas 62% of the little bustard collision events were concentrated in the dry months (July to September).

3.2. FACTORS INFLUENCING BUSTARDS' COLLISIONS

The original (with unconstrained variables) Boosted Regression Trees model for great bustard (Supplementary Figure 1 and 3) explained 20.4% of the total deviance (AUC: 0.85 ± 0.02; Pearson's correlation: 0.42 ± 0.03). The proportion of open habitat was by far the most important predictor, with a trend for increased likelihood of collision once this proportion reaches 50%. Survey effort, i.e. accumulated surveyed distance in all sampling visits (the larger the effort, the more likely a collision record, with an important threshold at about 120 km of accumulated effort) and power line configuration (lower likelihood of collision in small configuration) ranked second and third respectively. Wire marking and the dominant habitat near the section had lower importance. In the simpler model with the constrained variables (explained deviance: 15 ± 2.1%; AUC: 0.77 ± 0.01; Pearson's correlation: 0.45 ± 0.02) the order of variable importance remained essentially the same, although wire marking and dominant habitat became even less relevant (Figure 4). Fitted functions of this model are shown in Figure 5. The most important interactions between variables (Supplementary Figure 4) suggest that the risk of collision with small configuration, when compared with other configurations, was much lower in regions with higher open habitat availability, and the effect of survey effort was particularly important in line sections with higher cover of open habitat.

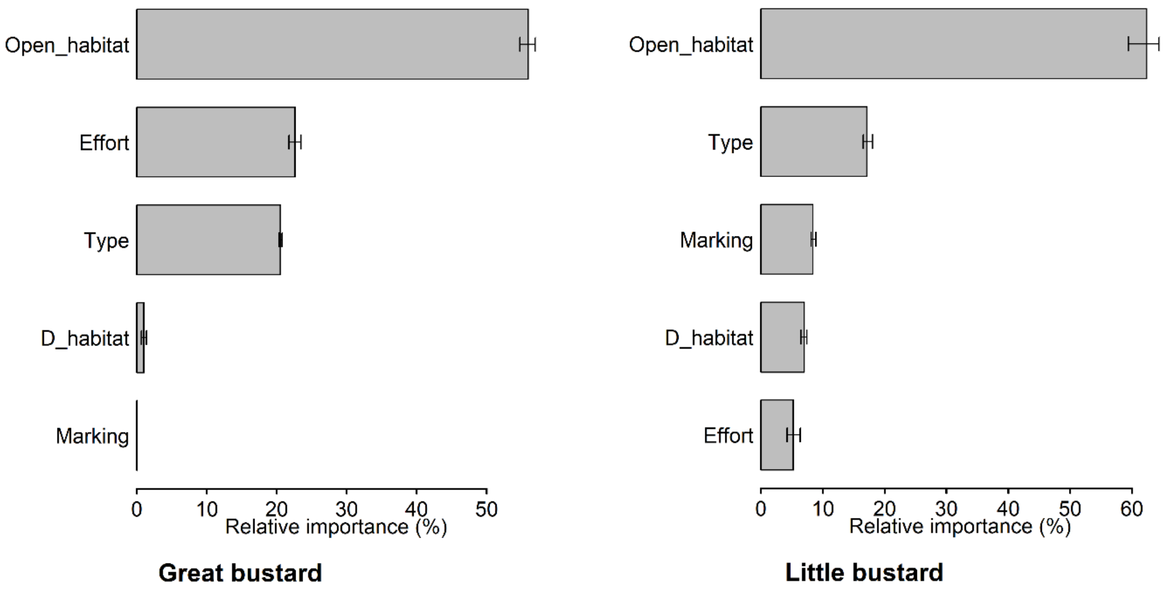
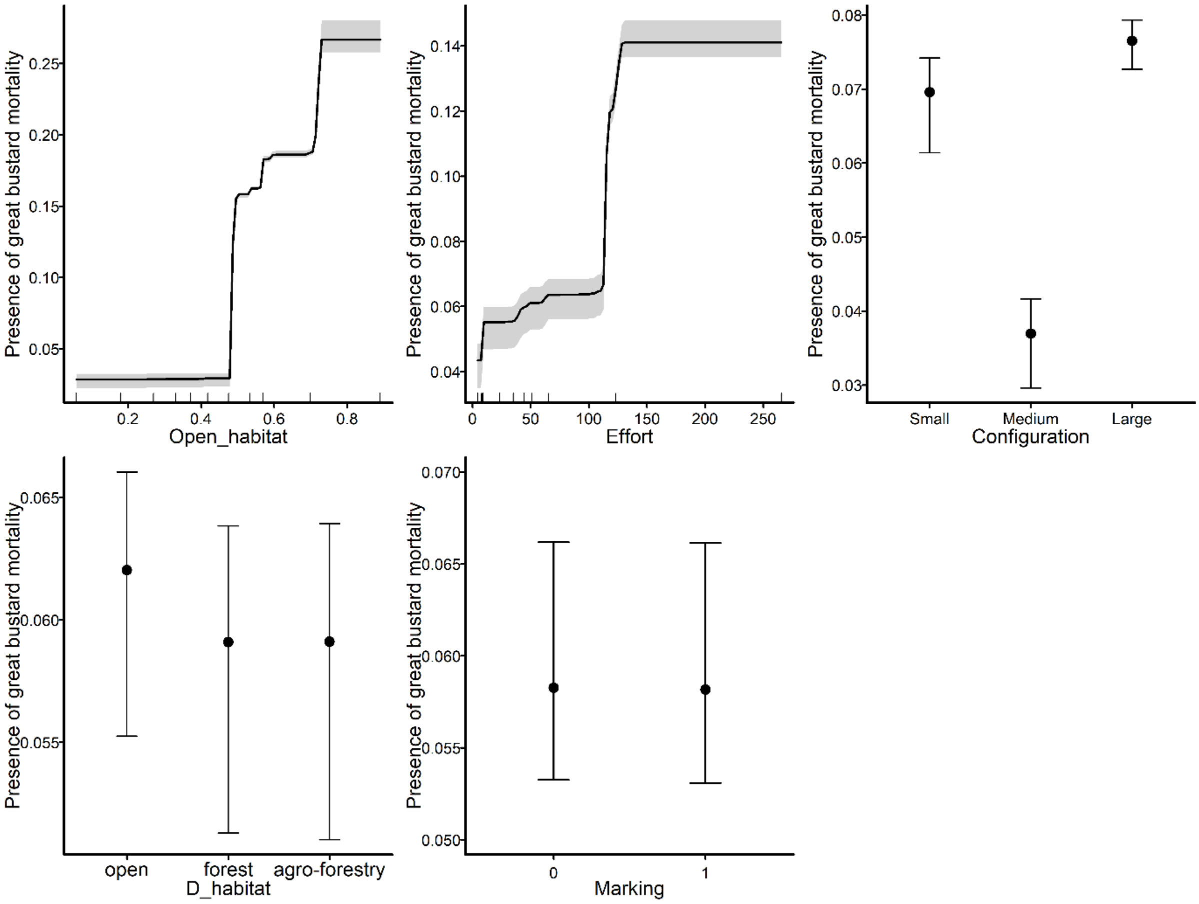


Figure 4. Relative importance (%) (means and 95% confidence intervals) of the predictor variables used to model the presence/ absence of mortality of great bustard and little bustard by collision with transmission power lines in Alentejo, Portugal. The models were fitted imposing a monotonic increase to the variables: proportion of open habitat and survey effort, and a monotonic decrease to wire marking.

Regarding the little bustard, the Boosted Regression Trees model with unconstrained variables explained 15.5% of the total deviance (AUC: 0.778 ± 0.01; Pearson's correlation: 0.46 ± 0.02) (Supplementary Figure 3) and was quite similar to the model with the constrained variables (14.8 ± 1.5% of explained deviance; AUC: 0.774 ± 0.01; Pearson's correlation: 0.46 ± 0.02). The proportion of open habitat was also the most important variable (although the shape of the fitted function suggested a continuously increasing effect, rather than a threshold as for the great bustard), followed by power line configuration (higher likelihood of collision in large configuration; Figure 4 and Supplementary Figure 3). The likelihood to register little bustard collisions decreased with wire marking and increased with survey effort. Interactions between variables suggest a higher risk of collision in the large configuration at intermediate levels of habitat availability, when compared with other power lines configurations (Supplementary Figure 5).

For all models, there was no significant auto-correlation in model residuals (Supplementary Figure 6).

a)



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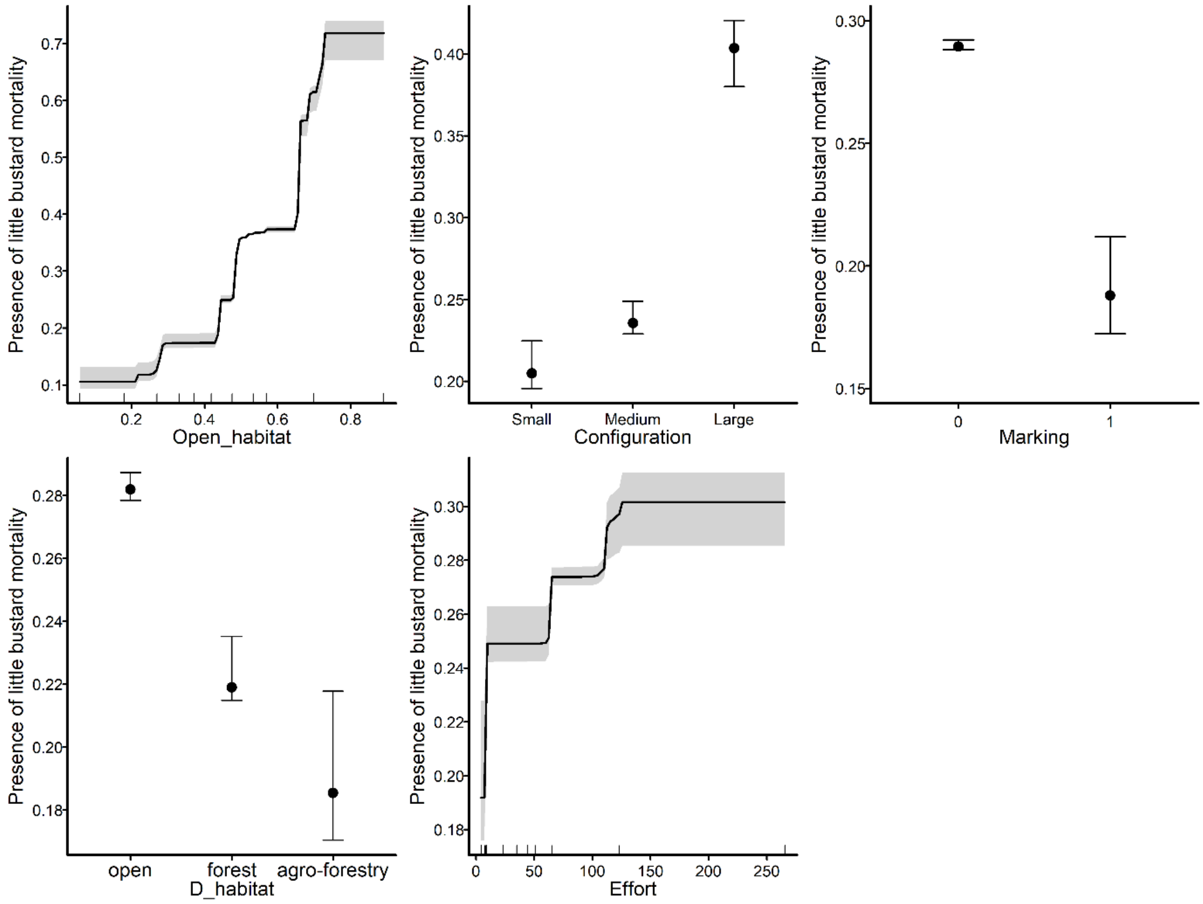

Figure 5. Partial dependence plots (means and 95% confidence intervals) for the predictor variables influencing the presence/ absence of mortality of a) great bustard and b) little bustard by collision with transmission power lines in Alentejo, Portugal. The models were fitted imposing a monotonic increase to the variables: proportion of open habitat and survey effort, and a monotonic decrease to wire marking. Configuration: small configuration, horizontal at 150 kV; medium configuration, horizontal at 400 kV; large configuration, vertical at 150 or 400 kV. Ticks across the bottom of each plot show the distribution of sites across the variable, in deciles. Intervals for fitted functions and relative importance represent the range (minimum and maximum values) for a set of 100 runs.

4. DISCUSSION

4.1. SPATIOTEMPORAL COLLISION PATTERNS

Both bustard species exhibited clustered spatial patterns of collision with power lines. These patterns are probably related with the species' distribution and abundance across the region, mainly determined by the availability of open habitats in flat areas and with lower human disturbance (e.g. Pinto et al., 2005; Silva et al., 2007; Equipa Atlas, 2008; Moreira et al., 2012). The importance of the spatial distribution of the species was also evident when comparing collision patterns across species: collision events of great bustard occurred in areas where collisions of little bustards also occurred, but the opposite was not true, as the little bustard fatalities, although clustered in contiguous sections, are more spread in the study area. This might be explained by the larger and more widespread population of little bustard (see Figure 1). For both species fatalities were recorded both inside and outside Special Protected Areas.

Temporal patterns in collisions across the annual cycle might be explained by differences in flocking behaviour, activity and flight patterns. In the case of the little bustard, the peak of mortality during the post-breading season is probably related with: (i) the migratory movements that some individuals perform from the breeding grounds to areas with higher food resources (Silva et al., 2007; García de la Morena et al., 2015) and the use of stop-over sites in areas with poor habitat conditions during such periods; (ii) the increased distance travelled daily searching for food (Silva et al., 2014); (iii) the higher frequency of flights at collision risk heights (Silva et al., 2014); and (iv) the gregarious behaviour during this season. The collision pattern of little bustard also varied across space: (i) there was a high number of collisions outside Special Protected Areas during summer (July to September), when birds leave the breeding grounds (Silva et al., 2007); (ii) there was a peak of mortality during the autumn (October to December) within Special Protected Areas, probably associated to the return to the breeding grounds after the onset of rains (García de la Morena et al., 2015); and (iii) a third mortality peak occurred during the beginning of the breeding season inside Special Protected Areas, which coincides with the onset of the mating period (March to May), when males settle in breeding sites and females perform movements between lekking areas.

For the great bustard, although the annual distribution of birds in Alentejo is not well known, there is evidence that it is influenced by bird behaviour and local movements, as in the little bustard. The majority of fatalities occurred in late summer and autumn (September to November), when a large number of birds leave their breeding grounds in search of areas with higher food availability and individuals tend to gather in larger flocks (Rocha, 2006). This temporal pattern also matches the higher frequency of flights crossing a transmission power line observed by Marques et al. (2007).

4.2. FACTORS INFLUENCING THE COLLISION RISK

The availability of open farmland habitat was the main determinant of collision risk in both species, revealing that the presence of bustards' habitat is the major collision driver for the species and suggesting that collision events are less frequent during the migratory journey, when birds cross other habitat types, probably flying high over power lines wires. The probability of bustard collisions increased with the availability of open farmland in the region, although the threshold differed across species: little bustard collisions increased when more than 20% of open habitat was available, while this threshold increased to 50% in the case of the great bustard. This difference may reflect a stricter requirement of great bustards for open areas, compared to little bustards (Suárez-Seoane et al., 2002). This variable expressing the amount of available habitat at a larger landscape scale was more important than the dominant habitat in the close vicinity of the power line. However, the dominant habitat in a 1-km buffer was also relevant for the little bustard.

The technical configuration of the power line also influenced collision risk. For the little bustard, the large configuration with four levels of wires, forming a bigger collision risk area (higher distance between top and bottom wires), posed a higher risk than the small and medium configurations, both with just two levels of wires. Also, the comparison between the two horizontal configurations (with similar distance between top and bottom wires) showed that higher lines pose a greater collision risk to little bustards. Although the effect of power line height on collisions is strongly dependent on flight altitude and maybe species-specific, higher power lines and the vertical configuration were pointed out as having a higher collision risk, as they represent a larger barrier to birds in flight, which tend to gain altitude to fly over the obstacle rather than passing below (Luzenski et al., 2016; Murphy et al., 2016; Bernardino et al., 2018). Such behaviour increases the likelihood of a bird collision with the earth wires, that are thinner and less visible when compared with the phase conductors (see Bernardino et al. 2018). We highlight that although the importance of power line configuration has been previously suggested by several authors, this is the first study that finds strong evidence of such effect.

For the great bustard, the large configuration also seemed to be riskier although the difference to the small configuration was not significant. However, our dataset may not be fully adequate to test different power line configurations in this species, as the three configurations were not evenly represented in the range of the species within the study area. In fact, most transmission lines crossing important areas for the great bustard were from the small configuration and only a few had medium configuration, which may explain the absence of records of collision with this type of power lines and the consequent predicted low collision risk

Additionally, our results also showed that the power line configuration may interact with habitat features, as we found that power lines with a large configuration pose a higher collision risk to little bustard in areas with intermediate levels of open habitats (ca. 20 – 65%), when compared to the small and medium configurations. This may occur because the species tends to use areas with less suitable or fragmented habitats during the non-breeding season (Silva et al., 2007), when the species also tends to fly at heights with higher collision risk (Silva et al., 2014).

The influence of power line configuration in bustards' collision risk suggests that distribution power lines, usually much lower and with a smaller collision risk area, are less risky to these birds when compared to transmission lines. However, the total length of the distribution grid is much larger (in Alentejo region the extension of distribution power lines is ca. 13,483 km (Silva et al., 2014) while the transmission network has 1,239 km), therefore it might represent an important mortality source as well.

Our results suggest that wire marking devices have a significant but minor effect in the reduction of collisions in the little bustard. Previous studies showed that wire marking devices have a limited effect on bustard species, and only large spirals were found to have some effect on the great bustard (Janss & Ferrer, 1998; Barrientos et al., 2012). The data obtained in our study was insufficient to evaluate the effect of wire marking on this latter species, as most of the transmission power lines crossing the main range of the great bustard had marking devices, so it was difficult to separate habitat and mitigation effects. In fact, this may explain why the model fitted without imposing a monotonic trend showed that the power line sections marked with spirals had a higher risk of collision to the species.

4.3. IMPLICATIONS FOR BUSTARD CONSERVATION AND POWER LINE MONITORING

The main determinant of collision risk for the great and little bustards is the amount of habitat in the region surrounding the power line route. Therefore, the best mitigation measure for future transmission power lines is to avoid the routing through areas with large expanses of open farmland habitat. For existing lines, burying the aerial wires would be the best practice for open farmlands (more than 50% of open habitats) at least in Special Protected Areas relevant for both bustard species, although this action is likely to be of difficult implementation due to its extreme high cost, and legal and technical issues (Raab et al., 2012; Bernardino et al., 2018). Whenever this is not possible, (1) we recommend the adoption of technical configurations with smaller pylons, a reduced number of collision levels (with less cables displaced vertically) and smaller distances between top and bottom wires. Additionally, (2) all transmission lines crossing areas with >20% of open habitats in a 5 km buffer should have marking devices to increase their visibility. Although this mitigation measure appears to have a fairly small effect on these species it can contribute to reduce the number of fatalities. The choice of the wire marking device should be based on the best scientific knowledge available, balancing the effectiveness and durability of each device (see Bernardino et al. 2018). Experimental designs focusing on bustard species, based on a Before-After Control-Impact approach, should be used to identify the best devices for this bird group.

The high prevalence of mortality caused by collision with power lines in both species (Palacín et al., 2017; Marcelino et al., 2017), indicates that reducing such anthropogenic mortality is likely to have a positive effect on their populations. Such mitigation would be particularly important for the little bustard, as its population halved over the last 10–14 years (Silva et al., 2018).

Our results also showed that the likelihood of finding a carcass increased with survey effort, mainly for the great bustard. Despite being larger birds, hence with a larger probability of detection during the carcass surveys (Ponce et al., 2010), a higher survey effort may be needed to detect great bustard collisions because those are uncommon events as (i) the species occurs in lower numbers when compared with the little bustard, and (ii) its fatality pattern is temporally more scattered, mainly outside Special Protected Areas. Therefore, monitoring schemes focussing on these species should include regular carcass surveys covering the whole spring, summer, and autumn periods.

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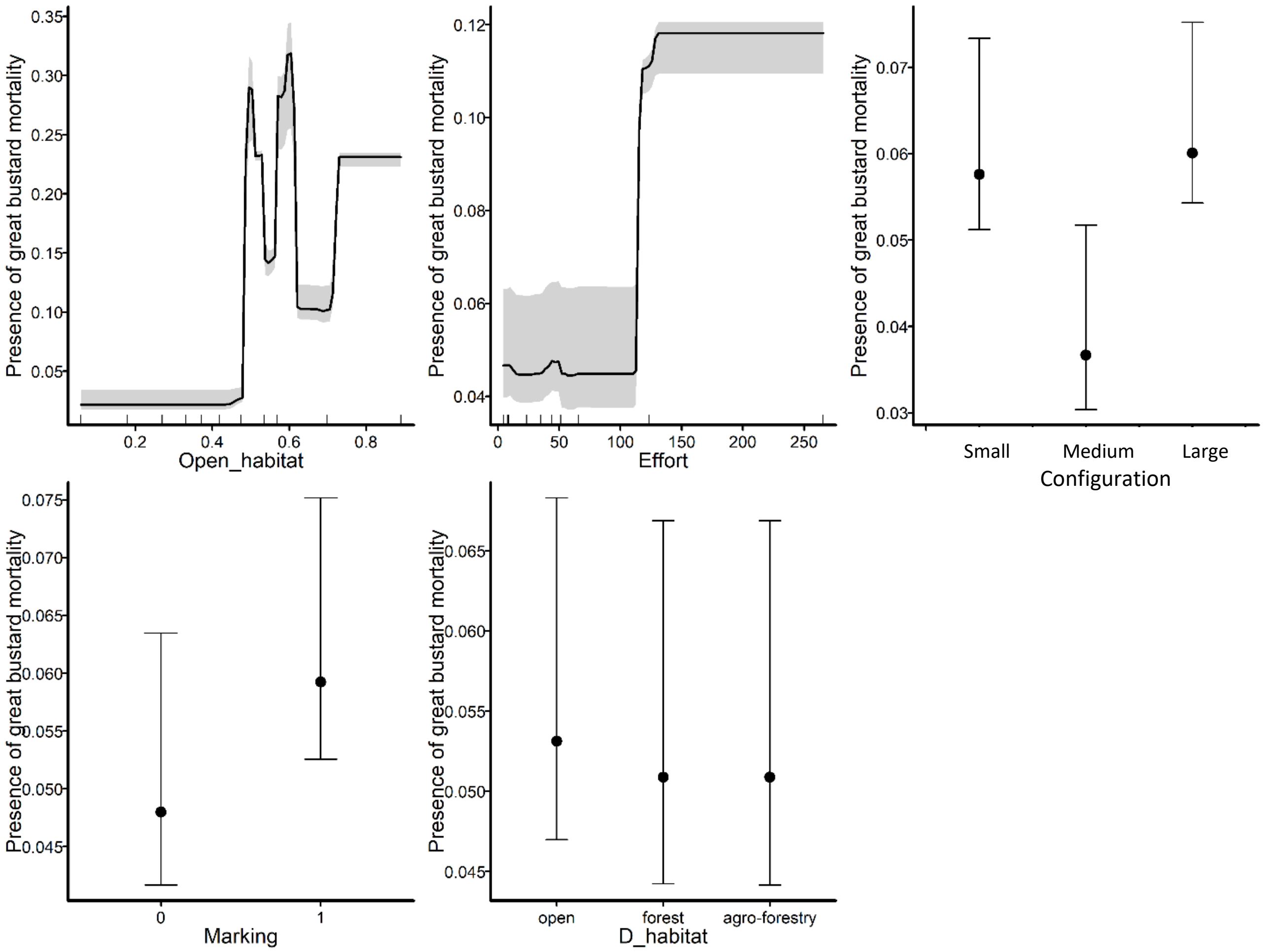
SUPPLEMENTARY MATERIAL

Table S1. List of studies on bird collision with transmission power lines in Alentejo region used in this analysis. The Table indicates the number of (2-km) power line sections surveyed, the power line configuration (S – small configuration, horizontal at 150 kV; M – medium configuration, horizontal at 400 kV; L – large configuration, vertical at 150 or 400 kV; see Figure 2), the total length of surveyed power lines (km), the study duration (months), the interval between consecutive surveys, and the total number of great and little bustard carcasses registered.

Source	No. power line sections surveyed	Power line configuration	Survey length (km)	Study duration (months)	Survey interval (days)	No. of carcasses	
						Great bustard	Little bustard
Neves et al., 2005 [A]	61	S, L	139	12	30 / 90	14	40
Marques et al., 2007 [B]	6	S	11.2	29	15	32	30
Marques et al., 2007 [B]	3	S	5.7	29	30	8	1
Marques pers. data [B]	1	L	2.7	12	30	3	2
Ecossistema 2007 [C]	15	S, M	41	12	30	0	11
Procesl 2007, 2010 [C]	12	L	25	67	15 / 30	2	6
Agripro Ambiente 2007, 2008, 2009 [C]	2		2.8	36	90	0	0
Ecosativa 2009 [C]	15	M	26.5	24	30 / 90	0	5
Infante et al. 2011 [B]	25	S	61.3	24	30	0	2
Procesl 2012 [C]	10	L	22.5	24	15	0	0
Procesl 2015 [C]	5	L	7.9	24	30	0	0

[A] - national assessment; [B] - Wire-marking effectiveness study; [C] – monitoring program (from Environmental Impact Assessment process)

a)



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b)

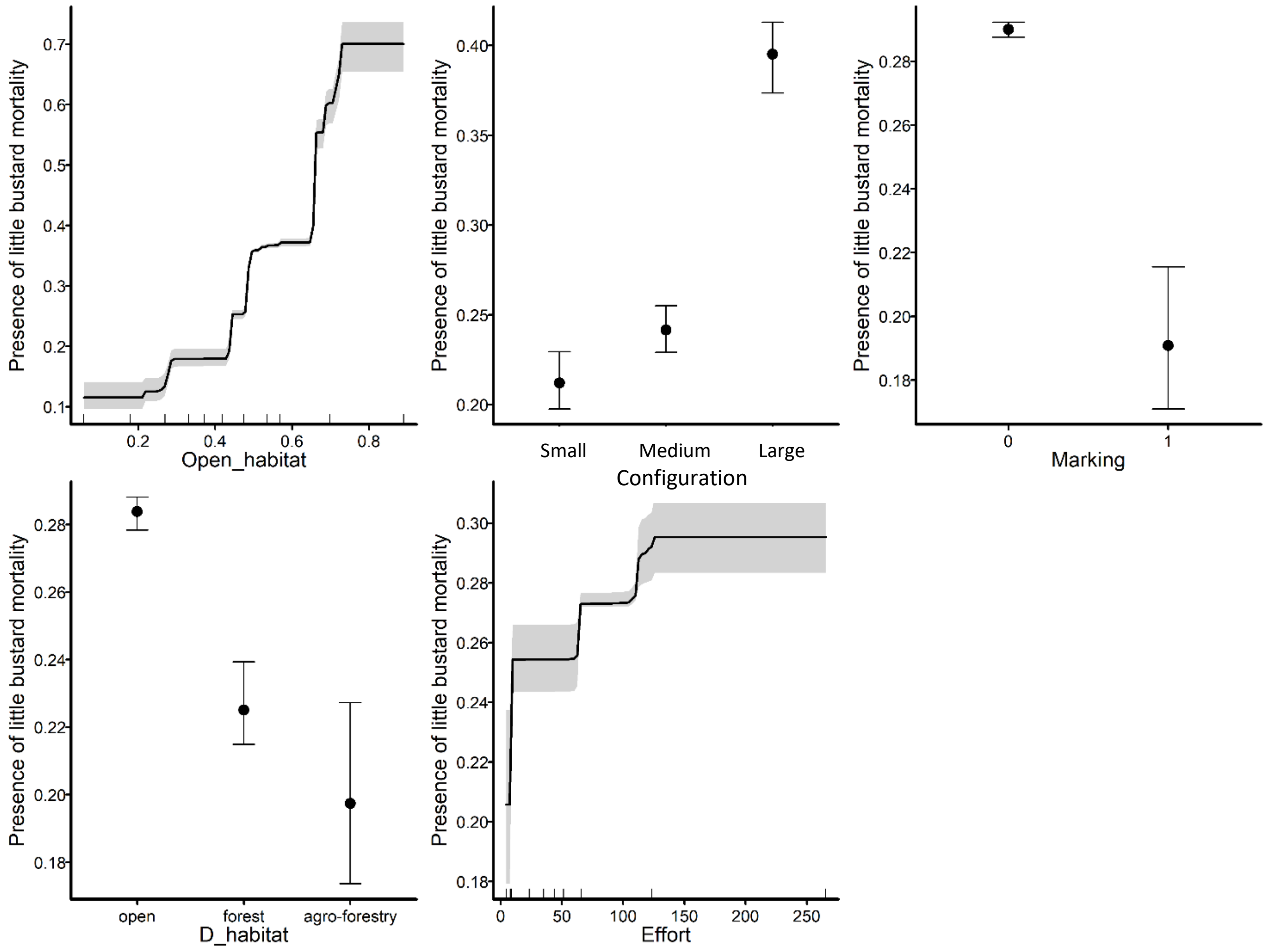


Figure S1. Partial dependence plots (means and 95% confidence intervals) for the predictor variables influencing the presence/ absence of mortality of a) great bustard and b) little bustard by collision with transmission power lines in Alentejo, Portugal. These models were fitted without imposing monotonic variations to the variables. Configuration: small configuration, horizontal at 150 kV; medium configuration, horizontal at 400 kV; large configuration, vertical at 150 or 400 kV (see Figure 2). Ticks along the xx axis of each plot show the distribution of sites across the variable, in deciles. Intervals for fitted functions and relative importance represent the range (minimum and maximum values) for a set of 100 runs.

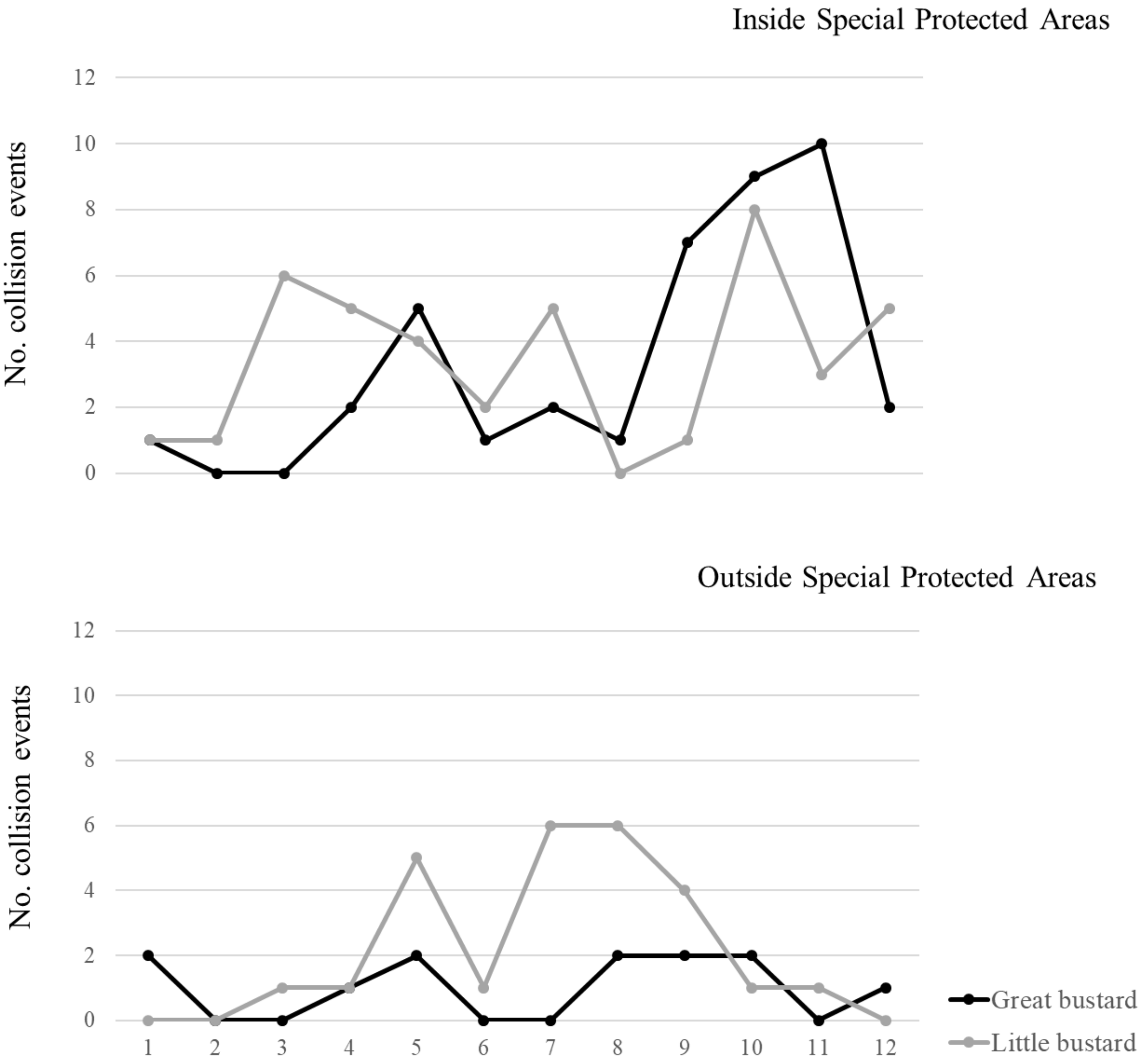


Figure S2 Seasonal variation in great bustard and little bustard collisions with transmission power lines (number of carcasses or remains) in Special Protected Areas (n = 40 great bustards; n = 41 little bustard) and outside Special Protected Areas (n = 12 great bustards; n = 26 little bustard).

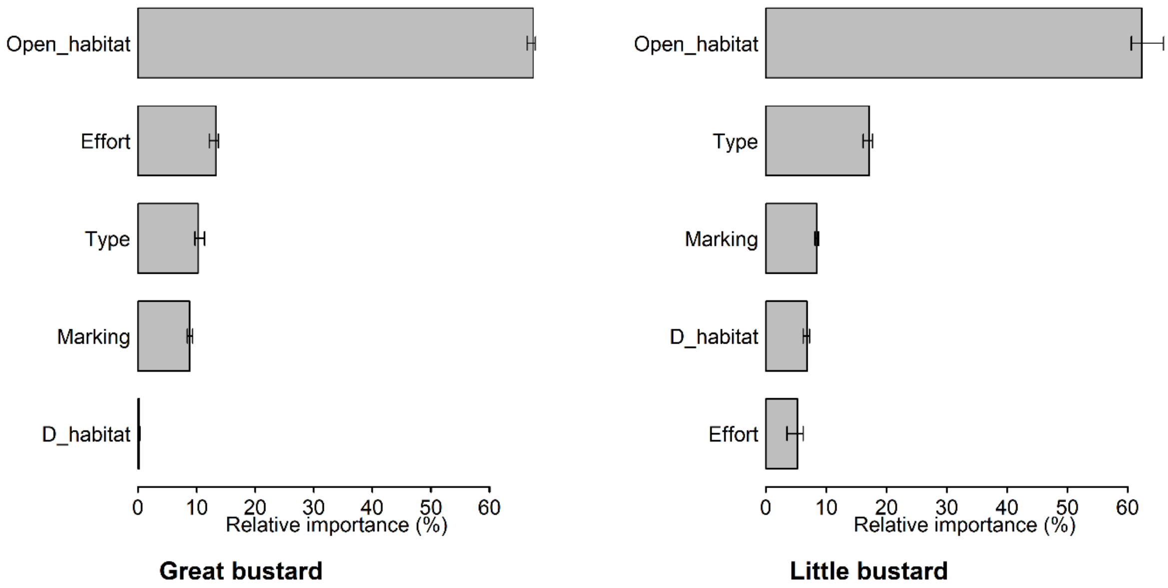
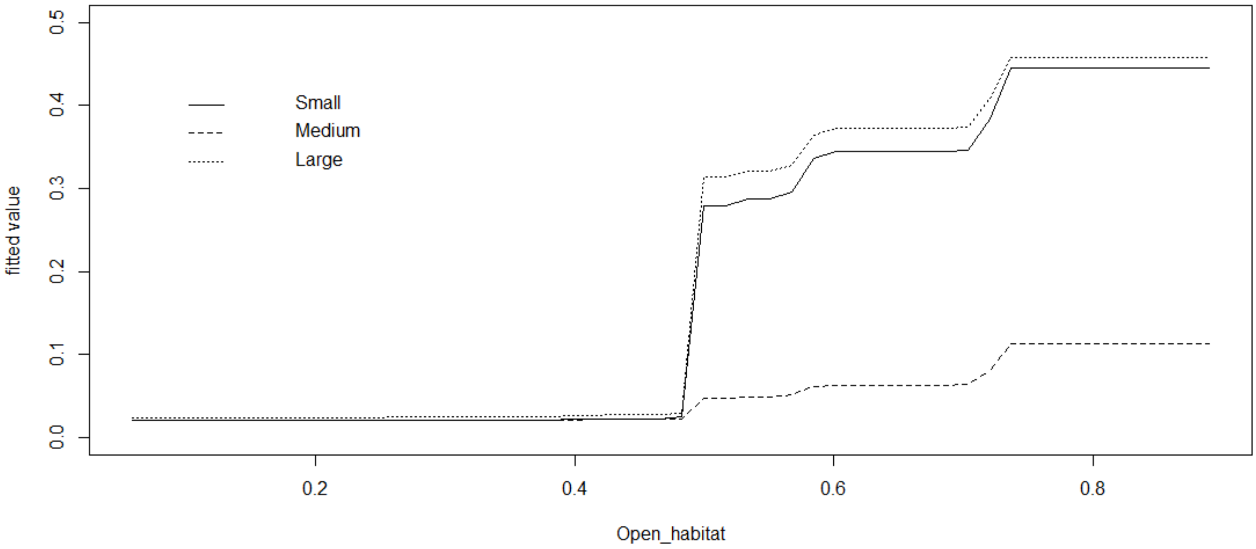


Figure S3. Relative importance (%) (means and 95% confidence intervals) of the predictor variables used to model the presence/ absence of mortality of great bustard and little bustard by collision with transmission power lines in Alentejo, Portugal. These models were fitted without imposing monotonic variations to the variables.

Great bustard model: 20.4 ± 1.9% explained deviance; AUC=0.849 ± 0.02 and Pearson's correlation of 0.42 ± 0.03
Little bustard model: 15.5 ± 1.6% explained deviance; AUC=0.778 ± 0.01 and Pearson's correlation of 0.46 ± 0.02

a)



b)

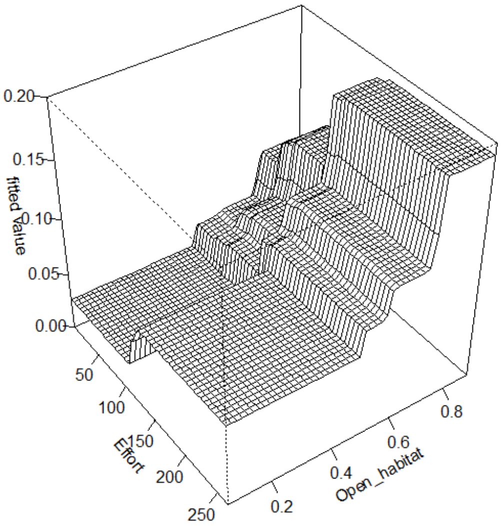


Figure S4. 3D plots showing the interaction between the predictor variables in the great bustard model: a) proportion of open habitat in a 5 km buffer and power line configuration (small configuration, horizontal at 150kV; medium configuration, horizontal at 400 kV; large configuration, vertical at 150 or 400 kV; see Figure 2); b) sampling effort and proportion of open habitat.

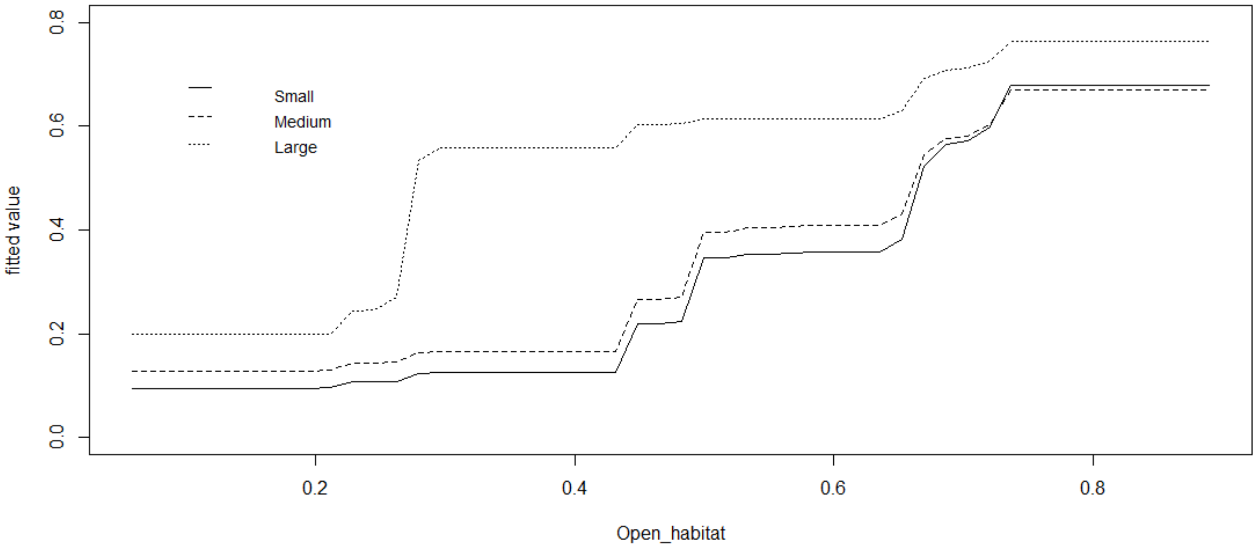
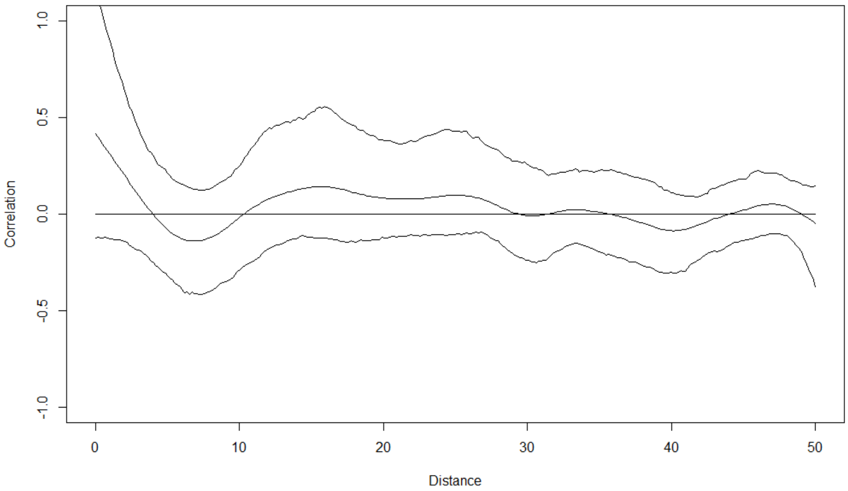


Figure S5. 3D plots showing the interaction between the predictor variables in the little bustard model: proportion of open habitat in a 5 km buffer and power line configuration (small configuration, horizontal at 150kV; medium configuration, horizontal at 400 kV; large configuration, vertical at 150 or 400 kV; see Figure 2).

a)



b)

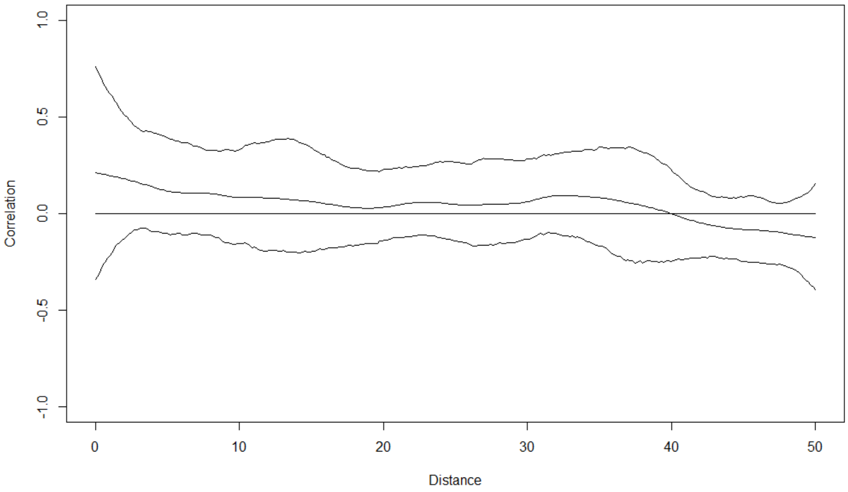


Figure S6. Spline correlograms describing spatial autocorrelation for the boosted regression trees residuals for models describing the presence/ absence of mortality of a) great bustard and b) little bustard in transmission power lines in Alentejo, Portugal. Lines represent the estimate (in the middle) and the 95% confidence envelopes (external lines) using 1000 bootstrap resamples (Bjørnstad and Falck, 2001).

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Chapter 4

Male post-breeding movements and stopover habitat selection of an endangered short-distance migrant, the Little Bustard *Tetrax tetrax*

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ABSTRACT

Migratory decisions, such as the selection of stopover sites, are critical for the success of post-breeding migratory movements and subsequent survival. Recent advances in bio-logging have revealed the stopover strategies of many long-distance migrants, but far less attention has been given to short-distance migrants. We investigated the stopover ecology of an endangered grassland bird, the Little Bustard *Tetrax tetrax*, a short-distance migrant in Iberia. Using high resolution spatial GPS/GSM data, 27 male Little Bustards breeding in southern Portugal were tracked between 2009 and 2011. We studied post-breeding movements using Dynamic Brownian Bridges models to identify the main stopover sites, and Generalized Linear Mixed Models to examine habitat selection in stopovers. During their post-breeding movements, males were essentially nocturnal migrants, making frequent stopovers, while maintaining a relatively fast pace to reach more productive agricultural post-breeding areas. Stopovers occurred in most post-breeding movements (83%) regardless of the total distance covered (average 64.3 km), and most stopovers (84%) lasted less than 24 hours. Birds used mostly agricultural non-irrigated and irrigated croplands as stopover sites, and avoided other land uses and rugged terrain. There was a negative relationship between stopovers and the proximity to roads, but not to power lines. The high frequency of stopovers during post-breeding movements, despite the short distances travelled, together with the nocturnal migratory behaviour of bustards, may impose additional risks to a bird mainly threatened by collision with power lines in non-breeding areas. We also conclude that even for short distance migrants, habitat connectivity between breeding and post-breeding areas is likely to be a key conservation concern.

Keywords: grassland bird, migratory connectivity, movement ecology, stopover site selection.

1. INTRODUCTION

Post-breeding migratory movements are usually associated with a predictable seasonal change of environmental conditions and/or food availability (Dingle & Drake 2007, Hedenström 2008), but are also influenced by individual factors such as sex, age or role specialization during reproduction (e.g. Palacín et al. 2009). Migratory strategies and decisions along the trajectory, such as interrupting migration at particular stopover sites for resting and/or refueling (Newton 2008), play a key role in the success of the movement and subsequent survival (Alerstam et al. 2003, Legagneux et al. 2012).

Therefore, understanding migratory decisions including stopover use and habitat selection on route, is crucial to estimate population trends and risks, predict changes in migratory behaviour and develop appropriate conservation strategies (Shuter et al. 2011). In this context, a good knowledge of migratory connectivity, which refers to the extent to which animals from the same breeding area move to the same non-breeding areas (Newton 2008), is also important, especially for species with highly selective habitat preferences (e.g. Briedis et al. 2016).

Recent advances in tracking technology have opened a new door for the study of avian migration (Robinson et al. 2010) and stopover ecology of a wider number of migrant species (e.g. Eraud et al. 2013, Lemke et al. 2013, Evens et al. 2017). Despite that, the knowledge of the stopover ecology of many avian groups and species, and particularly of short-distance migrants, is still very limited (but see Strandberg et al. 2009, Newton et al. 2017, Röseler et al. 2017).

The Little Bustard *Tetrax tetrax* is a medium-sized grassland bird, whose distribution is fragmented across the Palearctic range. Spain and Portugal are the stronghold of its western distribution, where the main breeding populations are mostly concentrated in the Extremadura, Castilla La Mancha (Spain) and Alentejo (Portugal) regions (De Juana & Martínez 1996, García de la Morena et al. 2006, Equipa Atlas 2008). The species has a Vulnerable conservation status in Europe, where it is mainly threatened by habitat loss and degradation (Silva et al. 2018), illegal killing and collision with power lines (Marcelino et al. 2017), and recent trends indicate a severe decline in their breeding numbers in parts of their range (Silva et al. 2018). Although Iberian Little Bustards have been considered mostly sedentary (e.g. Cramp & Simmons 1980, Villers et al. 2010), a recent and comprehensive tracking study found that most populations in the region are actually migratory or partially migratory (89% of all tracked individuals; García de la Morena et al. 2015), performing regular short or medium-distance movements to post-breeding and/or wintering sites (Silva et al. 2007, García de la Morena et al. 2015). The majority of male Little Bustards engage in these migratory movements in June/July, right after the breeding season and during the Iberian summer (García de la Morena et al. 2015) when temperatures and vegetation dryness reach their peak (Silva et al. 2007). In these post-breeding movements, birds head to northern, coastal or higher-altitude areas, where food availability and environmental conditions are expected to be more favorable (Silva et al. 2007, 2015, García de la Morena et al. 2015). Studies on stopover ecology of bustards are scarce and limited to a few long-distance bustard species/populations, such the Asian Houbara Bustard *Chlamydotis macqueenii* (e.g. Combreau et al. 1999, Tourenq et al. 2004, Burnside et al. 2017) or the Asian Great Bustard *Otis tarda dybowskii* (Kessler et al. 2013). The stopover ecology of short-distance migratory bustards, such as the Iberian Little Bustard population, is completely unknown.

In the present study, we used a high-resolution tracking dataset, collected over a three-year period, to investigate the stopover ecology of Iberian Little Bustards during their post-breeding movements. Our specific aims were to characterize their migratory behaviour and use of stopovers (occurrence, number, duration and site-fidelity), and to study the influence of habitat structure (land cover and topography) and linear infrastructures (roads and power lines) in stopover habitat selection during post-breeding movements.

2. METHODS

2.1. FIELDWORK

Capture and tagging of Little Bustards was carried out in several sites located in two main breeding areas, the Castro Verde and Vila Fernando SPAs (Special Protected Areas) (Figure 1), in the early breeding period (April to early May) of three consecutive years, from 2009 to 2011 (14, 7 and 6 individuals, respectively). The capture method was targeted at males, using snares and a female decoy (Ponjoan et al. 2010). A Solar GPS Platform Transmitter Terminal (30 g PTT; Microwave Telemetry Inc.) was deployed on 27 adult breeding males, using a full harness made of Ribbon Teflon, weighing less than 4.7% of the birds' mass. Transmitters were programmed to record a GPS position every 2 hours, with an accuracy of ± 18 m (Microwave Telemetry 2014). Eight of the 27 birds were tracked for more than one year (in one case up to three years).

2.2. PRE-ANALYSIS OF TRACKING DATA

Spatial data from the PTTs and cartographic data were handled with Quantum GIS 2.2.12 (QGIS Development Team 2013). Birds were considered sedentary whenever they remained within 15 km of their breeding site throughout the year (García de la Morena et al. 2015). A quarter of the post-breeding movements (25.7%, n = 35) were preceded by a long-term permanence in pre-migratory staging areas (or secondary breeding areas; average duration = 26.1 days, range = 10.7 - 38.9 days). These areas were close, although clearly separated from, the main breeding area (average distance ± SD = 13.4 ± 4.8 km) and were not considered part of the subsequent post-breeding movement.

Post-breeding movements were therefore only considered to occur when birds moved more than 15 km away from their breeding areas, between May and August. To set the limits of each individual post-breeding movement, we considered their breeding site or pre-migratory staging area as the 'origin point' of the migratory movement, while the 'end point' coincided with the arrival to the main post-breeding area, the furthest location from the breeding site, where the majority of birds stayed for at least two or three months. The boundaries of the movements were the last and first two fixes in the same position (or positions close to each other), located in the departure and destination areas, respectively. In a few cases (n = 6), birds had two main post-breeding areas, and their movement was subdivided accordingly. Those movements were included in all analyses, except for the estimation of arrival and departure dates, from breeding areas and to post-breeding areas, respectively.

2.3. IDENTIFICATION AND CHARACTERIZATION OF STOPOVERS

Movements and stopovers were characterized (occurrence, number and duration) through visual inspection of each individual movement. We considered areas in which birds stayed for at least two consecutive fixes along each individual's post-breeding movement as stopover sites, excluding the departure and destination areas. Our data collection settings (see above) did not allow for the detection of stopovers with duration inferior to two hours.

2.4. HABITAT SELECTION

To identify the stopover locations to be included in the habitat modeling analysis, we used Brownian Bridge Movement Models (BBMMs; Horne et al. 2007, Sawyer et al. 2009, 2011). The BBMM were used to estimate the utilization distribution (UD) of individual bustards along the movement route, incorporating the distance and elapsed time between successive fixes, as well as the location error and the Brownian motion variance (BMV; Horne et al. 2007, Sawyer et al. 2009). Since there is evidence that Little Bustards may migrate preferentially during the night (Silva et al. 2014), we assumed that their migratory behaviour was likely to differ between day and night. For that reason, we used a Dynamic BBMM, which is a version of BBMM that considers changes in behaviour when moving, namely changes in speed and direction, which can be defined for different time-windows (12 h in our case, to differentiate the expected night and day periods). Within the sliding window, a Dynamic BBMM calculates different BMV values and compares the model fit using one or two estimates of BMV (Kranstauber et al. 2012, Lai et al. 2015, Palm et al. 2015). UDs between 50% and 75% were used to outline the stopover areas, as they showed a good adjustment to the stopover relocations. The decision of using 50 or 75 UD was dependent on the extension of the movement, where after visual inspection, BBMM analysis of shorter post-breeding movements generally resulted in a good adjustment with 50% UD, while longer post-breeding movements showed better adjustments at the 75% UD level. Departure and arrival site locations (six fixes each) were included in the movement path considered in the Dynamic BBMM analysis, as a margin of fixes is required at each end of the window, depending on window and margin sizes (Kranstauber et al. 2012).

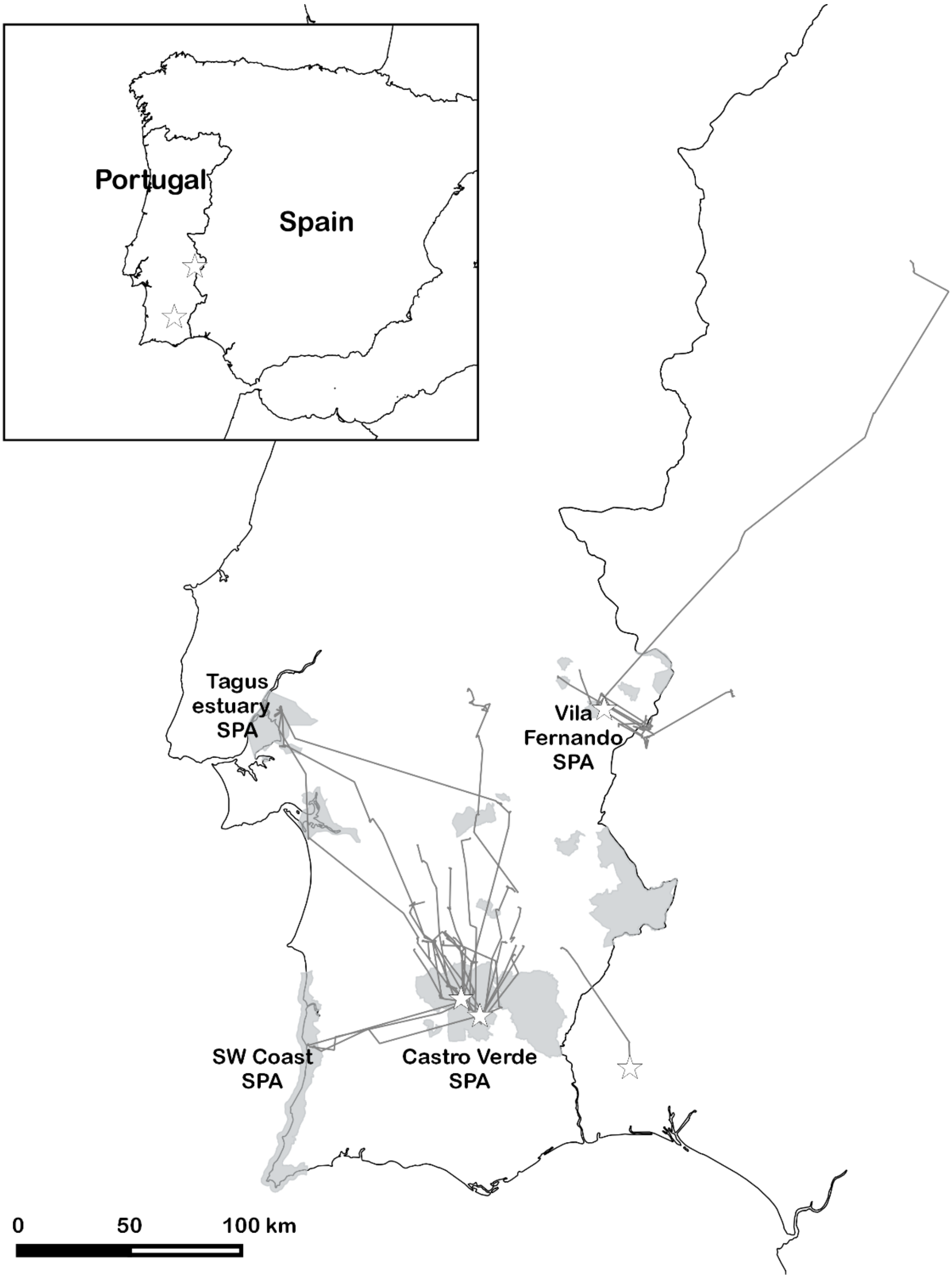

Figure 1. Outward post-breeding movements (*n* = 40) of Little Bustards (n = 27 individuals) breeding at Castro Verde and Vila Fernando SPAs. Capture locations (breeding sites) are indicated by white stars and special protected areas with importance for grassland birds are shown in grey.

To characterize stopover habitat selection, Little Bustard fixes inside stopover areas were compared to an equal number of random points located in a region defined as a 2-km buffer outside these areas; these locations were considered pseudo-absences for modelling purposes. This approach was selected for two key reasons. First, the goal of this analysis was to explore stopover habitat selection in the context of the migratory corridor rather than within the stopover site, and selecting potentially unused areas within the stopovers is likely to underestimate the availability of habitats in the surrounding landscape. Second, given that stopover areas were selected according to high UD areas, and considering the time interval between relocations (2 hours), this approach also maximizes the likelihood that locations selected as pseudo-absences represent unused, although available, locations.

Habitat selection analysis was then carried out with presence / absence locations in relation to landscape variables known to be relevant for the Little Bustard (Silva et al. 2004, 2007, 2010). Land cover data was originally obtained from CORINE Land Cover (CLC) 2012 version 18.5 (EEA 2016). Level 3 categories were reclassified into three relevant land cover categories: dry cropland, irrigated cropland, and other land uses (Table 1). Terrain ruggedness was calculated as the mean of absolute differences between the elevation of a cell and that of its surrounding cells (Wilson et al. 2007), using data from ASTER Global Digital Elevation Model (NASA 2009) and the function 'terrain' from the Raster package (Hijmans 2017) for R statistical software. Finally, we collected information on the distribution of the main roads from OpenStreetMap© contributors (classes: motorway, trunk, primary and secondary; Haklay & Weber 2008), and the distribution power lines for the whole study area and classified each point according to its distance to the nearest road and power line.

Table 1. Description and summary statistics of the predictor variables used to model the habitat selection of Little Bustard at stopover sites (*n* = 381 locations at 61 stopover sites) during post-breeding movements. Means and range are provided for the continuous variables, and frequency per class is presented for the categorical variables.

Variable	**Description (units)**	**Mean (sd) / Frequency**	**Range**
Land cover	Corine Land Cover 2012 classes: Dry croplands (non-irrigated arable land 2.1.1, pastures 2.3.1, natural grasslands 3.2.1); Irrigated croplands (permanently irrigated land 2.1.2, rice fields 2.1.3) and Other land uses (all remaining land cover classes)	Dry croplands: 436 Irrigated croplands: 97 Other land uses: 229	-
Ruggedness	Terrain ruggedness (30 m spatial resolution)	-0.43 (0.32)	-0.94 - 1.49
Distance to power lines	Distance to distribution power lines (m)	777.9 (666.3)	0 - 4801
Distance to roads	Distance to the main roads (m) (classes: motorway, trunk, primary and secondary of OpenStreetMap© (Haklay & Weber 2008)	2581 (1940.1)	0 - 11000

2.5. CONSISTENCY IN THE USE OF BREEDING, POST-BREEDING AREAS AND STOPOVERS

To quantify the fidelity to breeding and post-breeding areas, we calculated the percentage of spatial overlap between consecutive years of the same individual, given by the 95% UD (estimated by Brownian Bridges Models) in the breeding area (from 1 April to departure date) and post-breeding areas (see above) in each year. Similarly, the repeated use of stopover sites by the same individual in consecutive years was assessed by quantifying the overlap between stopover areas previously identified in the post-breeding movements (delimited by the 50-75% UD).

2.6. STATISTICAL ANALYSES

The effects of habitat, landscape and human infrastructure were tested using the presence and absence locations at stopover sites. We calculated the Pearson correlation coefficient and the variance inflation factor (VIF) between the explanatory variables to evaluate correlations and collinearity (Zuur et al. 2009). VIF values (all < 1.2) and pairwise correlations between explanatory variables (all $|r| < 0.60$) were low for our dataset, so all variables were used in the analysis.

Stopover habitat selection was modeled using Generalized Linear Mixed Models (GLMMs) with a binomial error distribution (Zuur et al. 2009). Bird identity was included as a random factor to address the spatial and temporal dependency of the replicated measures from each individual (Zuur et al. 2009). As we expected a response at short ranges from the linear infrastructures, we applied a log-transformation (log x+1) to the variables distance to roads and distance to power lines, so that short distances were more influential in the analysis. We computed GLMMs with all possible variable combinations, resulting in a total of sixteen models. To decrease model selection uncertainty and increase robustness of parameter estimates, we performed model averaging using an information theoretical approach by computing averaged parameter estimates from the best-selected models with $\Delta AICc < 10$ (Burnham et al. 2011). Model performance was assessed through the deviance explained and conditional R2 of each selected model (Nakagawa & Schielzeth 2013, Johnson 2014).

Analyses were undertaken in R (R Core Development Team 2014), using the package usdm to calculate VIF (Naimi et al. 2014), the package lme4 to run GLMMs (Bates et al. 2016) and the package MuMIn for multimodel selection and model averaging (Bartón 2013).

3. RESULTS

3.1. POST-BREEDING MOVEMENTS

From the 27 male Little Bustards tracked in the course of this study, only one individual from Vila Fernando showed a clear sedentary behaviour, remaining close to the breeding site all year round during two consecutive years (maximum distance from the breeding site = 7.7 km). All other individuals (96.3%) performed seasonal movements (Figure 1, mean departure date: 29 June), moving to areas further than 35 km (79% of all birds) from their breeding sites during the post-breeding period (average = 77.5 ± 65.5 km; range = 19.0 - 303.7 km). Most birds captured in Castro Verde (52%) headed north to post-breeding areas where irrigated agriculture is the dominant land use, while other individuals flew to more distant coastal SPAs (21%), such as the Tagus estuary and the Portuguese Southwest coast, also areas with a very high proportion of irrigated crops. Most birds from Vila Fernando moved east to the irrigated crops that surround the Guadiana river (70%). One individual engaged in a long-distance movement (of more than 300 km) reaching a post-breeding area located north of Plasencia, Spain. The large majority of post-breeding movements occurred during the night with 78% of these movements already starting in the night time period, and the remaining (22%) in late afternoon (roughly between 17:00 and 20:00) and finishing in the first hours of daylight or late night (Table 2). No birds were recorded flying in the hottest hours of the day, between 11 and 16h (considering all periods of continuous flight, including partial movements between stopovers and movements without stopovers, n = 124).

3.2. STOPOVERS

Eighty-four stopovers were identified and analysed through visual inspection. Stopovers occurred in more than 80% of the post-breeding movements (Table 2) and 76% of birds made one to three stopovers during their movements. There was a significant positive relationship between the distance travelled and the number of stopovers made by the birds (Pearson's correlation: r_{32}= 0.38, P = 0.028) although the occurrence of stopovers was still high (75%) in shorter-distance movements (< 50 km).

The vast majority of stopovers (84%) were of short duration (Figs. 2 & 3), lasting less than 24 hours (Table 2). These short stopovers lasted most of the daylight period (64% of short stopovers), with birds arriving at late night/early morning and departing in the late afternoon or during the night (Table 2). Despite that, a substantial part of these short stopovers were carried out exclusively during night-time (36%) lasting only a few hours (88% of these nocturnal stopovers lasted up to 4 h). The distance travelled between stopovers (including departure and arrival to post-breeding areas) was different in diurnal and nocturnal stopovers. While only 48% of diurnal stopovers were followed by a stop within the following ten kilometers of the movement, over 80% of night stopovers had a subsequent stop within the same distance (median distance travelled = 10.20 and 3.70 km, respectively; Mann-Whitney U = 445.0, n = 83, P = 0.008).

The majority of stopover locations during these post-breeding movements were located outside SPAs (82.2%), contrasting with locations during the breeding period, mostly located within SPAs (85.4%, this dataset).

Most birds tracked over consecutive years maintained a similar migratory behaviour (Figure 4 & Table 3), using the same breeding (88% of birds, n = 8) and post-breeding areas (63% of birds). One exception was a bird that in the second year dispersed to a new breeding site, 87 km away from its previous breeding area. Despite the fidelity to the same post-breeding areas over consecutive years (Figure 4), there were no repetitions in the use of stopover sites by the same individuals (Table 3).

Table 2. Description of stopovers during post-breeding movements of Little Bustards.

	Descriptor	**Value**
	Number of post-breeding movements	40
	Number of stopovers[1]	84
	Number of tracked individuals	27
Movement	Departure date[2]	179.5 ± 22.2 (184)
	Arrival date[2]	184.0 ± 23.4 (189)
	Duration of movements (days)[3]	2.4 ± 2.4 (1.4)
	Movement range (km)	64.3 ± 55.7 (41.5)
	Time of departure	23:21 ± 03:24 (00:00)
	Time of arrival	06:24 ± 03:47 (07:00)
Stopovers	Occurrence of stopovers[1]	83.0%
	Number of stopovers per movement[1]	2.5 ± 1.4 (2.0)
	Duration of stopovers (hours)	20.5 ± 24.6 (16.0)
	Time of departure	23:57 ± 04:09 (01:00)
	Time of arrival	05:53 ± 03:28 (06:00)
	Distance travelled between stops (km)	23.4 ± 27.8 (12.4)

[1] estimated from BBMM analysis and visual inspection;

[2] Julian date;

[3] Including stopovers; mean ± standard deviation, with median in brackets

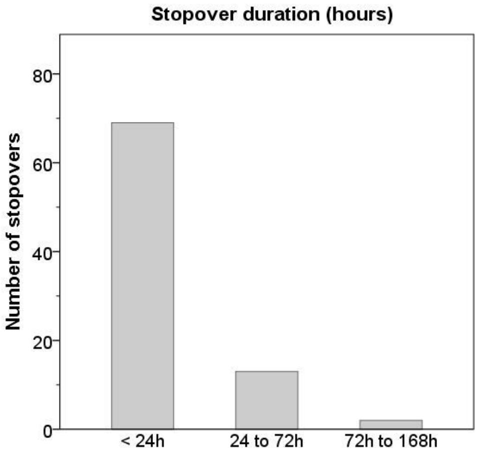

Figure 2. Number and duration (in hours) of stopovers (*n* = 84) during the post-breeding movements (*n* = 40) of Little Bustards.

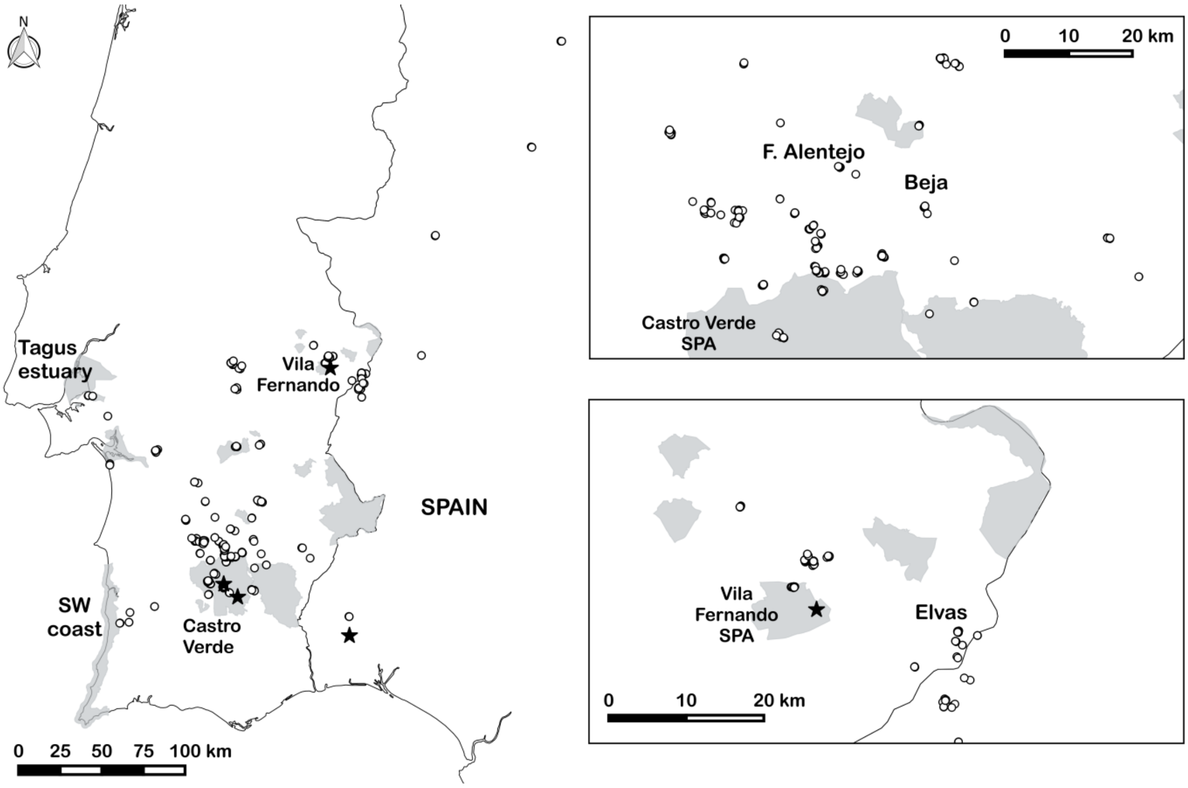

Figure 3. Stopover locations of Little Bustards during their outward post-breeding movements. Capture locations (breeding sites) are indicated by black stars and special protected areas with importance for grassland birds are shown in grey.

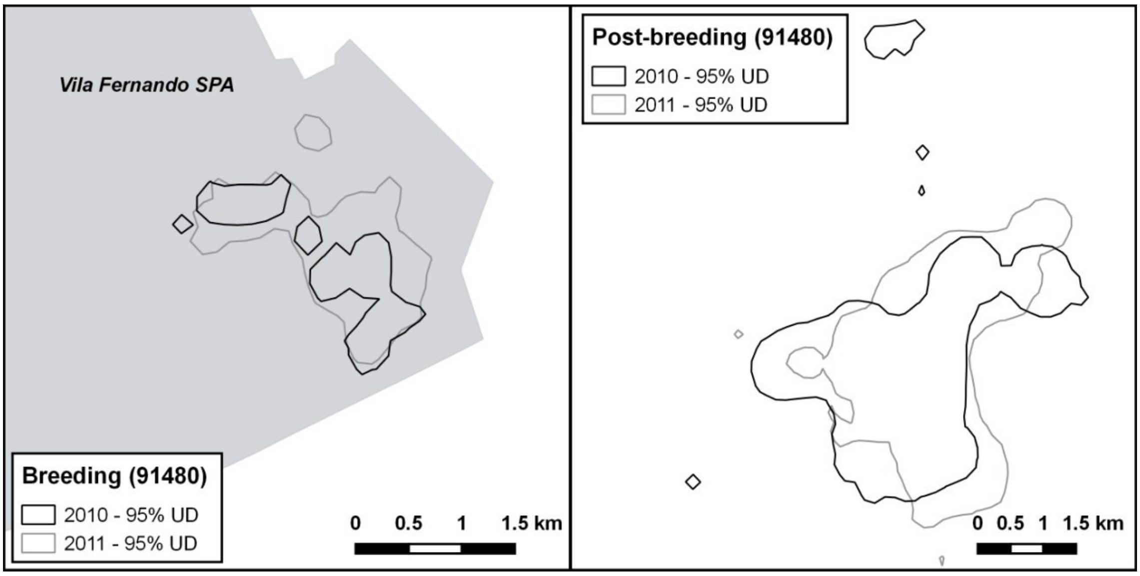

Figure 4. Breeding and post-breeding areas (kernel 95% UD) of an individual male Little Bustard (91480) in two consecutive years, 2010 and 2011.

Table 3. Percentage of spatial overlap in the use of breeding, post-breeding (50% and 95% UD) and stopover areas by eight male Little Bustards in consecutive years.

Individual	Number of years	% Breeding overlap (95% UD)	% Post-breeding overlap (95% UD)	Stopover overlap%
91469	2	20	77	0
91470	2	45	59	0
91471	2	37	0	0
91474	2	0	0	0
91479	2	38	11	0
91480	3	13 - 48	55 - 69	0
91481	2	14	0	0
91482*	2	37	30	-

* resident individual

3.3. HABITAT SELECTION ON ROUTE

Brownian bridge models allowed the identification of 75 stopovers to be used for habitat selection modeling (fourteen were excluded due lack of habitat data or close proximity to post-breeding areas). The stopover habitat selection model averaging process retained 4 models (ΔAICc < 10; AIC range: 932.94 - 942.21; deviance explained: 0.11 – 0.13; r2: 0.20 – 0.23). The selection of stopover sites was mostly influenced by land use and distance to roads, followed by terrain ruggedness (Table 4). In their stopover sites, Little Bustards used mostly irrigated cropland and non-irrigated areas composed by extensive traditional farming and pastures (see Figure 5). While there were no significant differences in the selection of the above land uses, other land uses were avoided, as was the proximity of main roads and more rugged landscapes (Table 4). The selection of stopover sites was not influenced by the distance to power lines (Table 4).

Table 4. Estimated coefficients of the model averaging procedure (based on four models with ΔAICc < 10), indicating the relative importance of the variable and the number of containing models.

(Conditional average)	Estimate	Std. Error	z value	p-value	Relative variable importance	No. of containing models
Intercept	1.623	0.584	2.774	0.006	-	-
Land cover:					1	4
Irrigated lands	0.219	0.255	0.855	0.392		
Other land uses	-1.706	0.209	8.152	< 0.001		
Ruggedness	-0.839	0.287	2.924	0.003	0.97	2
Log (Distance to power lines + 1)	-0.005	0.056	0.090	0.928	0.27	2
Log (Distance to roads + 1)	0.238	0.075	3.166	0.002	1	4

The category non-irrigated lands is represented by the intercept values

4. DISCUSSION

4.1. POST-BREEDING MOVEMENTS AND STOPOVERS

Although there is some evidence that Little Bustards migrate during the night (Villers et al. 2010), in contrast to other bustard species (e.g. Kessler et al. 2013), there is little information as to whether this is an obligatory or flexible migratory strategy. In this study, the great majority of male post-breeding movements were nocturnal or partially nocturnal (89.5%, n = 124) and birds avoided flying during most of the daylight period. One of the main potential advantages of nocturnal migration is to avoid predation (Alerstam 2009), but there are other compensations, such as using daylight hours to forage and refuel, minimizing load costs (e.g. Delingat et al. 2006). Furthermore, nocturnal migration has metabolic advantages, particularly for birds with an active flapping flight, as it is possible to minimize water loss (Klaassen 1996). Summer temperatures in Southern Portugal frequently exceed 35°C, particularly during midday hours, and Little Bustards are known to reduce their activity levels in response to extreme hot weather (Silva et al. 2015). For this relatively large bird species, flying preferentially during the night period will probably help to prevent water loss and avoid overheating during migratory movements. A potential disadvantage of night migration is an increased risk of collision with anthropogenic infrastructures, such as power lines, as many avian species show a weak or slower reaction to less-visible barriers during nocturnal flights, compared to during daylight (e.g. Deng & Frederik 2001, Murphy et al. 2016).

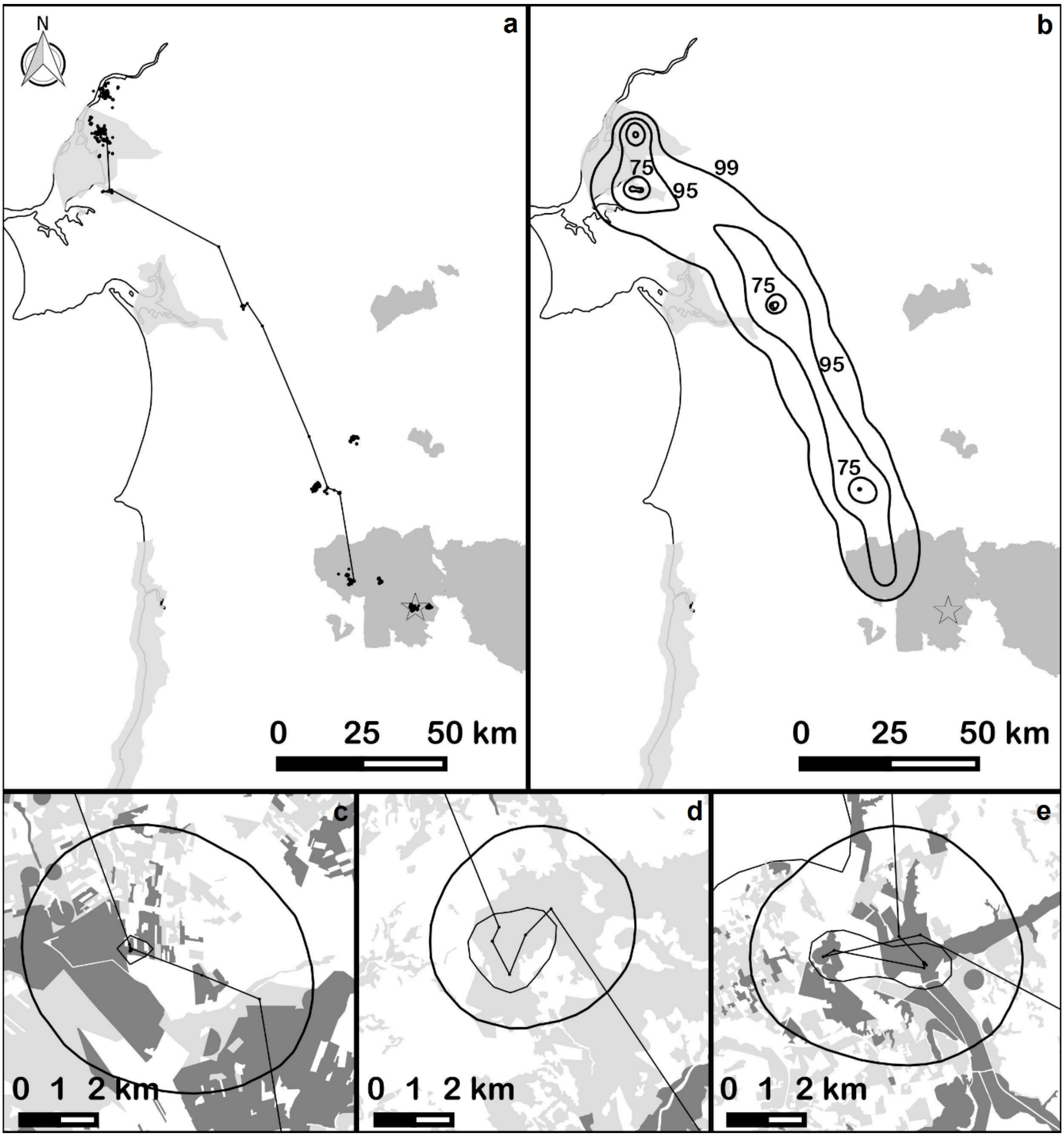

Figure 5. Example of a post-breeding movement of a Little Bustard (individual 91469_1_2009) that bred in Castro Verde in 2009: a) All fixes (black dots) during the year and post-breeding movement (black line); b) Utilization distribution (UD) during the post-breeding movement estimated from Dynamic Brownian Bridge models (stopover areas were identified using the 50 - 75% kernel UD); c) d) e) Stopover locations and land use (Light grey – Pastures and non-irrigated crops, Dark grey – irrigated crops, White – other land use). Star indicates breeding location. Note that the post-breeding movement was delimited between a pre-migratory/second breeding area (see methods) and the main post-breeding area.

During their post-breeding movements, male Little Bustards made one to three diurnal stopovers, which frequently lasted less than 24h (84%), between nocturnal flights. Overall, the occurrence of stopovers was high (> 80% of movements) even when the birds were covering a short migratory distance. The species is known to perform migratory movements of 400-600 km in a single night when crossing the Pyrenees (Villers et al. 2010), which is a much larger distance than the one covered by Little Bustards in the south Portuguese plains during the post-breeding period. Additionally, with a ground flight speed of 65 km/h (Villers et al. 2010) and no evident geographic barriers (except for one individual that crossed Sierra de Gredos, Spain), most of the tracked birds could have completed their post-breeding movements in a single nocturnal flight of a couple of hours. This raises the question: Why do male bustards make stopovers in these short-distance migratory movements?

The breeding period is an extremely demanding phase for male Little Bustards. Food resources are expected to decline throughout the breeding season (Silva et al. 2007) and their foraging activity is likely restricted due to high temperatures in early summer (Silva et al. 2015). In these short-distance movements, birds are also likely to perform their journeys in active flapping flight mode with high energy expenditure, rather than flying at altitudes where they could take advantage of tail winds (Liechti & Schmaljohann 2007, Mateos-Rodríguez & Liechti 2011). It is thus likely that the birds need to make stopovers to refuel and rest, even during relatively short migratory flights. By making these 'obligate' diurnal stops and moving preferentially during the night, Little Bustards may avoid unnecessary costs, while resting and refueling (also minimizing load costs) to resume the migratory movement in the subsequent night.

It remains uncertain whether this migratory strategy is also used by female Little Bustards, considering not only their distinct breeding phenology (females remain in breeding areas for longer periods, due to parental care duties), and smaller body size, as well as the potential higher flexibility in their migratory behaviour (e.g. Palacín et al. 2009). Indeed, in the sympatric Great Bustard, that shares a similar breeding phenology and habitat, females tend to remain sedentary in years when they are raising young (Palacín et al. 2009, 2011).

4.2. HABITAT SELECTION DURING STOPOVERS

Little Bustards, as other species from the Otitidae family, are extremely selective in relation to their habitat, particularly in the breeding and post-breeding seasons (e.g. Martínez 1994, Faria & Rabaça 2004, Silva et al. 2004, 2007). In southern Portugal, breeding Little Bustards tend to prefer agricultural fallow lands or extensive pastures, while in the post-breeding season birds move to more productive areas, usually occupied by irrigated fields (Silva et al. 2007). In stopover sites, dry crops and irrigated crops were both used by Little Bustards. Irrigated croplands were not significantly preferred in stopovers (compared to dry crops), which may be an indication that most birds were on the move, instead of prospecting potentially good foraging grounds or evaluating post-breeding areas. During stopovers, birds did avoid 'other land uses' as well as rugged terrain. These results suggest that male

Little Bustards are being less selective during short stopovers than in other periods of the year (showing a mixed preference for dry and irrigated crops), but still occupy areas that warrant a minimum protection from predators (areas with good horizontal visibility allow the early detection of predators; Metcalfe 1984) and potential foraging habitat.

Linear human infrastructures, such as roads and power lines, are known to negatively impact populations of many vertebrate species through habitat loss and degradation, barrier effects, increased human disturbance and mortality (Janss et al. 2000, Benítez-López et al. 2010, Silva et al. 2010, Barrientos et al. 2012). During the breeding season, Little Bustards seem to avoid the proximity of roads and power lines (Suárez-Soane et al. 2002, Silva et al. 2010; but see Martínez 1994, Faria & Rabaça 2004 for divergent results), and in the winter, when food resources are abundant, bustards have been found to avoid the proximity of roads and inhabited houses (Silva et al. 2004). In contrast, during the post-breeding period, these birds tend to use areas of intensified agriculture, moving closer to roads, which are abundant in those areas (Silva et al. 2007). Considering such variability regarding the response to linear infrastructures and human presence, it is likely that the importance of such drivers may vary according to the ecological context and individual requirements. The negative response of Little Bustards to roads suggests that during stopovers they still avoid proximity to some human infrastructures, also favoring areas with greater availability of food and cover. Nevertheless, Little Bustards showed a lack of response to the presence of power lines and, as in other heavy flight birds (e.g. Sandhill Cranes *Antigone canadensis*, Murphy et al. 2016), may be less able to detect the presence of these linear infrastructures during nocturnal flights.

4.3. INDIVIDUAL CONSISTENCY IN MIGRATORY BEHAVIOUR

To our knowledge, this is the first study quantifying the fidelity of male Little Bustards to their post-breeding areas, revealing a high level of fidelity to those areas (see also García de la Morena et al. 2015). This pattern is similar to that found in other short-distance migrant steppe birds in Iberia (Great Bustard, Morales et al. 2000, Alonso et al. 2001) and supports a strong migratory connectivity between Little Bustard breeding and non-breeding areas. Despite the similar migratory routes and high fidelity to post-breeding areas, there was no repetition by individuals in the use of stopover sites in consecutive years. Stopover site fidelity has never been investigated in short-distance migrants, but is known to occur in long-distance migrants that are highly selective in relation to habitat, such as waterfowl and shorebirds (e.g. Fox et al. 2002). Little Bustards are highly selective in relation to their habitat, but have shown to be less selective during post-breeding stopovers (see above). The short time spent in these post-breeding migratory stopovers (less than 24 hours) and availability of potential areas with adequate habitat may influence the non-repetition of the same stopover sites, but further studies are needed to support this hypothesis.

4.4. IMPLICATIONS FOR CONSERVATION

A good knowledge of the spatial distribution of migrant populations across the annual cycle is critical for their conservation (Shuter et al. 2011, Klaassen et al. 2014, Hewson et al. 2016). However, little is known about the migratory behaviour (including the selection of stopover sites) of many endangered short-distance migrants, or about the potential negative impact of human infrastructures during their migratory movements (e.g. Newton et al. 2017, Palacín et al. 2017).

Little Bustards, as most bustard species, are very prone to collision with overhead wires, particularly with power lines (Barrientos et al. 2012, Silva et al. 2014) due to their narrow binocular field of view, low flight maneuverability, gregarious behaviour and high flight speed (Martin & Shaw 2010, Barrientos et al. 2012). Therefore, the migratory strategy used by male Little Bustards (based on nocturnal flights interspersed with frequent stops) may impose additional risks to them, particularly during the post-breeding period, when birds may be crossing unknown areas, likely at collision-risk altitudes (Silva et al. 2014) and under low light conditions. For the Great Bustard *Otis tarda*, another short-distance migrant in Iberia and a collision-prone species, mortality is 2.4 to 3.5 times higher in migrants than in sedentary individuals, mostly due to collision with power lines (Palacín et al. 2017).

The rapid expansion of agricultural intensification in the south Portuguese plains, particularly of permanent crops, has been very significant over the last decade (e.g. Ribeiro et al. 2014). This widespread change in agricultural systems is affecting grassland bird populations all over Europe (Donald et al. 2006) and Little Bustards have declined by c. 50% in Portugal, possibly linked to habitat loss and degradation (Silva et al. 2018). The preservation of open habitat areas between their main breeding and post-breeding areas is a key conservation measure to ensure the availability of adequate stopover sites and guarantee connectivity, that should be considered in future management and conservation plans.

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Chapter 5

Wind turbines cause functional habitat loss for migratory soaring birds

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Wind turbines cause functional habitat loss for migratory soaring birds

ABSTRACT

1. Wind energy production has expanded to meet climate change mitigation goals, but negative impacts of wind turbines have been reported on wildlife. Soaring birds are among the most affected groups with alarming fatality rates by collision with wind turbines and an escalating occupation of their migratory corridors. These birds have been described as changing their flight trajectories to avoid wind turbines, but this behaviour may lead to functional habitat loss, as suitable soaring areas in the proximity of wind turbines will likely be underused.

2. We modelled the displacement effect of wind turbines on black kites (*Milvus migrans*) tracked by GPS. We also evaluated the impact of this effect at the scale of the landscape by estimating how much suitable soaring area was lost to wind turbines.

3. We used state-of-art tracking devices to monitor the movements of 130 black kites in an area populated by wind turbines, at the migratory bottleneck of the Strait of Gibraltar. Landscape use by birds was mapped from GPS data using dynamic Brownian bridge movement models and generalized additive mixed modelling was used to estimate the effect of wind turbine proximity on bird use while accounting for orographic and thermal uplift availability.

4. We found that areas up to approximately 674 m away from the turbines were less used than expected given their uplift potential. Within that distance threshold, bird use decreased with the proximity to wind turbines. We estimated that the footprint of wind turbines affected 3-14% of the areas suitable for soaring in our study area.

5. We present evidence that the impacts of wind energy industry on soaring birds are greater than previously acknowledged. In addition to the commonly reported fatalities, the avoidance of turbines by soaring birds causes habitat losses in their movement corridors. Authorities should recognize this further impact of wind energy production and establish new regulations that protect soaring habitat. We also showed that soaring habitat for birds can be modelled at a fine scale using publicly available data. Such an approach can be used to plan low-impact placement of turbines in new wind energy developments.

Keywords: aerial habitat; avoidance behaviour; migration; orographic uplift; raptor; thermal uplift; wind farms

1. INTRODUCTION

Wind energy generation has increased immensely over the last decades and this growth is expected to continue in the forthcoming years, with a predicted annual increase of 5% of the installed capacity until 2020 (GWEC, 2015; IPCC, 2011). Despite the immediate benefits for climate change mitigation, negative interactions between wind energy production and wildlife, mainly birds and bats, have been widely reported (Saidur et al., 2011). Soaring birds, including most raptors, storks and other large birds, are among the groups of highest concern, as their movement corridors have been populated by wind farms (Cabrera-Cruz, & Villegas-Patraca, 2016; Katzner et al., 2012; Martín et al., 2018) leading to high fatality rates through collisions with turbines (e.g. Barrios, & Rodriguez, 2004; Ferrer et al., 2012; Smallwood, & Thelander, 2008).

Soaring flight allows large birds to travel long distances with a reduced energetic cost (Duriez et al., 2014; Pennycuick, 1975). However, soaring depends on updrafts, which are relatively scarce and scattered across the landscape (Horvitz et al., 2014; Katzner et al., 2015). Two types of updrafts are commonly used by terrestrial soaring birds: (1) orographic uplift that results from the deflection of horizontal winds by sloping terrain and (2) thermal uplift that is formed during the day due to the heating of the land surface by solar radiation (Kerlinger, 1989). Soaring birds use orographic uplift either to gain altitude and glide downwards in a desired direction, or to travel along uplift-rich areas such as mountain ranges (Bohrer et al., 2012; Katzner et al., 2015). Orographic uplift is particularly useful when generated from mountain ranges oriented in the migration direction (Dennhardt et al., 2015; Kerlinger, 1989). In the case of thermal uplift, soaring birds typically climb in thermals using a circular trajectory from which they glide linearly towards the next thermal in the desired direction (Katzner et al., 2015; Kerlinger, 1989; Santos et al., 2017). Due to such specific requirements, soaring birds tend to move along areas with high uplift potential, often named corridors (sensu Dennhardt et al., 2015). Besides the physical requirements for soaring, the importance of different corridors may vary dramatically depending on their geographic position relative to migration routes of soaring birds. For example, areas in the vicinity of narrow sea crossings may experience higher traffic during migrations, as soaring birds avoid crossing large bodies of water (Newton, 2008).

Soaring birds and wind energy developments may compete for the same areas both at the local and regional scales. At local scales, wind turbines are frequently installed along the top of mountain ranges, in order to maximize exposure to horizontal winds, and these areas also tend to have high orographic uplift potential for birds (Katzner et al., 2012). At a broader scale, migratory bottlenecks of soaring birds often correspond to narrow sea crossings or mountain passes where the topography favours high wind speeds, thus also well suited for wind-power production (Hilgerloh, Michalik, &

Raddatz, 2011; Martín et al., 2018; Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014). Therefore, understanding how wind turbines impact movement corridors of migratory soaring birds is of utmost importance to better reconcile the production of wind power with wildlife conservation.

In general, birds tend to avoid wind turbines through evasive movements and changes in space use (May, 2015). Empirical evidence published on soaring birds has been showing they change their flight trajectories to avoid turbines (de Lucas, Janss, & Ferrer, 2004; Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014) and that their numbers decrease in the close proximity of the turbines (Barrios, & Rodriguez, 2004; Pearce-Higgins et al., 2009). Similarly, comparisons between the pre- and post-construction phases showed that soaring birds reduce their use of the areas where turbines are installed and their trajectories become more scattered in nearby areas (Cabrera-Cruz, & Villegas-Patraca, 2016; Farfan et al., 2017; Garvin et al., 2011; Johnston, Bradley, & Otter, 2014). While these avoidance behaviours suggest that soaring birds are to some extent able to cope with the presence of wind turbines (Marques et al., 2014), they may also cause functional habitat loss (i.e. loss of aerospace in movement corridors; Diehl, 2013), which is a potentially important, though largely neglected, impact of wind-power generation (Davy, Ford, & Fraser, 2017).

In this study we investigated the footprint of wind turbines on movement corridors of migratory soaring birds using high-frequency GPS tracking (1-minute temporal resolution or higher). GPS tracking is a powerful tool to investigate direct interactions between birds and wind turbines at multiple spatiotemporal scales, but it was only recently introduced in this field of study (e.g. Garthe, Markones, & Corman, 2017; Thaxter et al., 2015; Thaxter et al., 2018). We tracked 130 black kites (*Milvus migrans*) during the post-breeding migration in an area highly populated by wind turbines in the region of Tarifa, Spain. Black kites and other soaring birds concentrate in this region to cross the Strait of Gibraltar during their migration to Africa (MIGRES, 2009). Birds were captured and tracked during periods of strong crosswinds at the Strait of Gibraltar, which forced them to roam around Tarifa while waiting for conditions favouring the sea crossing. Bird movements were used to map space use intensity using Brownian bridge movement models. The influence of the wind turbines on the birds' use of the landscape was then modelled taking into account the main predictors of soaring flight, orographic and thermal uplift (Bohrer et al., 2012; Kerlinger, 1989). We hypothesised that (1) birds will use areas with greater uplift (orographic and thermal) more frequently, and (2) the area in the proximity of the wind turbines will be less frequented regardless of its uplift potential.

2. MATERIALS AND METHODS

2.1. STUDY AREA

This study was conducted in the region of Tarifa (36.0132ºN, 5.6027ºW), on the Spanish side of the Strait of Gibraltar. The Strait is a narrow sea crossing between Europe and Africa and is the main migration bottleneck for soaring birds travelling along the Western European–West African Flyway (Newton, 2008). The region of Cádiz (that includes Tarifa) is of high importance to the wind energy industry, with ca. 70 wind farms and over 1300MW of installed wind-power capacity (IECA, 2015). Our focal area had 160 operating wind turbines on seven wind farms, representing 132MW of power generation (Figure 1, Table S1). These turbines were mainly arranged in rows from North to South (Figure 1).

2.2. BIRD CAPTURES AND TRACKING

Our model species, the black kite, is an obligate soaring migrant, and one of the most common soaring species crossing the Strait of Gibraltar during the post-breeding migration (between 100 and 150,000 individuals are counted on an annual basis; Martín et al., 2016). These features make this species susceptible to interactions with wind turbines, and fatalities due to collision with wind turbines have been recorded in earlier studies in this region (Ferrer et al., 2012).

We captured and fitted 130 birds with GPS data loggers during the post-breeding migration (July to September) in 2012 and 2013 (Table S2). Birds were captured during periods of strong Levanter winds (5-15 m/s blowing from the east), which are frequent in the summer (Dorman, Beardsley, & Limeburner, 1995) and are known to prevent the passage of soaring birds to Africa, causing them to congregate around Tarifa for periods up to one week (Miller et al., 2016). Birds were captured in a walk-in trap (7 x 7 x 3.5 m) baited with carrion, located 3.5 km North of Tarifa (36.0426ºN, 5.6150ºW). We captured more birds than those eventually tracked, which enabled us to select similar numbers of adults and juveniles in each capture event. Overall, we tracked 72 adults and 58 juveniles. Sex ratio was also relatively balanced (69 females, 59 males and 2 unidentified, results from molecular sexing).

Birds were equipped with GPS-GSM data loggers (42g, TM-202/R9C5 module, Movetech Telemetry, UK, https://www.uea.ac.uk/movetech) attached as backpacks using Teflon ribbon. A weak-link was built in to each harness to allow the loggers to automatically detach. The weak-link was made from rubber band for the birds tagged in 2012 and from biodegradable plastic thread in those tagged in 2013. Previous tests showed that the rubber band breaks within two to four weeks when exposed to solar radiation and the biodegradable plastic thread within a year. Birds were released a few hours after capture, immediately after the tagging was completed. Loggers were set to obtain a GPS position at least once a minute. GPS mean error calculated from ca. 1500 fixes collected by two data loggers left at a fixed known position was 1.4 m in horizontal and 1.5 m in vertical, with maximum errors of 15 m and 31 m respectively. Data were uploaded to an online server via the GSM network every two hours.

The procedures involved in bird trapping and the GPS tagging were approved by the Consejería de Medio Ambiente of the Junta de Andalucía through the license to Alejandro Onrubia.

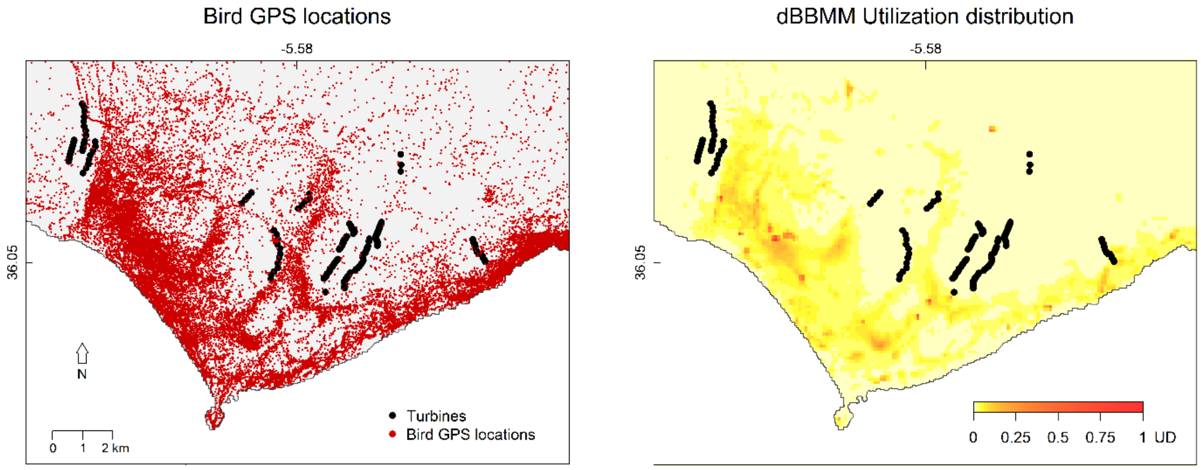

Figure 1. Use of the aerospace in the study area (Tarifa, Spain) by the black kites during the post-breeding migration of 2012 and 2013, and the locations of the wind turbines. Left panel: GPS locations of 130 tracked birds. Locations are only shown for birds flying (speed >1 m/s) during daylight in periods of Levanter wind (blowing from the east), and for the region where the concentration of bird movement was the highest. Right panel: cumulative Utilization Distribution modelled from dBBMMs. Map grid with 100m spatial resolution. Black dots in each map are the locations of wind turbines.

2.3. ESTIMATION OF OROGRAPHIC AND THERMAL UPLIFT

We used estimates of orographic and thermal uplift to test our first study hypothesis. The orographic and thermal uplift velocities were estimated using a modified version of the methodology employed by Bohrer et al. (2012) and Brandes and Ombalski (2004) for high resolution spatial data, described in Santos et al. (2017). The estimation of orographic uplift uses parameters from local topography (terrain aspect and slope) and wind (direction and speed). Local topography was obtained from a Digital Elevation Model of 30 m spatial resolution available at http://gdex.cr.usgs.gov/gdex/ (NASA JPL, 2009). Wind direction and speed was obtained at a weather station in Tarifa (36.0138ºN, 5.5988ºW). Measurements of wind for the whole migration season of black kites (mid-July to mid-September; MIGRES, 2009) during in 2012 and 2013 lead to the conclusion that there are two predominant wind conditions: (1) strong Levanter winds (wind direction from 80 to 120º; speed from 4 to 15 m/s) lasting for periods up to a week; and (2) western breeze (wind direction from 270 to 310º; speed from 1 to 6 m/s), typically occurring between Levanters (Figure S1). These wind conditions match with that generically described for the summer at the Strait of Gibraltar (Dorman, Beardsley, & Limeburner, 1995). In this context, we decided to build three different orographic uplift models, the first representing uplift for average conditions of wind during the collection of our tracking dataset (direction = 97.8º, speed = 8.8m/s), and the other two models representing the average conditions of Levanter wind (direction = 100º, speed = 7.7m/s) and western breeze (direction = 290º and speed = 4.1m/s) observed during the whole migration season of black kites in 2012 and 2013. The uplift estimated from the first model was used as predictor in bird space-use models (described in the section below), while the estimates of the remaining two uplift models were used in the calculation of general scenarios of habitat loss during Levanter wind and western breeze (shown in Figure 5).

The estimation of thermal uplift velocity according to Santos et al. (2017) uses land surface temperature derived from LANDSAT imagery. In general, satellite images obtained in the same season show high correlation in reflectance values if no major changes of land use are observed (Zhu, 2017). Consequently, high correlation is also expected for thermal uplift models built from those images. Santos et al. (2017) confirmed that uplift models built for the study area in different days during the summers of 2012 and 2013 are highly correlated ($r > 0.77$). Therefore, we decided to build a single thermal uplift model that used land surface temperature estimated from a LANDSAT 8 OLI/TIRS image acquired on July 17th 2013, available at http://earthexplorer.usgs.gov/ (NASA Landsat Program, 2015). The model was representative of uplift at 225 m height, which is the mean flight height of birds in our tracking dataset, and its spatial resolution was 100 m, corresponding to that of the LANDSAT 8 OLI/TIRS thermal band.

2.4. BIRD MOVEMENT MODELLING

Our modelling approach followed the concept of Resource Utilization Function (RUF) proposed by Marzluff et al. (2004). RUF uses a two-step analysis, the first that estimates the density or intensity of space use (i.e. Utilization Distribution; UD) over the geographic domain of interest and the second links the space use to a set of spatially explicit covariates in a regression model (Hooten et al., 2017).

Our modelling dataset included GPS positions of flying birds (i.e. GPS speed >1 m/s, Figure S2) collected during daylight and in days of Levanter wind (direction: mean = 97.8º, SD = 0.22, range = 83.2-116.3º; speed: mean = 8.8m/s, SD = 2.2, range = 4.2-12.7 m/s). Very few tracking data were collected with different wind conditions than Levanter because birds cross the Strait of Gibraltar as soon as the Levanter ceases (Miller et al., 2016). These data were thus excluded from the analysis. We also concentrated the analysis in the area where the concentration of bird movement was the highest (represented in Figure 1).

We used dynamic Brownian bridge movement models (dBBMM; Kranstauber et al., 2012) to estimate the UD of each bird in each day on a 100x100m grid. Contrasting to conventional methods of UD estimation, the Brownian bridge movement model quantifies the UD based on the movement path of animals rather than individual points (Horne et al., 2007; Kranstauber et al., 2012). A major advantage of this method is that it accounts for temporal autocorrelation in the data, which is a fundamental problem of tracking data, particularly for GPS data obtained at high frequency (Kranstauber et al., 2012). The dBBMM were implemented in R (R Core Team, 2016) with the function brownian.bridge.dyn of the package move (Kranstauber, Smolla, & Scharf, 2017), using a window size of 15 locations and a margin of 5 locations following the recommendations of Kranstauber et al. (2012). The UD calculated for each bird in each day were summed in order to produce a general UD for our study area. This UD was used as a response variable in the models described below.

In order to specifically test our study hypotheses, we fitted a generalized additive mixed model (GAMM) using distance to wind turbines and the orographic and thermal uplift velocities as predictors of bird UD. Orographic and thermal uplift are the most important drivers of soaring flight on land (Kerlinger, 1989), thus we expected bird UD to be fundamentally determined by those factors but potentially affected by the proximity of wind turbines. We selected GAMM as modelling technique because it simultaneously allowed the use of non-linear predictors and accounting for spatially correlated data (Beale et al., 2010; Zuur et al., 2009). The model was fitted with the function gamm of the R package mgcv (Wood, 2018). Bird UD and all predictors were represented by single values in the 100x100m grid generated in the dBBMM interpolation. We must emphasise that orographic and thermal uplift estimates result from static uplift models, representing the generic conditions for the period of tracking data collection (see section above). We added a Gaussian spatial correlation structure to the model to account for spatial autocorrelation (Beale et al., 2010; Dormann et al., 2007; Wood, 2017). This was done with the function corGaus of the R package mgcv (Wood, 2018) following Zuur et al. (2009). Bird UD was log-transformed to normalize its distribution. No random factors were included in the model. In a first approach, the degree of smoothing of predictors (k) was left free to be optimized by cross-validation (the default method of the gamm function). However, we found that the effects of uplift predictors on bird UD were approximately linear in the regions well supported by data (Figure S3). Therefore, we set these two predictors as linear in our final model. The modelling dataset was restricted to grid cells at distances up to 2 km from wind turbines (i.e. 9,136 grid cells), as the influence of wind turbines on bird UD is expected to dissipate with distance.

A second model was built for grid cells positioned far away from the influence of the wind turbines (1 to 2 km away from turbines) using only the orographic and the thermal uplift velocities as predictors. We used this model to estimate soaring suitability in the absence of wind turbines (used for the results presented in Figures 4 and 5). This model was a Generalized Least Squares (GLS) since it did not include non-linear predictors. The model was fitted with the function gls of the R package nlme (Pinheiro et al., 2018). As in the GAMM model, in this model we used function corGaus to account for spatial autocorrelation of the data, and the bird UD was log-transformed to normalize its distribution.

Both models were validated through 10-fold cross-validation. The original dataset was randomly split into a training subset with 90% of the data that was used to fit the model, and a testing subset with 10% of the data against which the model is tested. This procedure was repeated 10 times in a way that the training and testing subsets of each run were complementary and cover all the original dataset (Geisser, 1993). The precision and predictive performance of models were evaluated from their Normalized Root Mean Square Error (nRMSE), defined as the root mean square error divided by the range of the model response variable. The Root Mean Square Error (RMSE) is a commonly used metric for regression models accuracy and performance that quantifies model error in the units of the observed data (Kuhn, & Johnson, 2013). Normalizing the RMSE facilitates the comparison between models built at different spatial and temporal scales (e.g. Bocinsky, & Kohler, 2014; Feilhauer et al., 2010).

For both models, fitting assumptions were checked from diagnostic residual plots of R the packages mgcv and nlme (see Figure S4), and spatial autocorrelation correction was validated from plots of residual autocorrelation generated with the function correlog of the R package ncf (Figure S5, Bjornstad, 2018).

3. RESULTS

We tracked 130 individual black kites for an average of 3 days each, generating ca. 220,000 GPS locations (Figure 1 left panel). Movements were concentrated within a radius of ca. 40 km from Tarifa, with individual birds moving about 120 km on average before they crossed the strait of Gibraltar (see Figure S6 for examples of tracks). From the original dataset, 77,228 GPS locations were used for modelling purposes (Figure 1 left panel, Table S2; see methods for details on data selection).

The UD estimated from dBBMMs showed an uneven spatial pattern, with reasonably defined areas of concentration of movement (Figure 1 right panel). Higher intensity of movement was observed along two central areas aligned approximately North-South and along the coastline (Figure 1 right panel).

The estimates of uplift showed highly heterogeneous distributions (Figure 2). The highest orographic uplift velocities during the period of data collection were estimated along the east-facing mountain slopes in the most western and eastern regions of the study area (Figure 2 left panel). In contrast, the highest estimates of thermal uplift were concentrated in a valley located in the centre of the study area (Figure 2 right panel). Orographic uplift was spatially more concentrated with more extreme velocities than thermal uplift, but the latter showed higher values on average (orographic uplift velocity: mean of grid cell values = 0.35m/s, SD = 0.72, range = 0-6.18m/s; thermal uplift velocity: mean of grid cell values = 1.69m/s, SD = 0.26, range = 0.10-2.19m/s).

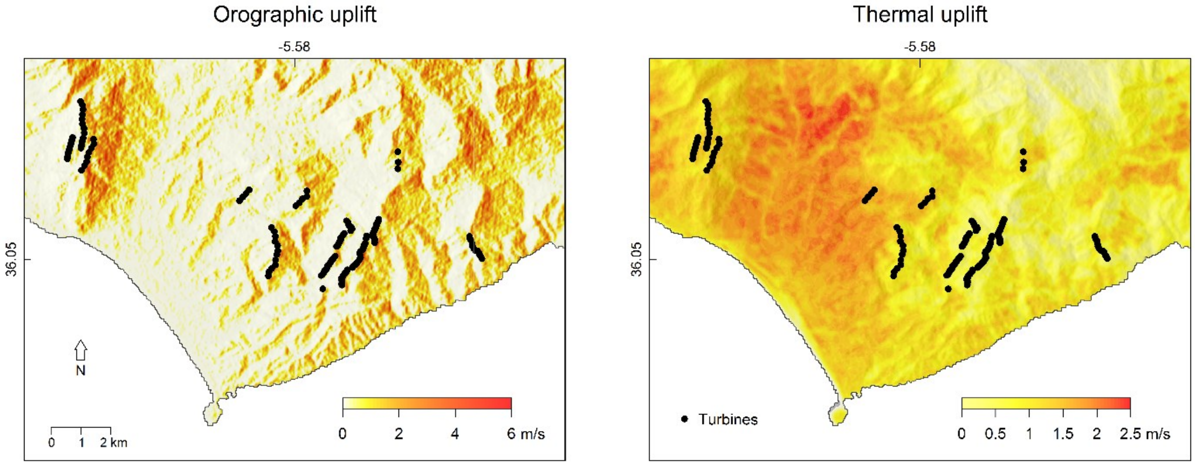

Figure 2. Estimated orographic (left) and thermal (right) uplift velocities in the study area. Orographic uplift represents deflected Levanter winds during the period of bird tracking (wind direction: mean = 97.8º, SD = 0.22, range = 83.2-116.3º; wind speed: mean = 8.8m/s, SD = 2.2, range = 4.2-12.7 m/s). Thermal uplift velocity was modelled for 225m height (mean flight height of birds) using land surface temperature estimated from a Landsat 8 OLI/TIRS image acquired in July 17th 2013 (NASA Landsat Program, 2015) (available at the USGS archive, http://earthexplorer.usgs.gov/). Light hill shading was added to illustrate interaction between topography and uplift. Black dots represent wind turbines.

GAMM results showed that bird UD was significantly affected by the distance to wind turbines and the two types of uplift (Table 1, Figure 3). A negative effect of wind turbine proximity on bird UD was observed up to a distance of approximately 674 m (i.e. the maximum of the curve of Figure 3 left panel), which dissipates beyond that. However, it should be noted that there was a slight drop of bird

UD after the 674 m. Both orographic and thermal uplift velocities had a positive effect on bird UD (Table 1, Figure 3).

The GLS model, fitted with data obtained beyond the influence of the wind turbines (i.e. 1 to 2 km from wind turbines), showed effects of orographic and thermal uplift velocities on bird UD similar to those of the GAMM (Table 1, Figure S7). Predictions of the GLS model applied to areas up to 674 m from the wind turbines were significantly higher than the dBBMM estimates for the same areas (Figure 4). This indicates that birds used areas close to turbines less than expected based on their soaring suitability. After extrapolating this model to the entire study area we found that between 3 and 14% of the area suitable for soaring was within the area of influence of wind turbines (i.e. within 674 m of wind turbines), these being similar during Levanter wind (4-14%) and western breeze (3-14%; Figure 5).

Table 1. Summary statistics for the two models explaining black kite UD. The first model tested the effect of wind turbines on bird UD while accounting for the effects of uplift. The model was a GAMM fitted with grid-cell data at distances up to 2 km from wind turbines, and included the distance to the wind turbines, the orographic and the thermal uplift velocities as predictors. The second model was designed to evaluate soaring suitability grid cells independently of the effect of wind turbines. The model was a GLS fitted with data obtained far from the influence of wind turbines (between 1 and 2 km distance) and used only orographic and thermal uplift velocities as predictors. Both models were corrected for spatial autocorrelation (see methods for details). Fitting and cross validation Normalized Root Mean Square Error ($nRMSE_{fit}$ and $nRMSE_{cv}$) are shown for the evaluation of precision and predictive performance of the models respectively. For $nRMSE_{cv}$ we show the range of the nRMSE calculated for the 10 models produced in the cross validation procedure (see methods for further details). SE – Standard error; t – T statistics; edf – Estimated degrees of freedom; F – F statistics.

	Estimate	**SE**	**t**	**edf**	**F**	**P-value**	**$nRMSE_{fit}$ (%)**	**$nRMSE_{cv}$ (%)**
Model: Effect of wind turbines							13.7	13.6 – 16.5
Intercept	-10.59	0.26	-41.33					
s(distance to turbines)				5.22	12.95	<0.001		
orographic uplift	0.11	0.01	8.03			<0.001		
thermal uplift	2.70	0.15	18.17			<0.001		
Model: Soaring suitability							14.5	14.8 - 17.9
Intercept	-10.42	0.36	-28.74					
orographic uplift	0.12	0.02	5.96			<0.001		
thermal uplift	2.62	0.21	12.68			<0.001		

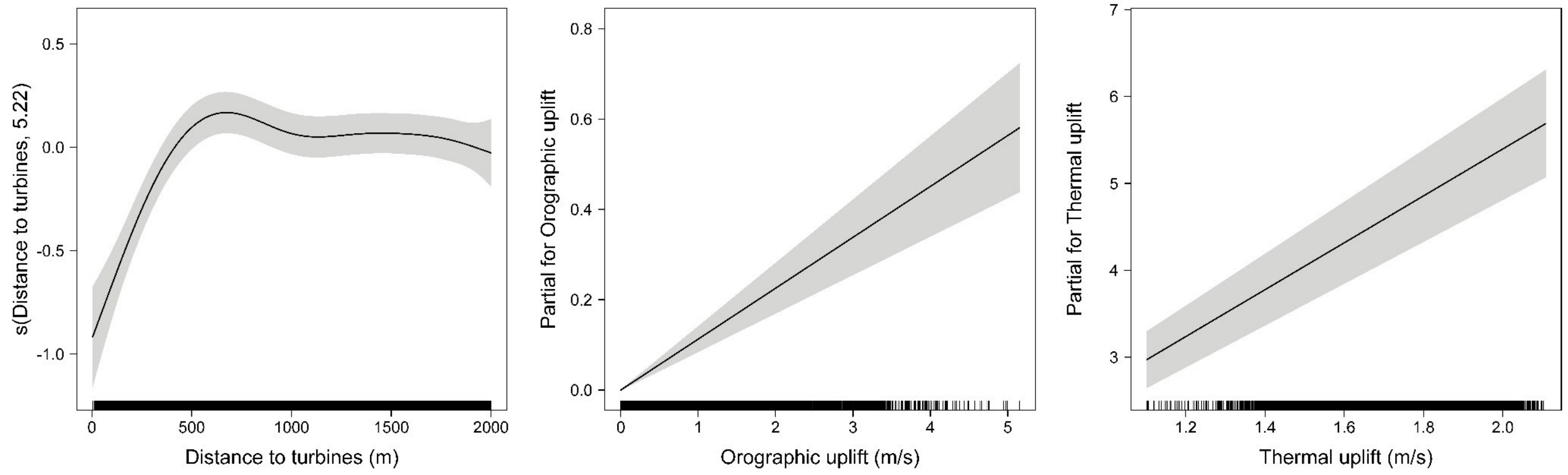

Figure 3. GAMM partial effects of distance to turbines, orographic uplift and thermal uplift on black kite UD. Shaded areas represent 95% confidence intervals. Modelling dataset includes grid cells up to 2 km from wind turbines.

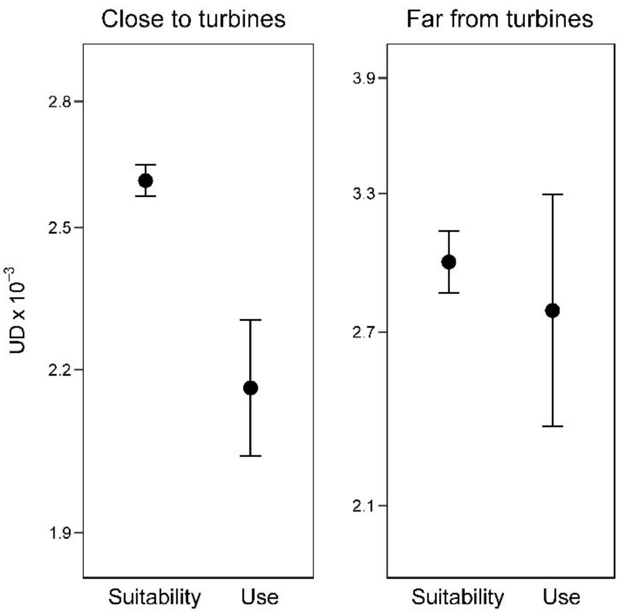

Figure 4. Comparison between soaring suitability and the use by black kites of the areas close to wind turbines (up to 674 m of distance) and far from wind turbines (located at 1 to 2 km distance from the closest turbine). Bird use corresponds to the UD obtained directly from the dBBMM, and the soaring suitability is the UD predicted from a GLS fitted with orographic and thermal uplift velocities as predictors and the dBBMM UD as response variable (see methods for further details). The GLS model was fitted with data of grid cells placed far away from the influence of wind turbines (between 1 and 2 km distance of the closest turbine). These data were randomly divided in two datasets, the first was used to fit the GLS model (with 90% of the data) and the second was used to represent bird use far from turbines in the plot (with 10% of the data). Error bars in the plot represent 95% confidence intervals.

4. DISCUSSION

We found that wind turbines affect a large area of potentially suitable soaring-habitat around them. GPS-tracked black kites showed a reduced use of the areas up to approximately 674 m away from the wind turbines (corresponding to an area of ca. 143 ha around each turbine), this effect being stronger at shorter distances (Figure 3), which proves our second study hypothesis. We also demonstrated that areas within 674 m of the wind turbines had suitable uplift conditions for soaring flight but they were used less than expected by the black kites (Figure 4). Interestingly, there was a slight peak of bird use at areas near the 674 m threshold (Figure 3) that might have been a consequence of birds changing direction to avoid entering the areas adjacent to the turbines (Cabrera-Cruz, & Villegas-Patraca, 2016; Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014). Additionally, we showed clear increasing relationships between orographic and thermal uplift and bird UD (Figure 3 and Figure S5), proving the first hypothesis of this study.

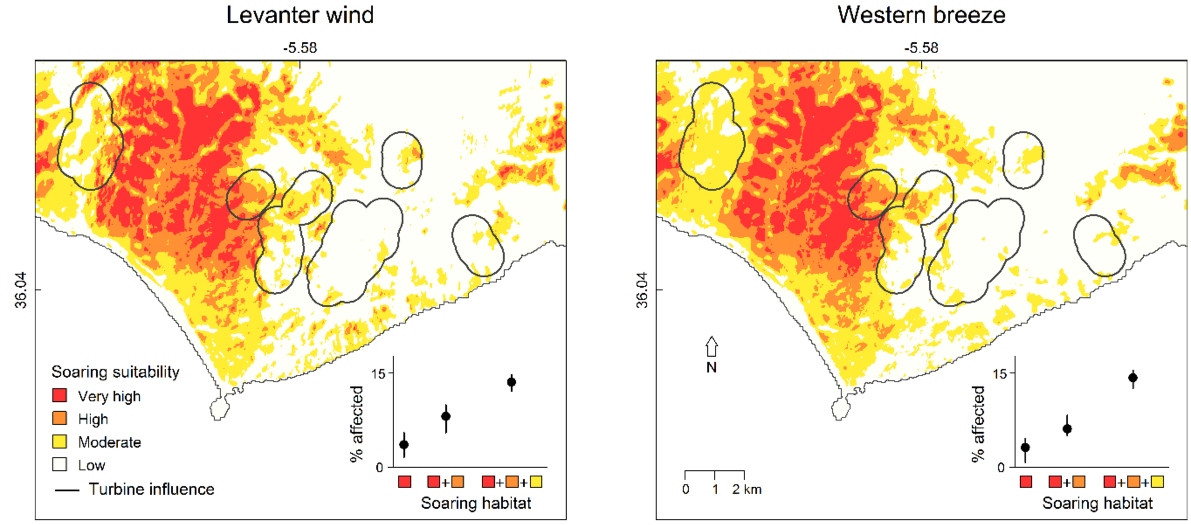

Figure 5. Soaring habitat affected by wind turbines for average conditions of Levanter wind (blowing from the east) and western breeze observed during the migration seasons of the black kites in 2012 and 2013. Wind turbine influence is represented by circles of 674 m radius around each turbine (this distance resulted from the GAMM model shown in Table 1 and Figure 3). Soaring suitability resulted from predictions of a GLS model (detailed in Table 1 and Figure S7) using thermal and orographic uplift estimates for the whole study area and for the two sorts of wind observed during the migration seasons of the black kites in 2012 and 2013. The UD predictions produced from the GLS model were simplified in soaring suitability categories: very high suitability – are the 10% highest UD values; high suitability – are the following highest 15% UD values; moderate suitability – are the following highest 25% UD values; and low suitability – are the lowest 50% UD values. The inset plot shows the percentage of area under the influence of wind turbines considering different scenarios of soaring suitability. Confidence intervals in the plot result from confidence intervals of fitted values of GLS model predictions.

We must emphasise that our models include some level of error (see Table 1), likely because that were other environmental variables influencing the movement of the birds that were not included as predictors. However, that amount of error is comparable to that found in previous studies linking bird soaring behaviour to uplift proxies (Bohrer et al., 2012; Dodge et al., 2014; Hernandez-Pliego, Rodriguez, & Bustamante, 2015; Santos et al., 2017; Sapir et al., 2011). The fact that uplift predictors were estimated for a single generic circumstance in time may also have added inaccuracy to our models. Tracking data used in the models were collected in highly uniform conditions of wind direction, therefore we do not expect that the areas with orographic uplift potential to change spatially in time. However, the variation observed in wind speed may have affected overall uplift intensity of those areas. This could potentially have influenced the birds' trade-off in using orographic uplift or thermal uplift in nearby areas. Regarding the thermal uplift, a considerable temporal variation is expected within a day and between days mostly due to the amount of solar radiation heating the earth surface (Stull, 1988). As in the case of orographic uplift, we do not expect such variation to promote spatial changes in uplift but some intensity variation is expected that could represent a trade-off in the use of alternative sources of uplift.

The displacement effects of wind-power plants have been demonstrated in earlier studies for soaring birds (Barrios, & Rodriguez, 2004; Cabrera-Cruz, & Villegas-Patraca, 2016; de Lucas, Janss, & Ferrer, 2004; Garvin et al., 2011; Johnston, Bradley, & Otter, 2014; Pearce-Higgins et al., 2009; Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014). However, to the current date only a single study quantified the extent of the area affected by this phenomenon (Pearce-Higgins et al., 2009). That study reports lower densities of two species of raptors during their breeding season in areas up to 800 m from turbines, coarsely matching the estimates of our model. Our study is the first attempt to quantify the proportion of soaring habitat lost or negatively affected by the presence of wind farms. We estimated that 3-14% of the areas suitable for soaring in our study area were impacted by wind-energy production, this estimate being similar for Levanter winds and western breeze (Figure 5). These two sorts of wind comprise most wind conditions found in Tarifa during the migration season of black kites (Figure S1). The magnitude of this impact is likely similar in other critical areas for migratory soaring birds where new large wind-power projects are being constructed, such as the Gulf of Suez in Egypt (Hilgerloh, Michalik, & Raddatz, 2011) or the Isthmus of Tehuantepec in Mexico (Villegas-Patraca, Cabrera-Cruz, & Herrera-Alsina, 2014). It should be emphasized that soaring birds are restricted to fly in soaring corridors (e.g. Leshem, & Yom-Tov, 1998; Santos et al., 2017; Shamoun-Baranes et al., 2003), thus, small losses of suitable area may have large constraints for their vital activities. Losses in movement corridors may be particularly important during migrations, as soaring birds already experience considerable mortality while overcoming natural barriers, such as deserts and sea stretches (Bildstein et al., 2009; Klaassen et al., 2014; Strandberg et al., 2010). Suboptimal soaring conditions may force birds to delay or suspend migration or to use flapping flight, which is energetically unsustainable for most species (Newton, 2008).

The reason why migratory soaring birds avoid wind turbines is still unclear. The fact that birds are displaced far beyond the areas occupied by the physical infrastructure of wind-power plants could be a consequence of neophobia, as turbines do not belong to their natural environment (Walters, Kosciuch, & Jones, 2014), but it could also be a consequence of earlier negative experiences, such as birds being caught in the airflow around turbines, or even witnessing fatalities of conspecifics. In addition, the functioning of wind turbines disturbs local airflow regimes (e.g. Magnusson, & Smedman, 1999; Sorensen et al., 2015), which may compromise uplift generation. However, this is expected to affect only the areas downwind the turbine rotors (e.g. Magnusson, & Smedman, 1999; Sorensen et al., 2015). We should also recognize that the avoidance of turbines varies considerably among soaring species, their life stage and their annual cycle (May, 2015), thus the range of influence of wind turbines found in this study is not necessary replicable in other contexts.

Our findings indicate that the negative effects of wind-power developments on soaring birds may be far more extensive than the commonly reported mortality caused by collision (Marques et al., 2014). Avoidance behaviour may suggest that soaring birds, as well as other birds, are partly able to cope with the existence of wind turbines (Marques et al., 2014). However, our results make clear that this is a simplistic interpretation and may lead to the underestimation of the real impacts of wind-power generation. We recommend that the authorities responsible for wildlife protection and wind industry regulations recognize the loss of aerial habitat caused by wind turbines and the potential associated negative impacts on soaring birds. It becomes clear from our results that individual turbines greatly differ on their impact depending on their geographical position (Figure 5), thus it is possible to significantly reduce overall impact of wind-power production with adequate planning. The method we used to map updrafts uses only data that is publicly available (Santos et al., 2017) and can be used in environmental impact assessment studies to guide the selection of low-impact locations for new wind turbines. We are convinced that wind-energy production is necessary to face global warming, but the accelerating increase of wind-power developments needs to be accompanied by science-based solutions to minimize its impacts on wildlife.

Acknowledgements

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SUPPORTING INFORMATION

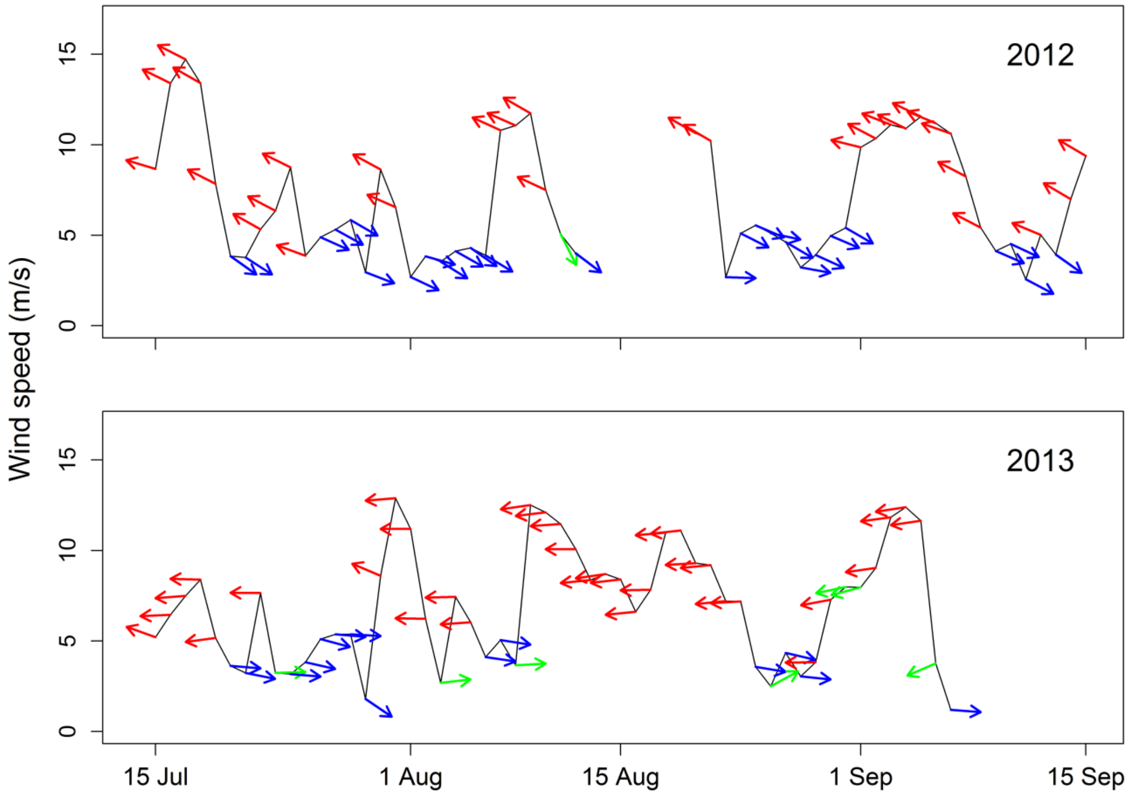

Figure S1. Wind conditions in Tarifa during the migration season of black kites (mid-July to mid-September; MIGRES, 2009) in 2012 and 2013. Wind speed is represented by the black line, while arrows refer to wind direction. Daily means are represented in both cases. Red arrows refer to strong Levanter winds (wind direction from 80 to 120º; speed from 4 to 15 m/s), blue arrows refer to western breeze (wind direction from 270 to 310º; speed from 1 to 6 m/s), and green arrows to any other wind conditions.

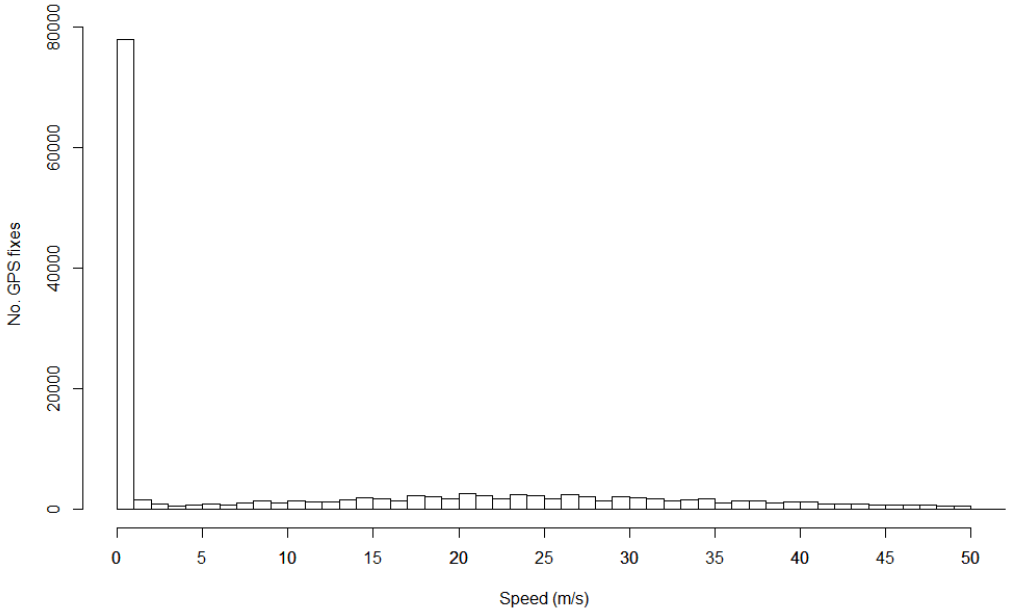

Figure S2. Distribution of GPS speed values from tracking data of black kites recorded in Tarifa (Spain) between 2012 and 2013. Birds were considered to be flying when speed was greater than 1 m/s.

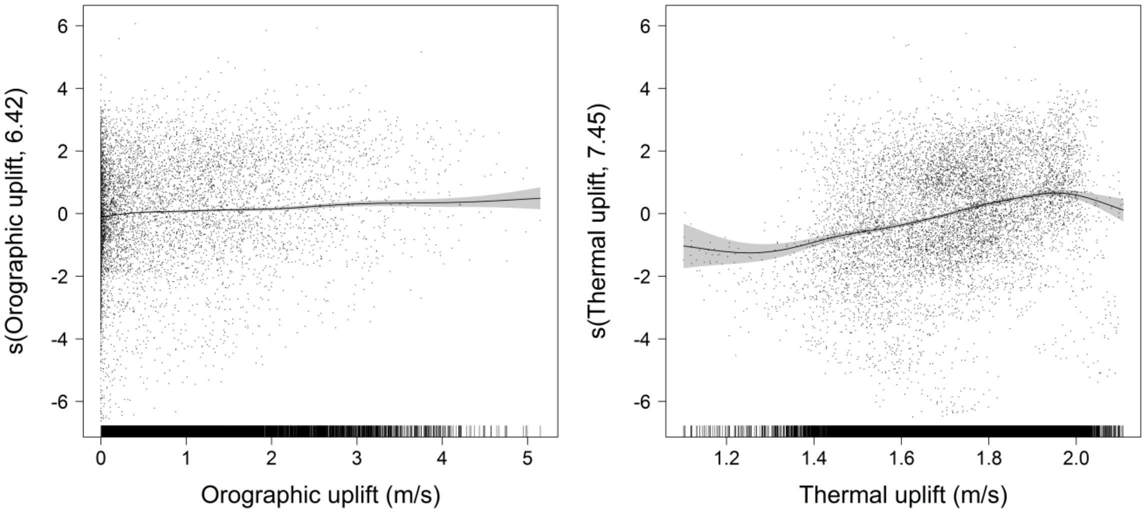

Figure S3. GAMM partial effects of smoothed uplift predictors. The degree of smoothing (k) was optimized by cross-validation. Shaded areas represent the 95% confidence intervals and overlaid dots represent the model residuals.

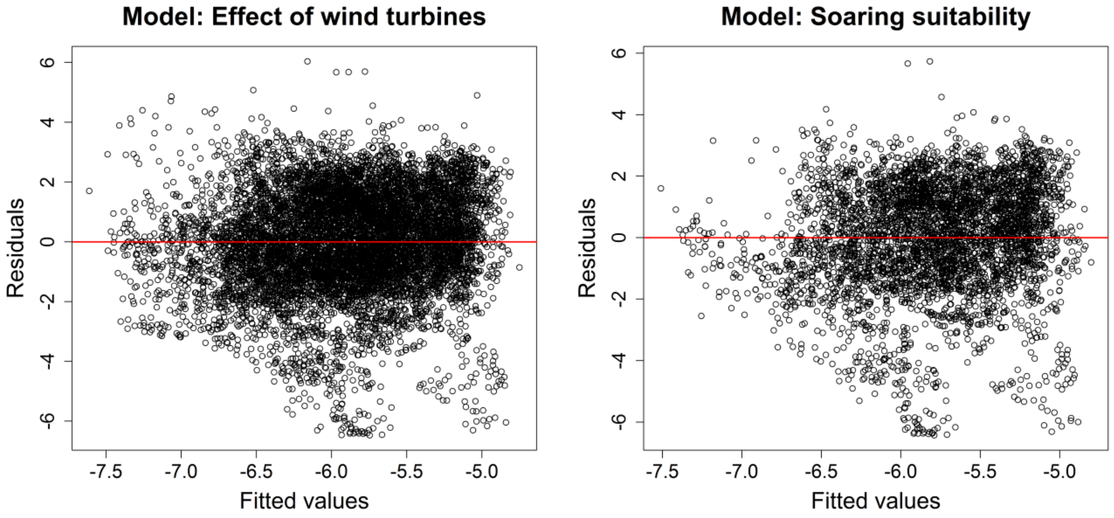

Figure S4. Diagnostic plots for the two models of this study (see Table 1 for further details on the models). In both cases, there is no pattern on the variance of the residuals along the fitted values that indicate problems of homoscedasticity.

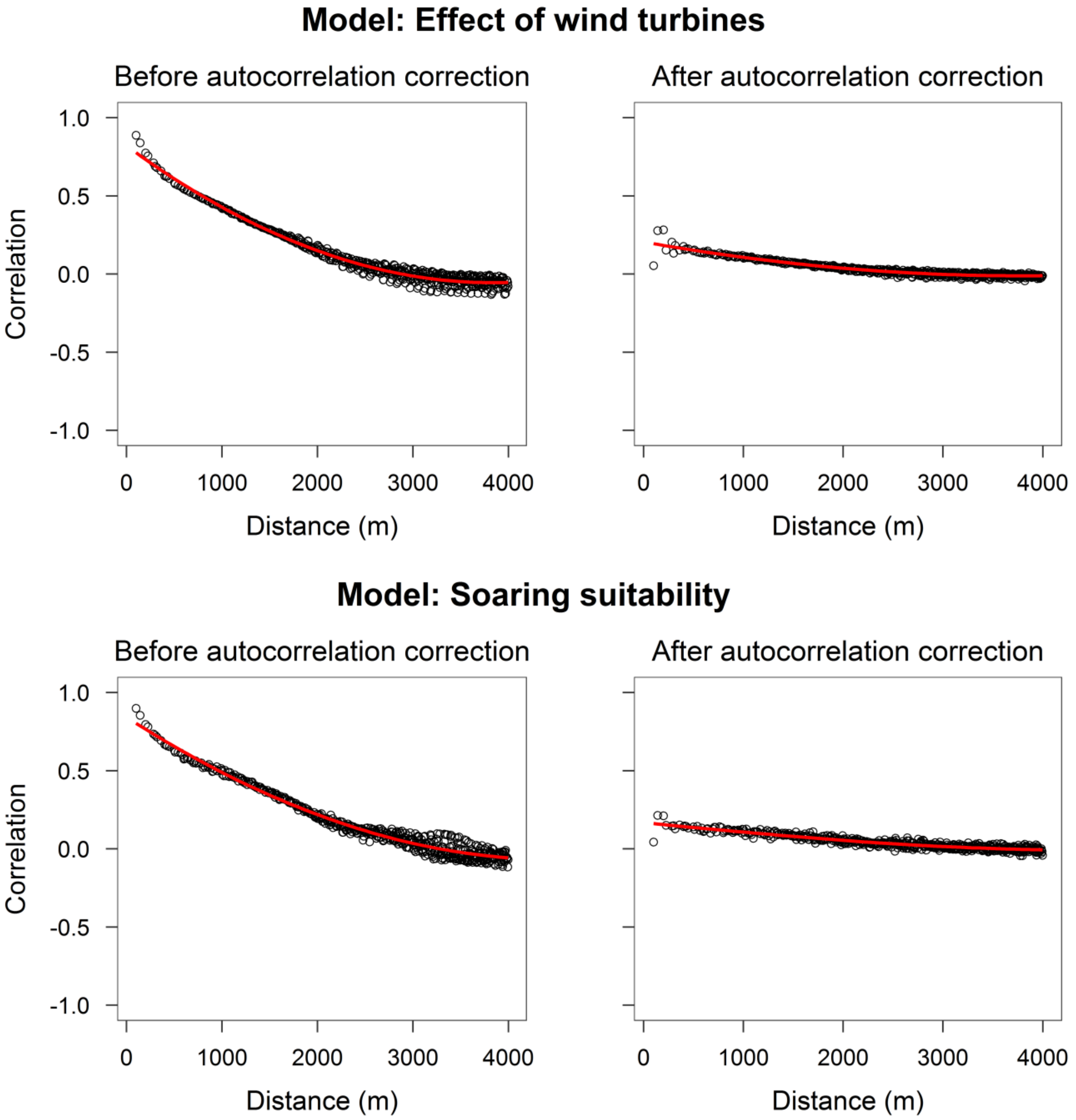

Figure S5. Spatial autocorrelation of the residuals for the two models of this study before and after being formulated with Gaussian spatial correlation structures (see Table 1 for specifications on the models and the methods section for details on the spatial correlation correction). Correlation values were computed with the function correlog of the R package ncf (Bjornstad, 2018). Trend lines in red are LOESS curves.

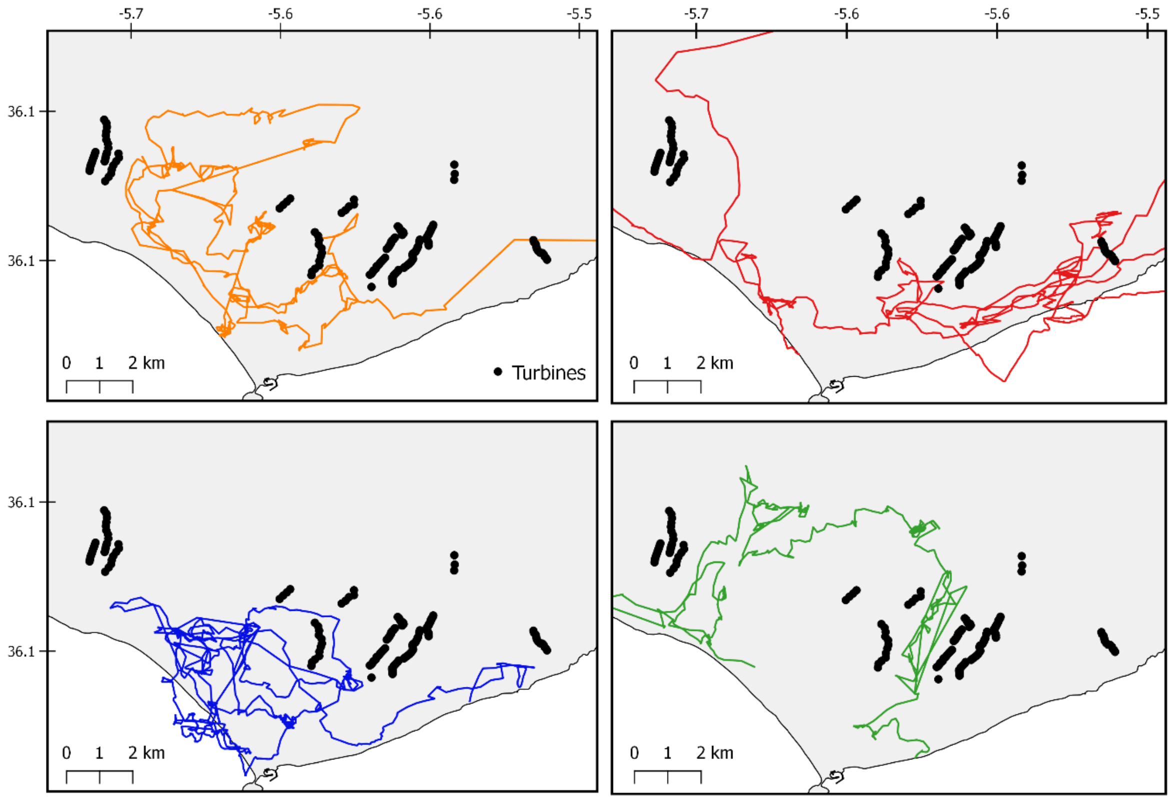

Figure S6. Examples of black kite GPS tracks recorded in the study area (Tarifa, Spain) during the post-breeding migration of 2012 and 2013, and the locations of the wind turbines. Birds were tracked with GPS-GSM dataloggers.

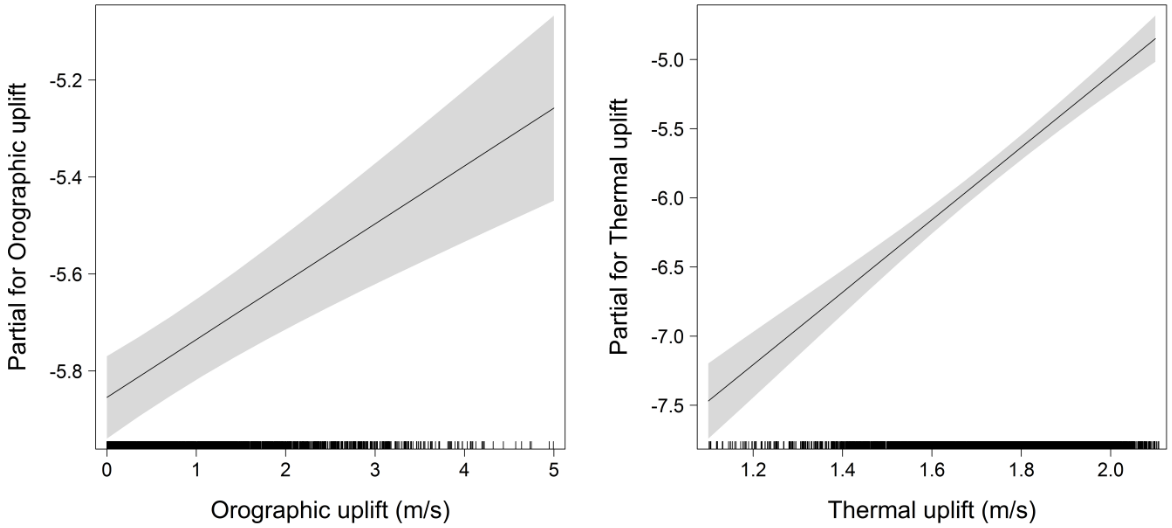

Figure S7. GLS model partial effects of uplift predictors on black kite UD (see model details in Table 1). Shaded areas represent 95% confidence intervals. Modelling dataset includes grid cells placed far away from the influence of wind turbines (between 1 and 2 km distance of the closest turbine, see methods for further details). Y-axis are represented on the scale of the response variable (i.e. log(UD)).

Table S1. Wind farms operating in the study area and their main features: total nominal power (MW), number of turbines, rated power (kW), hub height (m) and rotor diameter (m).

Wind farm	**Total nominal power (MW)**	**Nº turbines**	**Rated power (kW)**	**Hub height (m)**	**Rotor diameter (m)**
WF1	10,68	17	660/600	43,5/45/55	46/44
WF2	32	16	2000	57/64/75/85/98/114	71
WF3	42	21	2000	57/64/75/85/98/114	71
WF4	1,65	1	1650	60/78	66
WF5	36,9	90	410	25/31	33
WF6	2,42	3	1300/800/330	58,5/50/60/30	61/52/30
WF7	6	12	500	35	37

Table S2. Summary of tracking data from black kites fitted with GPS-GSM dataloggers in Tarifa (Spain) between 2012 and 2013: total number of tracking days and corresponding number of GPS fixes per bird, and the same variables for the data used for modelling purposes.

Bird ID	**Trackig period (days)**	**Total GPS fixes**	**Modelling period (days)**	**Modelling GPS fixes**
2	1	249	1	216
4	2	247	1	209
5	1	1568	1	1351
6	6	2346	1	230
7	2	991	1	723
8	4	4409	1	1138
9	1	1647	1	1015
11	6	2514	1	669
12	7	2637	2	1679
13	7	2217	1	549
15	2	110	1	83
16	4	1339	1	57
17	2	1095	2	835
18	2	496	2	186
19	4	1095	3	439
21	3	2583	2	1267
22	4	3572	2	2035
23	3	1209	1	813
24	2	467	2	367
25	3	1452	2	1230
26	3	919	2	533
27	3	667	2	163
28	8	1618	1	14
29	3	1762	2	1157
30	2	547	1	406
32	1	62	1	62
33	3	542	1	200
35	2	722	2	598
37	1	300	1	91
38	2	535	2	388
39	3	2041	2	1359
40	3	1412	1	760
41	2	116	1	47
42	2	489	1	237
43	3	975	2	257
44	3	1118	2	532
45	6	1749	3	552
46	5	1164	3	493
47	5	1226	2	455
48	11	1401	2	82
49	3	1336	1	523
50	2	871	1	706
51	4	1596	2	430
53	2	1860	1	822
54	2	578	1	379
57	2	165	1	55
58	1	458	1	425
59	4	2850	1	1413

Bird ID	Trackig period (days)	Total GPS fixes	Modelling period (days)	Modelling GPS fixes
60	2	866	1	409
61	5	1598	2	421
62	6	1876	2	350
63	7	3608	1	1542
65	3	4093	1	579
66	3	3308	1	1433
67	2	2143	1	1119
34b	3	1025	2	437
kite1	2	775	2	147
kite10	2	838	2	482
kite11	2	869	2	275
kite12	2	326	1	95
kite13	4	2502	2	60
kite14	3	1769	2	926
kite15	2	894	1	517
kite16a	1	324	1	48
kite16b	2	591	1	27
kite17	3	2455	2	1816
kite18	2	914	1	388
kite19	2	1038	2	738
kite2	1	454	1	270
kite20	3	3059	2	1807
kite21	2	953	2	614
kite22	4	1660	1	26
kite23	2	1175	2	750
kite24	3	1874	1	209
kite25	2	2981	1	76
kite26	1	1240	1	527
kite27	1	3449	1	1493
kite28	1	461	1	234
kite29	1	2319	1	386
kite3	2	780	2	165
kite30	1	1046	1	509
kite31	3	8638	1	251
kite32	2	2494	1	71
kite33	2	4075	2	691
kite34	2	3592	1	582
kite35	1	1629	1	342
kite36	2	3104	1	502
kite37	2	2445	1	609
kite38	1	2163	1	932
kite39	2	1768	1	504
kite4	5	2633	2	1011
kite40	1	1696	1	284
kite41	2	2019	1	34
kite42	2	2692	2	131
kite43	2	2741	1	109
kite44	3	2459	3	915
kite45	5	1992	4	739
kite46	1	212	1	41
kite47	3	2515	1	1635
kite48	4	2559	3	1528
kite49	4	1505	1	31
kite5	3	1753	1	833
kite50	4	2067	3	923
kite51	4	3547	2	955
kite52	2	601	1	84
kite6	1	1383	1	893
kite7	2	4252	1	166
kite9	2	772	1	34
logger102	4	1472	1	34
logger104	3	1327	3	756
logger106	4	1478	4	940
logger108	4	1833	4	784
logger110	4	3071	3	2047
logger113	3	834	3	458
logger114	4	1625	3	865
logger119	4	1582	2	872
loggertest	4	2007	3	793
p1	1	129	1	121
p10	2	1163	2	767
p11	13	2074	2	68
p12	3	1564	2	797
p13	4	1619	1	73
p15	1	83	1	79
p182012	4	3932	4	1300
p182013	4	1688	1	449
p19	2	492	1	398
p26	7	3787	1	764
p28	2	1570	1	568
p3	3	3819	2	1342
p5	3	1651	1	1018
mean	3,0	1697,6	1,6	594,1
SD	1,9	1212,5	0,8	483,1

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Chapter 6

Dispersal movements and habitat suitability of a globally threatened raptor revealed by high resolution tracking

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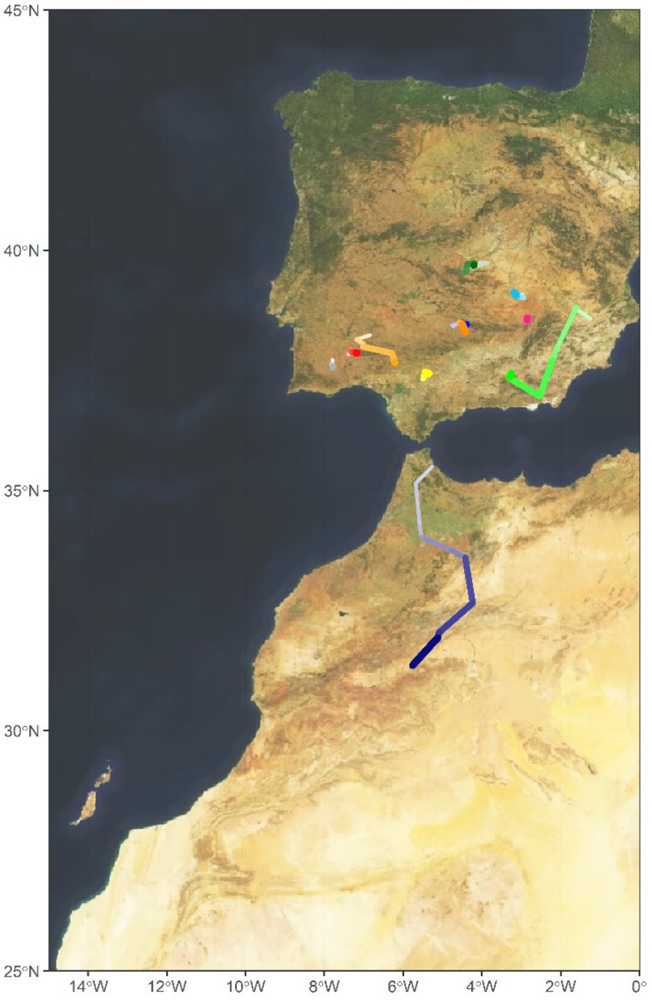

Dispersal movements and habitat suitability of a globally threatened raptor revealed by high resolution tracking

ABSTRACT

Advances in movement ecology, mainly new tracking devices with high spatial and temporal resolution, are improving our ability to study highly mobile and erratic life-cycle periods or animals, and to propose more suitable conservation measures. In this work we used GPS-GSM tags to study the spatial and temporal movements patters, and the habitat suitability of immature Iberian imperial eagles. We followed 12 birds for on average for 243 days during the dispersal phase, and collected ca. 38.000 bird locations. Brownian Bridge Movement Models were used to identify settlement areas, and Maxent models were applied to predict suitable areas for non-territorial birds in the Iberian Peninsula. Birds' travelled mainly in the centre and southern part of Iberia, where there are higher levels of habitat suitability for the species, and one eagle even crossed the Strait of Gibraltar to the north of Africa. Young eagles settled for most of their immature life (ca. 90%), typically travelling between different settlement areas in rotation. Settlement areas located at a mean distance of 208 km from their birth nest. Birds' exhibited a sedentary behavior during the coldest months, performing fewer movements than during the rest of the year. Spatial distribution models show that birds prefer landscapes dominated by agroforestry systems and shrublands, with a smooth topography and lower levels of the aridity index. Our results suggest that the immatures eagles are travelling longer and settling in areas located further away from their origin than earlier known, maybe because the species population is increasing and competition is forcing birds' to find alternative locations. This may also be responsible for the expansion of the range of the species, including the breeding range. Our predictive model showed a good fit, and can help to guide future management actions focusing on this species.

Keywords: *Aquila adalberti*; Spanish imperial eagle; movement ecology; settlement areas; spatial ecology; floaters

1. INTRODUCTION

Movement ecology is a rapidly growing and novel science that is enabling significant advances in knowledge on how species move and use space across their range, ultimately improving our ability to preserve and manage wild populations (Allen and Singh, 2016). The distribution of a species can be dynamic in space and time, with individuals having regular and predictable movements, such as migrations, or erratic and resource-driven nomadism (Runge et al., 2014). Changes in the way space is used can occur during the life-span of a single individual. Long-lived raptors, for example, are usually territorial during the breeding season and show fidelity to their breeding location, but can have a long dispersal and transient period before establishing a territory (Newton, 2010). Knowledge on how species use the landscape and how this changes through the environment or individual-context (e.g. age, reproductive state, etc.) can be of major relevance to outline sound conservation strategies.

The Iberian imperial eagle *Aquila adalberti* is a large non-migratory raptor, endemic to the western Mediterranean region. Currently, it breeds exclusively in Iberia (Spain and Portugal), with less than 500 breeding pairs (Birdlife International, 2017; Sánchez et al., 2008). Although its population is presently increasing, the species is one of the rarest raptors in the world and is classified as globally Vulnerable (Birdlife International, 2017; Sánchez et al., 2008).

The historical range of the Iberian imperial eagle contracted ca. 90% by the mid-20th century (Deinet et al., 2017), when it was close to extinction, with only 30 breeding pairs remaining in the wild during the 1970s (Luis M. González et al., 1989; Sánchez et al., 2008). Human persecution and the massive decline of its' main prey, the European rabbit *Oryctolagus cuniculus* (due to viral diseases), explains the decline of the species (Sánchez et al., 2008). The eagle population has been recovering since the end of the 20th century (Ortega et al., 2009), which can partially be attributed to successful conservation actions addressing key threats (González and Oria, 2004).

The juveniles of this species, like in other long-lived raptors, have a long dispersal period before exhibiting a territorial and breeding behavior, which usually starts when birds are 4.5 years old (González et al., 2006). During dispersal, the immature eagles (or floaters) make long-distance trips away from the natal area and use several temporary settling zones, i.e. settlement areas, spending their non-adult life travelling between them (Ferrer, 1993; L.M. González et al., 1989). The range of these non-breeding animals tends to be similar to the breeding range of the species, although a few individuals have made forays into North Africa, which was part of the historical breeding range of the species but where it does not presently nests (González et al., 2008). Young eagles tend to settle in open landscapes, often dominated by *Quercus* sp. agroforestry systems and with reduced human disturbance (Ferrer and Harte, 1997). However, the environmental and climatic drivers underpinning the selection of these settlement areas are still mostly unknown.

The dispersal stage is long and sub-adult birds suffer higher mortalities rates than adults (González et al., 2007). Therefore, temporary settlement areas should be considered key locations for the conservation of the Iberian imperial eagle (Ferrer and Harte, 1997; Penteriani et al., 2005). During this period, young eagles are particularly vulnerable to electrocution with power lines poles (González et al., 2007), and mitigating such non-natural mortality is considered of high priority for the conservation of the species (González et al., 2007; López-López et al., 2011; Sánchez et al., 2008).

Detailed knowledge about settlement areas can guide the management actions focusing the species, which is particularly relevant when the population is increasing and the range of the species is expanding. New tracking technologies can contribute to understand the use of the landscape by dispersing eagles with high spatial and temporal resolutions. Previous studies of immature Iberian imperial eagle were conducted mostly using VHF technology, which, although provide valuable information, has a limited spatial and temporal resolution (Ferrer, 1993; Ferrer and Harte, 1997; González et al., 1989; Muriel et al., 2016). Therefore, in this study we use state-of-the-art GPS tracking to (i) describe the movement patterns of the immature Iberian imperial eagles in the months after leaving the parents' territories and (ii) reveal the patterns of spatial and temporal use of the settlement areas. We also use tracking data to (iii) identify areas that are suitable for the settlement of the species in the Iberia peninsula, which is the first attempt to model the species distribution during the dispersal period at such spatial scale.

2. MATERIAL AND METHODS

2.1. CAPTURING, TAGGING AND TRACKING

We monitored a total of 12 birds from 2014 to 2018 (Table 1). Eleven were juveniles, born in five nests in Portugal (Idanha-a-Nova, Mourão and Mértola regions; Ramos et al. 2019) and one was an immature dispersing in the southern part of the country. The juveniles were tagged in the nest before the first flights attempts (49-55 days old) and the immature, aged 18-24 months, was captured in a baited clap trap. Birds were fitted with GPS/GSM solar tracking devices from Movetech Telemetry (87 × 40 mm and 78g; http://movetech-telemetry.com), using a backpack-style breakaway harness of Teflon, weighing less than 3% of the birds' mass. Transmitters were programed to record a GPS position every 20-60 minutes, and data were uploaded to an online server via the GSM network.

Tagging procedures were undertaken by the Portuguese national authority for nature conservation, Instituto da Conservação da Natureza e das Florestas and Dirección General para la Biodiversidade/Ministerio de Medio Ambiente from Spain (permits: 148/2014/CAP, 391/2015/CAP, 684/2016/MANUS and 170/2017/CAP).

Table 1. Description of movements, number and distance between settlement areas of immature Iberian imperial eagles, during the dispersal period.

Bird	Settlement tracking period (days)	GPS fixes	Minimum distance travelled per day (km)	No. settlement areas	Distance between settlement areas and nest (km) mean (range)[1]	Distance between settlement areas (km) mean (range)[1]
Male 1	32	551	70	2	125 (51-198)	159
Female 4	47	752	60	2	195 (8-383)	391
Male 6	53	969	91	5	406 (3-567)	312 (31-571)
Male 5	128	1840	48	5	141(6-234)	145 (27-239)
Male 4	178	2147	56	7	214 (2-426)	198 (50-426)
Female 2[2]	183	2322	35	3	-	252 (62-377)
Male 7	196	3096	25	5	140 (54-216)	111 (20-179)
Male 3	348	4595	43	6	239 (10-631)	326 (66-687)
Female 1	389	5995	51	5	108 (9-180)	155 (70-256)
Male 8	408	7345	33	3	128 (12-309)	311 (54-318)
Female 3	410	5600	64	4	258 (10-433)	231 (67-430)
Male 2	542	10336	52	12	330 (9-678)	341 (37-930)
Total (x̄)	243	3796	52	5	208 (2-678)	244 (20-930)
Males (x̄)	236	3860	52	6	215(2-678)	238(20-930)
Females (x̄)	257	3667	53	4	187(8-433)	259(62-440)

[1] distance was measured in relation to the centroid of the settlement area (kernel 90% UD)

[2] immature bird that was tagged with 18-24 months

2.2. BIRDS MOVEMENT DYNAMICS

We filtered our tracking database keeping a single location per hour for each eagle, to get a uniform data collection frequency across bird. We also excluded locations during the dependence period, i.e. when juveniles returned to overnight in the territory of their parents (Ferrer, 1992), which in our tracked birds occurred until they were 93 to 153 days old (Ramos et al., 2019). One of the males exhibited territorial behavior earlier than usual, i.e. was highly faithful to an area and was repeatedly seen with a female. Data on this bird was only included until the last displacement movement (ca. 26 km distance travelled).

Brownian bridge movement models (BBMM; Horne et al. 2007; Kranstauber et al. 2012) were used to identify the settlement areas used during the dispersal period. BBMM uses information on the sequence of locations of tracking data, allowing for the identification of highly used areas and also the movement corridors between them. The BBMM were implemented in R (R Core Team, 2016) with the package move (Kranstauber and Smolla, 2017), using a window size of 12 locations and a margin of three locations, following the recommendations of Kranstauber et al. (2012).

We defined settlement areas has the areas more intensively used by birds during the dispersal period, and used utilization distribution (UD) of 90% to outline the boundaries of settlement areas (Figure S1). Additionally, we only considered an area as a settlement area if the eagle occupied it for a continuous period over 3 days.

To characterize the movements across time we calculated the daily distance between each overnight location and the nest, for the eleven eagles tagged in the nest. To reduce the variation in the data and simplify the analysis, we present such variable based on the median of a 10-days window.

2.3. HABITAT SUITABILITY MODELLING

We selected a set of seven, not highly correlated ($r < 0.70$), environmental and climatic predictors to model the potential habitat suitability of the Iberian imperial eagles' during the dispersal period (Table 2). These predictors were chosen based on previous knowledge of the species ecology, mainly the fact that the species is associated to the Mediterranean climate, prefers agroforestry systems and avoids areas with high human disturbance and paved roads (Ferrer and Harte, 1997; González et al., 1992, 1990).

For modelling we used MaxEnt, a machine-learning algorithm that models the relationship between species presence and associated environmental data to predict the probability of species occurrence across the landscape (Elith et al., 2011; Phillips et al., 2006). This analysis was performed for the whole Iberia peninsula, using a UTM 10 km cell grid. Cells coinciding with a settlement area (as identified by the BBMM models, above described) and that simultaneously had eagle GPS locations were included in the model as presences (n=358). As the eagles' movements and the areas overflown by the birds conditioned the selection of settlement areas, as the sampled birds could not have selected areas that were not surveyed, we included a bias layers to guide the selection of the background points (n = 5,000). This was achieved through the use of a density map of all the birds' GPS fixes, based on the number of GPS fixes in a 250 km buffer. Such approach allowed us to account for our sample selection bias (Phillips et al., 2009), by selecting a higher number of background points in areas overflown by the birds. The model was fitted using only linear, quadratic, and product features, in order to produce more interpretable model responses (Merow et al., 2013).

The model was evaluated through the area under the receiver operating characteristic curve (AUC), mean and standard deviation values of 50 replicates, and the relative contribution of each predictor was estimated with the jackknife test. The MaxEnt model was built in R (R Core Team, 2016), using the dismo package (Hijmans et al., 2016).

Table 2. Description of the predictor variables used to model the habitat suitability of the Iberian imperial eagle at settlement areas, during the dispersal period.

Variable	Description	Source
Aridity	Global Aridity Index quantify the precipitation availability over atmospheric water demand (30 arc second spatial resolution). The index is lower in more arid conditions.	Global Aridity and PET database (Trabucco and Zomer, 2009; Zomer et al., 2008)
Roughness	Measurement of terrain heterogeneity generated in R using the raster package (Hijmans and Van Etten, 2014), calculated using a 30m spatial resolution digital elevation model	ASTER Global Digital Elevation Model (NASA JPL, 2009)
Roads	Total length of paved roads (km)	OpenStreetMap (Haklay and Weber, 2008)
AgroForest	Proportion of agro-forestry areas (CLC code: 244) (100m spatial resolution)	Corine Land Cover (CLC) 2012
Forest	Proportion of forestry areas (CLC codes: 311, 312, 313) (100m spatial resolution)	
Open	Proportion of open areas: dry or irrigated temporary crops, natural grasslands and pastures (CLC codes: 211, 212, 213, 231, 321) (100m spatial resolution)	
Shrubs	Proportion of areas with shrubs (CLC code: 244) (100m spatial resolution)	

3. RESULTS

3.1. SPATIAL MOVEMENT PATTERNS

We obtained a total of 2.914 tracking days of the Iberian imperial eagles during the dispersal period, corresponding to a mean value of 243 days (SD = 163, range = 32-542) per bird (Table 1). Birds travelled ca. 53 km per day throughout both Portugal and Spain, mainly in the center and southern part of Iberia (Figure 1). One of the eagles (male 2) crossed the Strait of Gibraltar to the north of Africa in October, traveling ca. 3.700 km from Spain to Morocco, Algeria, Mauritania and Western Sahara (the distance was measured from the overnight location of the last day in Spain before the bird crossed to Africa, until we arrived in the settlement area in Morocco), and after settling down in Morocco, moved back to Iberia (Figure 1, Table 1).

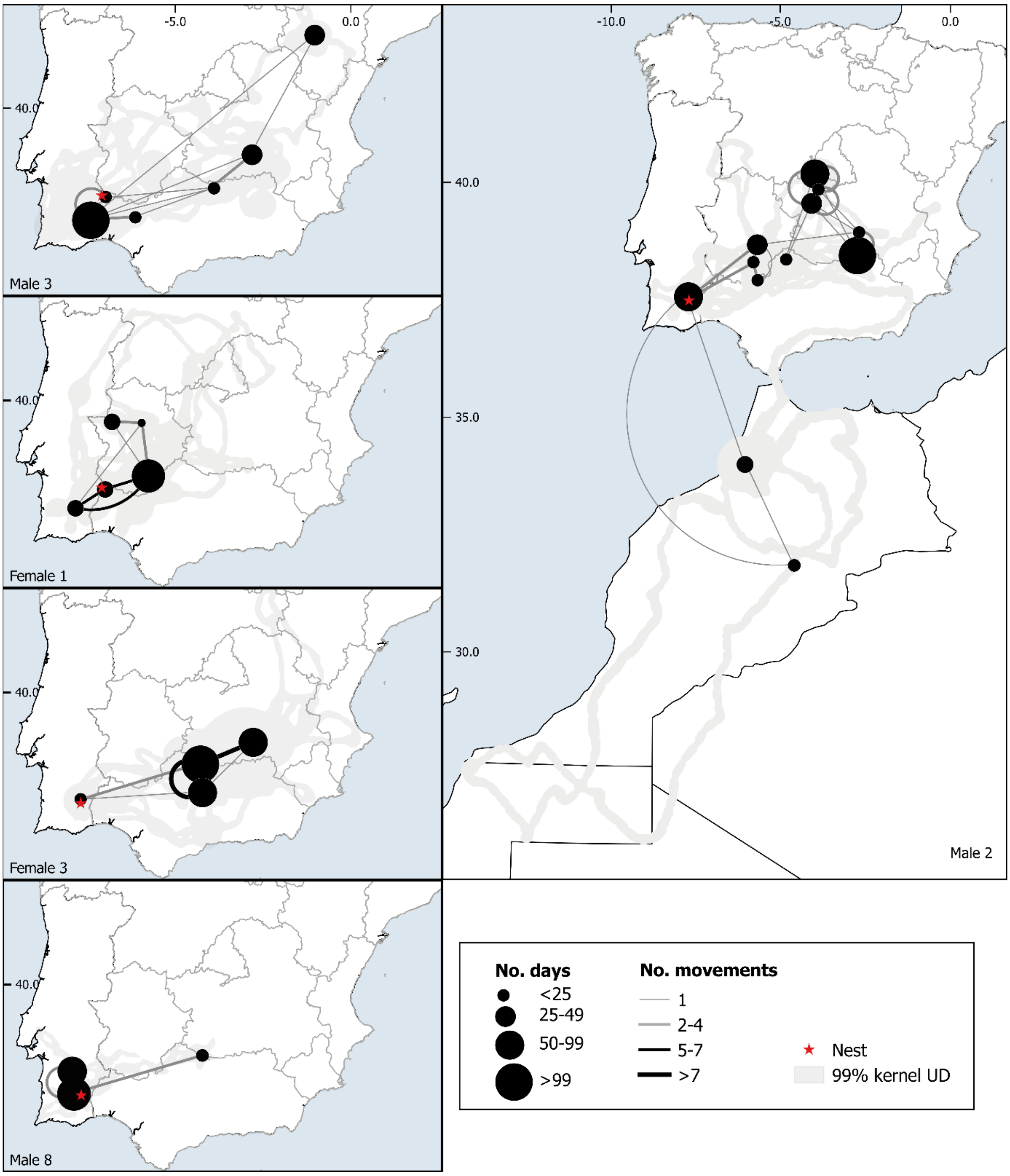

Figure 1. Settlement areas (circles represent the centroid of settlement areas) and total number of days spent in each one (circle size), for the five Iberian imperial eagles tracked for more than 300 days during the dispersal period. The thickness of the black lines is proportional to the number of movements between settlement areas (proportional to line width) and the grey area represents the movement corridors used by the birds (kernel 99% utilization distribution (UD)).

Most immature Iberian imperial eagles used different temporary settlement areas in rotation, which were located at a mean distance of 208 km from their birth nest (range 2 - 678 km) and 244 km from each other (range = 20-930; Table 1). Settlement areas were usually located on or adjacent to known breeding areas within its range in Iberia. However, two birds used particularly distant locations in the extremes of the birds' range, one in the Rabat region of Morocco and the other nearby Zaragoza, Spain

(Figure 1 and Figure 2). Some settlement areas were used by several individuals. In Portugal the region of Baixo Alentejo (mainly Castro Verde and Mértola) was used by all twelve birds monitored in this study. In Spain, Zafra (Badajoz province) was used by five individuals, Campo de Montiel and Sierra Morena (both in Ciudad Real province) were used by four individuals and finally an area south of Toledo was used by three individuals.

The eagles that were tracked for over 300 days spent ca. 88% of their dispersal period inside the settlement areas, although the use of such locations varied considerably between individuals (Figure 1, Table 1). Some birds used a lower number (<4) of settlement areas and settled there for longer periods, e.g. female 1 and male 8 spent over 60% of their tracking period in a single area. Other birds used from 5 to 12 settlement areas, traveling more frequently, but spent the majority of the tracking period in three different areas (53%, 65% and 73% for male 2, female 3 and male 3, respectively).

3.2. TEMPORAL MOVEMENT PATTERNS

Birds used, on average, 2.2 (SD = 1.3; range = 1-7) settlement areas per month (Figure 3). In the beginning of the dispersion period they seemed to be exploring the range and in the first month of independence they used 2.8 (SD = 1.3; range = 1-7) settlement areas. In later months they mostly revisit previously known settlement areas, and only 0.2 (SD = 0.6; range = 0-3) new areas were visited each month. In the beginning of the dispersal period male and female eagles tend to use areas at similar distances from their natal location, but nine months after emancipation and onwards, i.e. during the second year, females tend to use areas further away (Figure 4).

Figure 5 shows that during most of the year birds moved quite frequently between settlement areas. However, in the coldest months, from late November to the end of February, they all had a very sedentary behavior, performing far fewer movements than during the rest of the year (Levene's Test for Homogeneity of Variance: F-value = 632.55, Pr(F) < 0.000).

Some individuals return to their parents’ territories months after their independence (Figure 5). Male 2, for example, returned five, seven and eight months after emancipation, while female 3 visited her natal location nine months after dispersing.

Two of the male birds died during the tracking period, one from illegal poisoning in Andalusia and a second by electrocution in a distribution power line in Extremadura. A male (male 8) started to exhibit territorial behavior unusually early, during its second year, and we were able to confirm in the field that he was actively defending a territory and a nest in the company of an adult female, ca. 3,5 km from its birth nest.

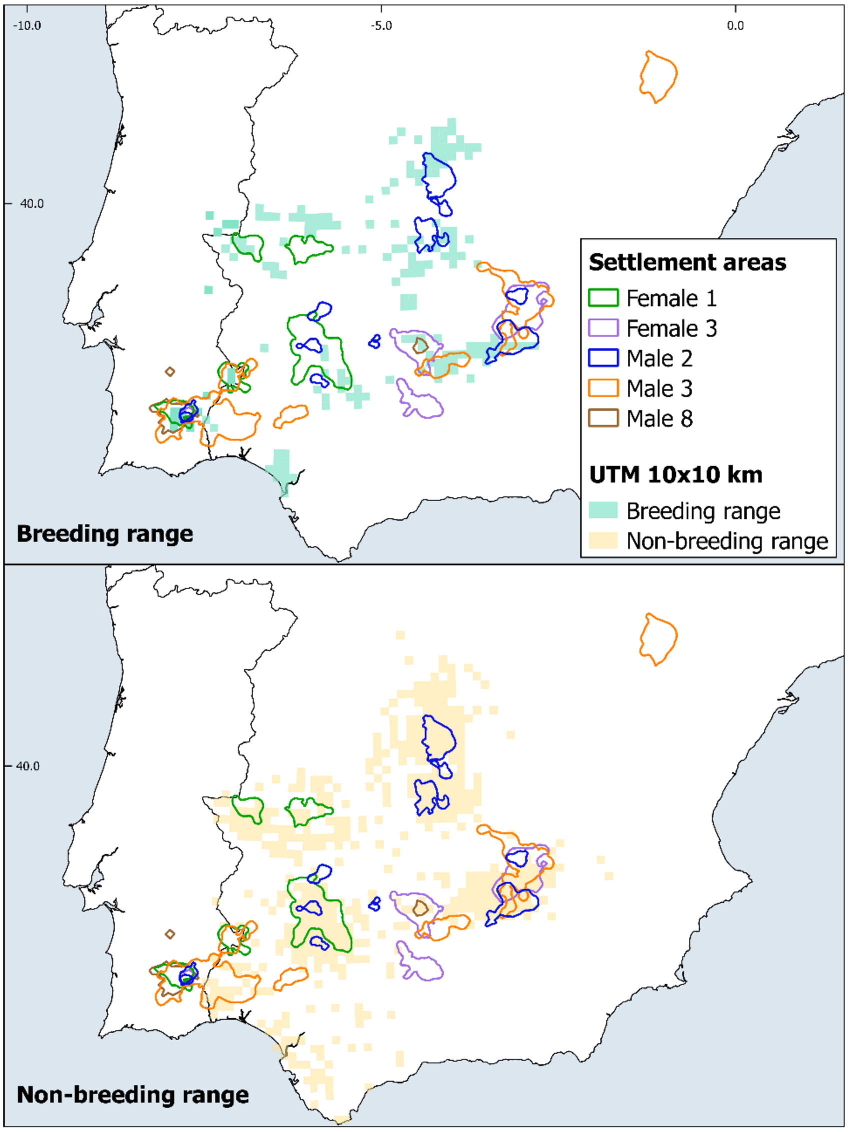

Figure 2. Settlement areas (kernel 90% utilization distribution (UD)) of the 5 Iberian imperial eagles tracked for more than 300 days during the dispersal period; species breeding range in Spain (Martí and Del Moral, 2003) and Portugal (C. Carrapato, *pers. Data; C. Pacheco com. pess.*) and non-breeding dispersion previously described (González et al., 2008).

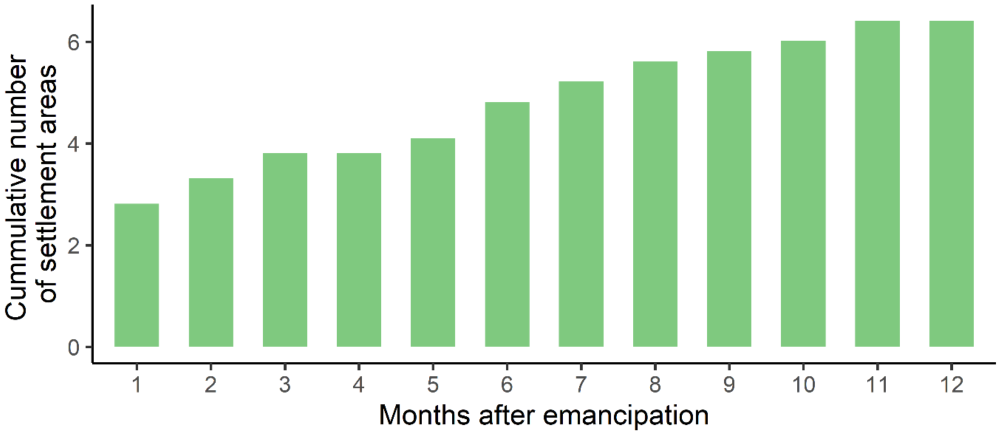

Figure 3. Cumulative number of settlement areas used by young Iberian imperial eagles.

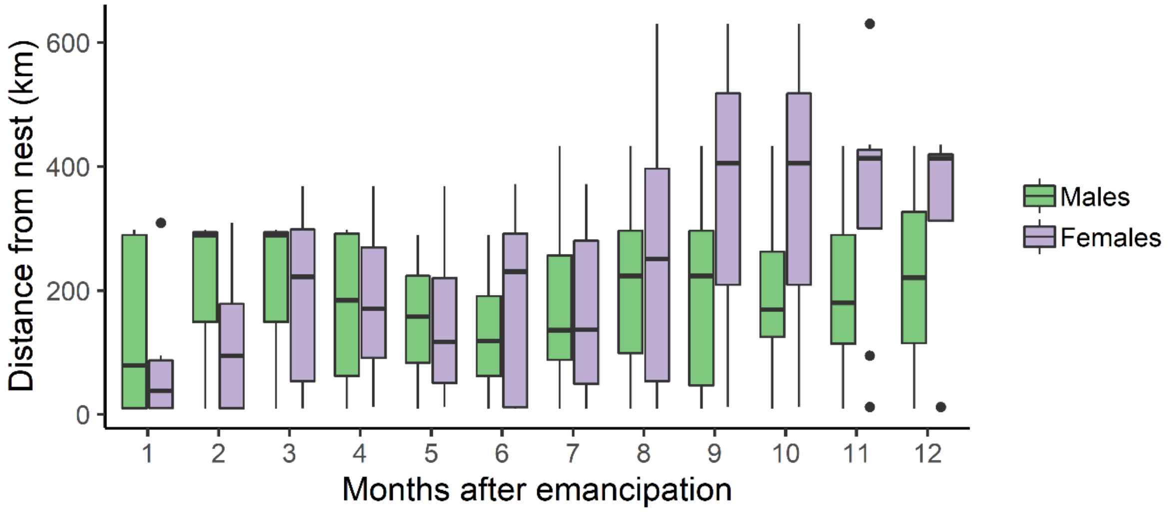

Figure 4. Temporal variation of the distance between the settlement areas and the birth nest (km) for male and female birds. Only towards the end of the first years after emancipation females start settling further than males.

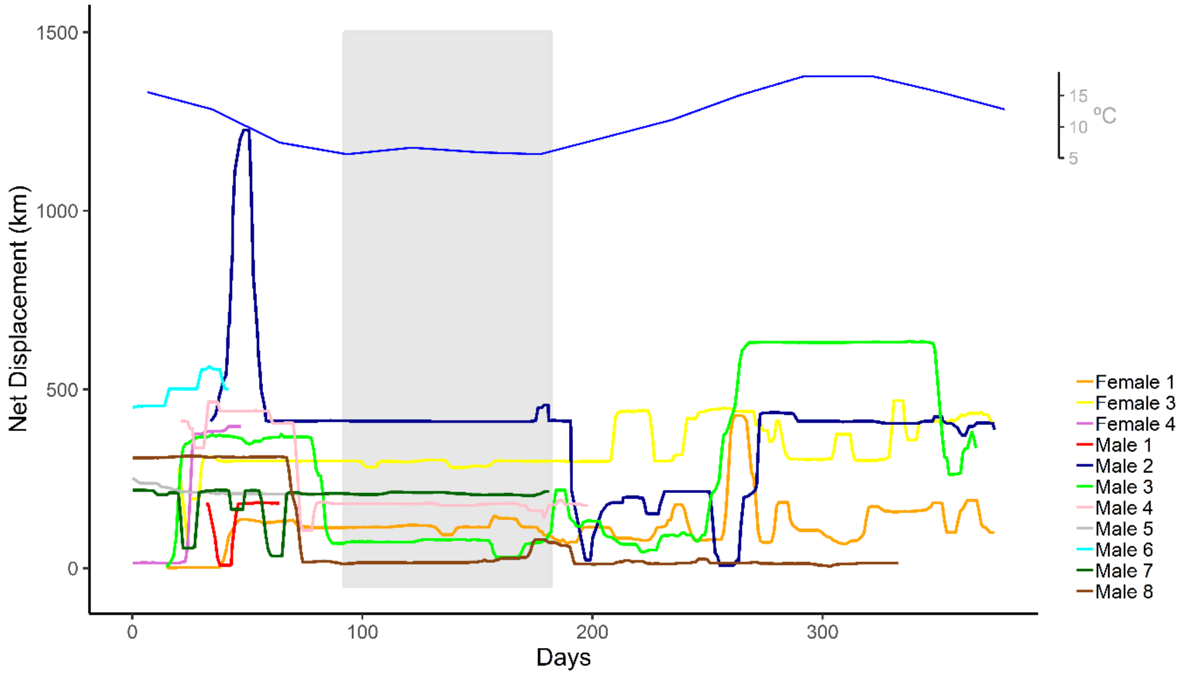

Figure 5. Median distance from nest (km) measured in a 10-days window per bird tracked and mean monthly minimum temperature (measured in Spain during 2016; AEMET 2019). Day 1 represents 1st September. Grey areas represent period between December and February, the coldest months.

3.3. HABITAT SUITABILITY MODELLING

The MaxEnt model showed a good adjustment to our data (AUC = 0.842 ± 0.048). The probability of Iberian imperial eagles' presence during the dispersion period increases with lower levels of the aridity index (i.e. lower levels of water availability, see Table 2), decreases with terrain roughness, and increases with cover by agroforestry systems and shrubs (Figure 6). The most suitable areas for the dispersing eagles are located in central and southwest of the Iberian Peninsula, while its north and northwest are unsuitable (Figure 7).

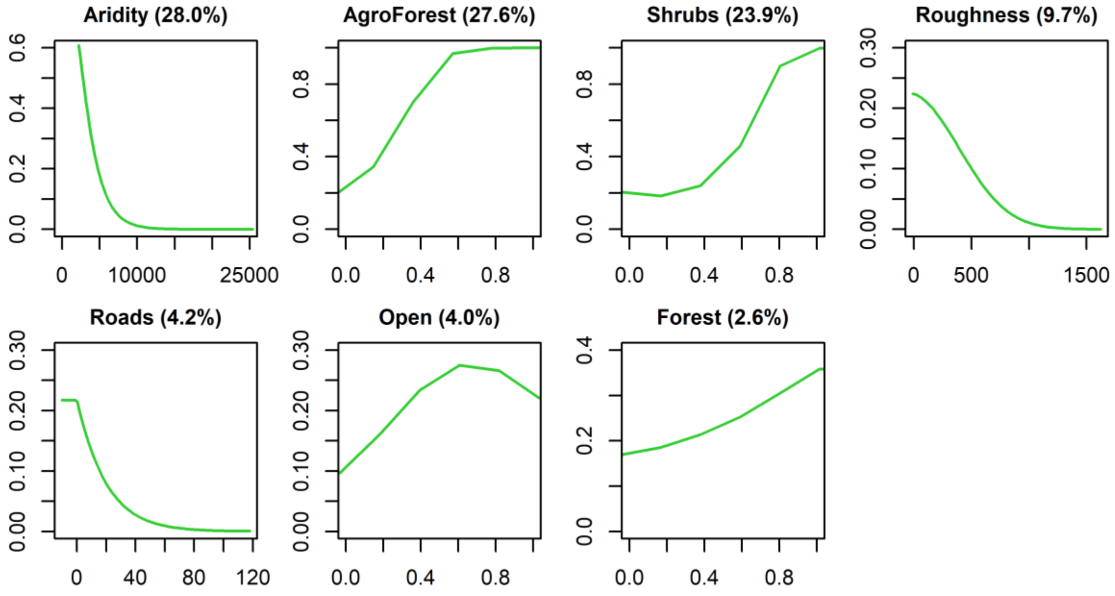

Figure 6. Response curves for the predictors used to model the habitat suitability for the settlement areas of Iberian imperial eagle in Iberia.

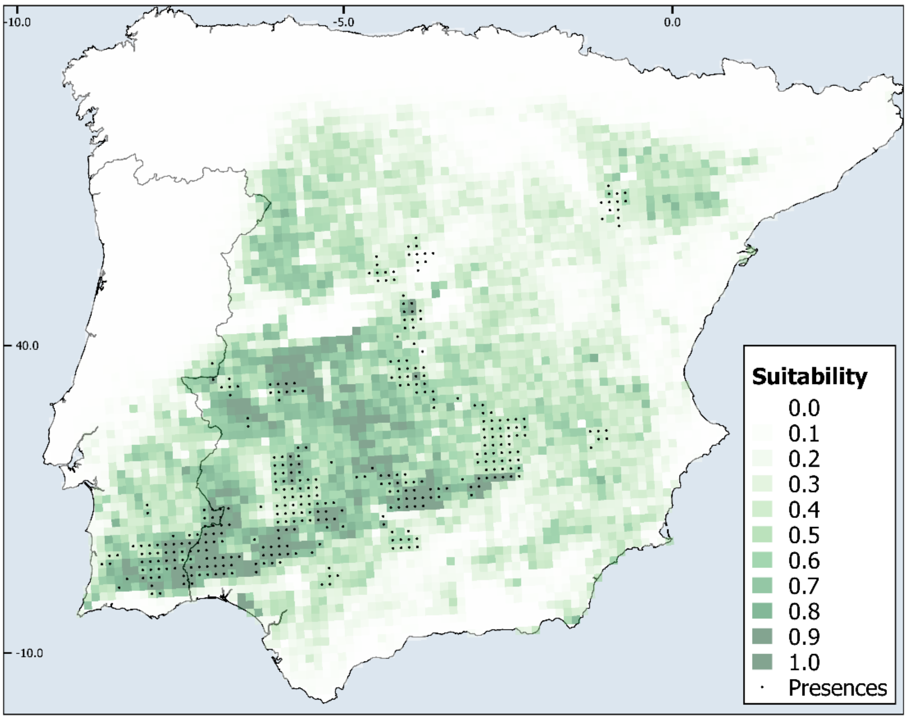

Figure 7. MaxEnt Spatial predictions (UTM 10 km grid) for the habitat suitability for settlement areas of Iberian imperial eagle in Iberia and cell grids used as settlement areas by the 12 tracked birds' (presences).

4. DISCUSSION

4.1. SPATIAL MOVEMENT PATTERNS

Immature Iberian imperial eagles dispersed throughout most of central and southern Iberia and North Africa, settling in specific areas for variable periods. All the birds used several settling areas, but while some spent most of their time in a single area others moved more frequently and divided their time more evenly across multiple settlement areas. Such variable strategies may be related to the availability of food resources at each location, as raptor distribution during pre-adult life is highly related with such factor (Caro et al., 2011; Mañosa et al., 1998).

In general, settlement areas were located within the breeding range of the species (Figure 2). This result suggests that the broad scale habitat requirements for dispersing birds are similar to those of nesting animals, or that social information and conspecific cueing plays an important role in the selection of settling areas by young eagles (Muriel et al., 2016). However, it is worth noting that this pattern was observed at a relatively coarse spatial scale and may not occur at finer scales, because it is unlikely that immature birds settle within adult territories (Ferrer, 1993; Ferrer and Harte, 1997).

The birds tracked in this study (2014 to 2018), made longer movements and settled further from the natal locations ($\bar{x}$ = 208 km) than the birds from Doñana ($\bar{x}$ = 84 km) studied from 1986 to 2009 (Muriel et al., 2016), or birds from southwest Spain ($\bar{x}$ = 162 km) studied from 1984 to 1986 (L.M. González et al., 1989). One possible explanation for this difference is that the recovery of the eagle population may be increasing intraspecific competition, forcing young birds to settle further from their nest. In fact, interference competition is known to be a major driving force limiting space use and distribution in top predators (Linnell and Strand, 2000; Martínez et al., 2008; Rebollo et al., 2017). Such interactions may be promoting the expansion of the species range and could explain the use of settlement areas in regions that are presently not used by breeding adults (e.g. Zaragoza, Figure 2). This hypothesis is supported by the establishment of the breeding nucleus of Mértola - Castro Verde (southern Portugal), an area that does not result from the expansion of a preexistent nucleus; it was first used by juveniles and immatures eagles, before the firsts breeding attempts (Catry et al., 2010). However, the largest distances for the settlement areas found in our study can also be related to the use of GPS tracking devices, which offer more reliable tracking and unlimited spatial range for data collection, when compared with the radio-transmitters used in the previous studies.

4.2. TEMPORAL MOVEMENT PATTERNS

The first days and weeks after emancipation are likely key for the young eagles, because during them the birds gather invaluable information about potential settlement areas to be used in the forthcoming months (Figure 3). In fact, some of this information may have been acquired before emancipation, during the pre-emancipation exploratory flights, when Iberian Imperial eagles juveniles can fly up to 441 km away from the nest (Ramos et al., 2019).

While we did not observe gender differences in range during the eagle's first year, in their second year of life females moved to areas further away from the natal region (Figure 4). Muriel et al. (2016) described a similar pattern in birds from southern Spain, but González et al. (2006) found no differences between males and females. Such variable findings seem to support the hypothesis that the Iberian imperial eagle is a philopatric facultative species, which tend to recruit within or close to the natal population, while some individuals emigrate to other breeding nuclei according to the metapopulation structure (Muriel et al., 2016). Such hypothesis is supported by the fact that both male and female immature birds regularly visit their natal territory, as observed in this study and by Muriel et al. (2016), possibly in search of vacant territories (Ferrer, 1993). What is not yet totally clear, because of the relatively small sample size of the existing studies, is if the species is a female-biased disperser (i.e. males are more philopatric than females), like most known birds species (Greenwood, 1980).

We were able to confirm a philopatric behaviour for one of the tracked male eagles. As described above, male 8 (Table 1) showed a territorial and breeding behaviour during its second year, establishing a territory ca. 3,5 km from its origin natal area, after having used distant settlement areas (62 and 309 km), and having returned twice to its natal territory.

The consistent sedentary behaviour found in all tracked individuals during the coldest months (late November to February) is a novel and unexpected finding. It suggests that the Iberian imperial eagle strongly depends on thermal uplifts to make long distance flights, which are less frequent and weaker during this time of the year. Terrestrial soaring birds rely on orographic and thermal uplift to travel long distances with a low energetic cost (Pennycuick, 1975). Uplift formation depends on the interaction of local weather conditions with the underlying landscape. During the winter, thermal uplift is expected to be low, as it is formed when the solar radiation heats the land surface, but orographic uplift should be higher as it is moulded by horizontal winds in slopes (Kerlinger, 1989). It is known that climacteric conditions may force soaring birds to interrupt their migratory journey for some hours or even days (Allen et al., 1996; Miller et al., 2016), but the absence of exploratory movements of the immature eagles for weeks or even months is a major behavioural change. This temporary sedentary behaviour may have important consequences, as birds may be restricted to an area with limited food resources during a season with shorter days and, therefore, reduced time to forage.

4.3. HABITAT SUITABILITY MODELLING

This study was the first attempt to model the Iberian imperial eagle distribution during the dispersal period at the scale of Iberia. Suitable habitats for dispersing eagles are associated to the Mediterranean region of Iberia, in the center and south of the Peninsula, where agroforestry systems dominated by *Quercus* sp. and shrublands are present in areas with a smooth topography. Beyond the known range for the species (Figure 2), the model also predicts high suitability in the Aragón region (Northeast Spain), where male 3 settled for ca. three months, in western part of Castilla y León province of Spain and in southern Portugal. Our results are in accordance with the known general habitats requirements of the species (Cabral et al., 2005; González et al., 2008; González and Oria, 2004) and with the results of studies of the immature eagles (Ferrer and Harte, 1997). However, we did not find a negative effect of paved roads as previously described by Ferrer & Harte (1997), probably due to the distinct spatial scale used across studies. Higher suitability levels were also scored in areas that traditionally have higher densities of European rabbit (Virgós et al., 2007), the main prey of the Iberian imperial eagle (Ferrer and Negro, 2004; R. Sánchez et al., 2008), however, there is presently no data on European rabbit abundance to add this variable to the models at this scale.

Our model showed a good fit, hence the generated potential suitability map can help to spatialize priority areas for management actions focusing on the immature birds of this species.

4.4. CONSERVATION IMPLICATIONS

The conservation of the Iberian imperial eagle depends on factors that include the preservation and improvement of their habitat, mainly the increase of the availability of the European rabbit and the reduction of the relatively high anthropogenic mortality rate (Ferrer and Negro, 2004; González et al., 2007; González and Oria, 2004).

Temporary settlement areas are of great importance, as young eagles spend ca. 90% of their time there and, in some cases, seem to be forced to stay in a single area during the coldest months. Therefore, settlement areas should be considered a priority for the conservation of the species, as previously pointed out by Ferrer & Harte (1997), and predictive cartography, like the one produced in this study, may help the identification of such priority locations. Additionally, there is a strong relation between the habitat and spatial areas used by adult and immature eagles, at least at broader scales, so the knowledge of settlement areas can inform on potential new breeding locations for the species. The results of our study suggest that the region of Aragón may be a future breeding area for the species, as it has high levels of habitat suitability for immatures and one of the tracked birds settled there.

The Iberian imperial eagle is highly dependent on the availability of its main prey, the European rabbit (Ferrer and Negro, 2004; R. Sánchez et al., 2008), and management actions aiming to increase rabbit populations in areas with high suitability for the species can be a strategy to promote the expansion of this raptor, fixing breeding pairs in new locations.

We were able to confirm that two out of the twelve studied eagles died at the end of the first winter, both by anthropogenic causes: one by electrocution with power lines and the other by illegal poisoning. Such observations highlight the importance of addressing anthropogenic mortality of the species during the dispersal period.

Nowadays, there are several technical options to prevent the electrocution of big raptors in power lines poles (Chevallier et al., 2015; Tintó et al., 2010), and it has been proven that such mitigation is effective to reduce the mortality of the Iberian imperial eagle (López-López et al., 2011). Even though this is the main cause of anthropogenic mortality of non-adult eagles (González et al., 2007), power lines retrofitting has been focusing primarily on the breeding territories (SPEA and QUERCUS, 2012), as the consequences of the loss of an adult bird on population dynamics are greater than those of the loss of non-breeding individuals (López-López et al., 2011). However, with the increase of the population numbers and range, and the establishment of new breeding areas previously used by transient immatures, the management of the settlement areas gain an even greater importance in the conservation of the species.

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SUPPLEMENTARY MATERIAL

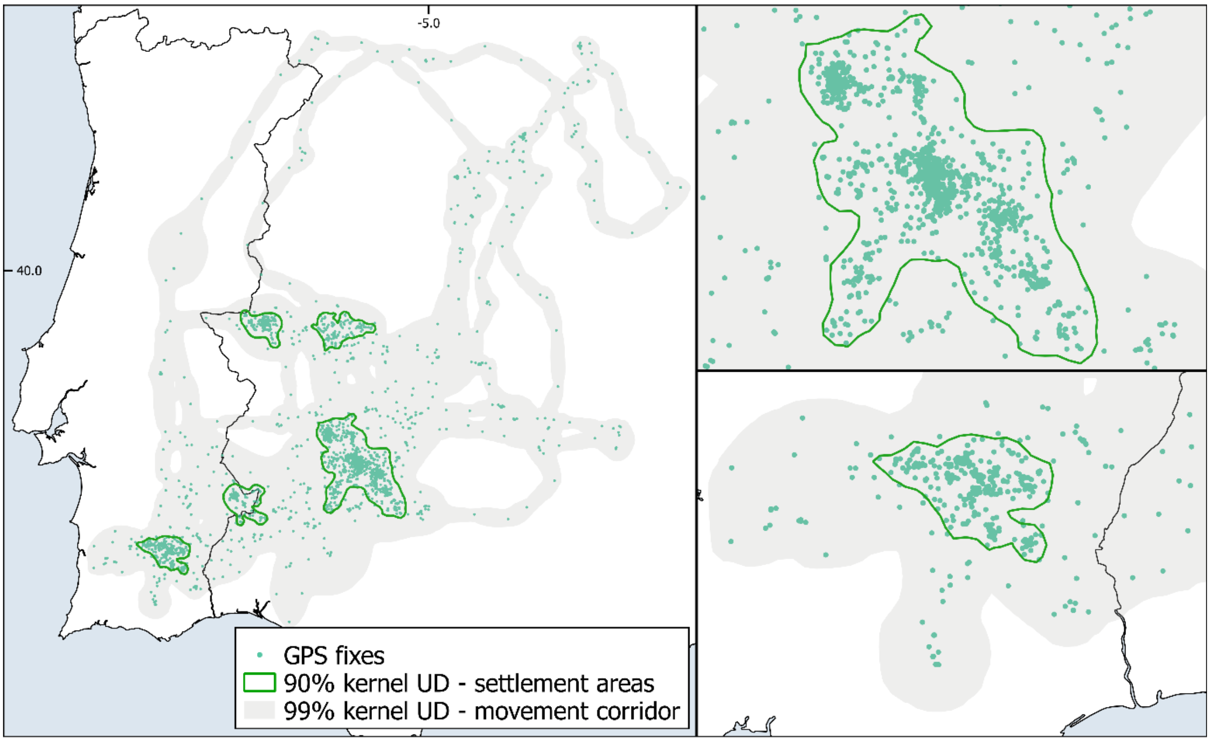

Figure S1 – Example of the settlement areas definition for the female 1.

Chapter 7

General discussion

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General discussion

Anthropogenic infrastructures affect wildlife in multiple and complex manners. Habitat and behavioural effects, as well as mortality, are particularly noticeable when considering birds' species. Overall, this thesis aimed to study how anthropogenic infrastructures influence the distribution and movements of several bird species with the purpose of identifying management actions and support conservation strategies. Here, I highlight the key findings of this thesis and relate them to the literature. Additionally, I outline some of the major conservation implications and discuss some methodological challenges for studies on the interactions between birds and infrastructures.

1. EFFECTS OF INFRASTRUCTURES ON RAPTORS AND BUSTARDS

1.1. HABITAT AND BEHAVIOURAL EFFECTS

Habitat loss, habitat fragmentation and behavioural effects caused by anthropogenic infrastructures are widely described in the literature (Andrews, 1990; Fahrig and Rytwinski, 2009; Laurance et al., 2009; Pearce-Higgins et al., 2009; Rytwinski and Fahrig, 2015; Sánchez-Zapata et al., 2016; Trombulak and Frissell, 2000; Walters et al., 2014), and some of them have been identified in this thesis (chapters 2, 4 and 5).

In chapter 2 we studied the drivers behind the steep decline of the little bustard (*Tetrax tetrax*) population in Iberia since the beginning of the 21st century, including the effect of habitat availability, grazing management, linear infrastructures density and implementation of agri-environmental measures. Our results suggest that linear infrastructures, particularly power lines, cause a decrease in habitat quality for the little bustard, adding up to other major habitat concerns, such as high livestock density and grassland management. In fact, when the species occurred in high densities we did not observe an effect of linear infrastructures, whilst when the population dropped, areas with higher density of power lines had lower bird densities. Moreover, higher losses in little bustard numbers were registered in areas with higher density of power lines, probably because birds start avoiding linear infrastructures selecting optimal habitat locations, but also because of bird mortality at breeding locations, as there are high collision rates in the beginning of the breeding season (see chapter 3).

In chapter 4 we studied the stopover ecology of little bustard during the short-term migration and the habitat characteristics selected at stopover sites. Our results showed that birds were preferentially nocturnal migrants, making frequent and short-term (<24h) stopovers. They selected stopover locations avoiding the proximity of paved roads but did not avoid power lines. Previous work found that little bustards avoid the proximity of power lines during the breeding season (Silva et al., 2010) and during Summer (Lourie, 2016), so we were expecting an effect of such structures in the selection of stopover sites. We hypothesise that these birds are not able to see power lines in poor lighting conditions, as they arrive mostly late at night to the stopover locations. This may also help explain why the species has a high collision rate during the migration period, as we show in chapter 3.

The displacement effect of wind turbines in soaring birds has been previously identified by several authors (Barrios and Rodríguez, 2004; Cabrera-Cruz and Villegas-Patraca, 2016; de Lucas et al., 2004; Garvin et al., 2011; Johnston et al., 2014; Pearce-Higgins et al., 2009; Villegas-Patraca et al., 2014) but only Pearce-Higgins et al. (2009) quantified the extent of such effect (up to 800 m) just for two species during the breeding season. In chapter 5 we were able to isolate and quantify the displacement caused by wind farms for a migratory soaring bird, the black kite (*Milvus migrans*), at a migratory bottleneck region. We found that wind turbines cause underuse of good soaring areas up to a distance of 700 m, and estimated that 3-14% of the areas suitable for soaring in the study site have already been occupied by wind energy production. Additionally, we showed that this species used areas with high availability of orographic and thermal uplift, resources that occur in a patchy way throughout the landscape.

1.2. MORTALITY

Bird mortality due to the presence of anthropogenic infrastructures is common, due to collisions with travelling vehicles, collision with the structure itself or electrocution (Bevanger, 1998, 1994, Drewitt and Langston, 2008, 2006; Forman et al., 2003; Janss, 2000; Loss et al., 2015).

In chapter 3 we studied the mortality patterns in transmission power lines for two collision prone species, the little bustard and the great bustard (*Otis tarda*). From our analysis it was clear that collisions do not occur randomly. We found spatial and temporal patterns of mortality highly related with species' ecology, particularly distribution, movements and flight behaviour. Overall, bustards tend to collide in areas with greater habitat availability, during periods of high mobility (moving towards areas with greater food availability at the end of the breeding season) and mainly in tall structures. Such incidents seem to occur during daily movements and at stopover locations (see the previous section), but not when birds are engaged in migratory flights, where birds fly at higher altitudes (Silva et al., 2014), probably not interacting with transmission power lines. Although we did not study the population effects of mortality due to collisions with power lines, the results from chapters 2 and 3 suggest that this source of mortality is contributing to the decline of the little bustard. In fact, power lines are responsible for the high levels of non-natural mortality observed in this species (Marcelino et al., 2017) and there is a peak of collision events during the breeding season, mainly at its beginning (chapter 3), that partially explains why areas with higher densities of power lines are the ones where the species declined the most (chapter 2).

In chapter 6, even with a small sample size (12 birds), we registered an Iberian imperial eagle (*Aquila adalberti*) electrocution in a power line pole just a few days after leaving their parent's territory. This illustrates the high vulnerability of this raptor species to power lines, as birds disperse through a large range increasing the likelihood of interacting with power line poles. This threat had been previously identified by other authors (González et al., 2007).

2. IMPLICATIONS FOR SPECIES CONSERVATION AND MANAGEMENT

Throughout this thesis, I was able to demonstrate that infrastructures can play an important role in species distribution (chapters 2, 4 and 5) and may even contribute to accentuate population trends (chapter 2). The case of little bustards is of high concern, as the species is sharply declining and linear infrastructures seem to be contributing to such decline, due to high mortality rates by collision with power lines (Marcelino et al., 2017) and to habitat degradation resulting from the increase of power line and road densities.

This work also generated results relevant for the management of infrastructures and for outlining conservation measures. Such outputs can be included in the two first steps of the mitigation hierarchy, avoidance and minimization of impacts (see chapter 1). Avoidance aims to place infrastructures away from key ecological locations for sensitive species, and is the primary strategy to reduce overall impacts on biodiversity (Bernardino et al., 2018; Laurance et al., 2014; Marques et al., 2014; Phalan et al., 2018; Sánchez-Zapata et al., 2016; Weller, 2015). The relevance of such a strategy is of high importance for bustard species, as areas with higher densities of infrastructures are the ones with greater losses of little bustard density (Chapter2) and because the amount of suitable habitat was the main driver of collision risk in transmission power lines for both little bustard and great bustard (chapter 3). Due to the high vulnerability of these species and their high conservation status, the planning of a new linear infrastructure (mainly roads, railways and power lines) in Iberia should always include a conditioning layer identifying key areas for both species, comprising the main reproduction locations, wintering grounds, and movement corridors (including stopovers).

In chapter 5 we stress the need for new regulations for wind-power production that take into consideration not only the risk of collision of soaring birds but also the loss of aerial habitat caused by wind turbines. This is particularly important in keys areas for migration, such as migratory bottlenecks, as these locations frequently have good wind resources and are thus targeted by the wind industry.

We demonstrated that in areas of high relevance for soaring birds, the sitting of new wind farms or the repowering of existing ones, should take into account the uplift potential of the landscape. Uplift maps can help to identify high risk areas and can be generated for most part of the world using public information: orographic uplift potential can be predicted with a digital elevation model and wind data (speed and direction), and thermal uplift can be estimated from land surface temperature derived from Landsat imagery (Bohrer et al., 2012; Brandes and Ombalski, 2004; Santos et al., 2017).

Minimization aims to reduce impacts by choosing technical options that are less deleterious for wildlife. In chapter 3 we had two major outputs regarding these mitigation steps: power lines crossing bustard habitats should have smaller configurations (lower poles and a reduced number of vertical wires) and wire marking devices, which can help to reduce, but not eliminate, bustards' collisions. In fact, we found that transmission power lines with a large configuration and four levels of wires, forming a bigger collision risk area (higher distance between top and bottom wires), have higher collision risk than smaller configurations, at least for the little bustard. This effect has been suggested in the literature but this is the first study to demonstrate it. Moreover, we found that wire marking devices have a significant but small effect in the reduction of collisions in the little bustard, confirming previous studies that showed that cable marking solutions have less effect on bustard species than on other birds (Barrientos et al., 2012; Janss and Ferrer, 1998).

In chapter 6 we followed a different approach to contribute to the minimization of the impacts of anthropogenic infrastructures on a critically endangered raptor, the Iberian imperial eagle, by generating predictive cartography of habitat suitability to identify priority locations to intervene. Iberian imperial eagles, and mainly immature birds, are highly vulnerable to electrocution in distribution power lines poles (González et al., 2007); most old structures have designs with high electrocution risk for large raptors. Although nowadays the industry uses safer pole designs and new technical solutions that prevent bird electrocutions, there are still problematic operating structures throughout the landscape. Fortunately, this source of mortality can be successfully suppressed (Chevallier et al., 2015; López-López et al., 2011; Tintó et al., 2010), with the right amount of resources and planning. That is why predicting suitable areas for the Iberian imperial eagle during the non-adult period can be important for the conservation of the species. The data collected in chapter 6 also confirmed that the Mértola and Castro Verde regions (Baixo Alentejo, Southern Portugal) are of high relevance for dispersing Iberian imperial eagles, as all the tracked birds settled there for variable periods. Additionally, we found that the species has a sedentary behaviour during the coldest months (late November to February), what was a novel finding. This behaviour highlights the importance of conserving settlement areas, as bird movements seem to be constrained when climatic conditions are not favourable for flights powered by thermal uplift conditions.

In addition to the outputs related to the anthropogenic infrastructures, this thesis highlights the need to adjust livestock production in Iberian grasslands to make it compatible with the conservation of grassland birds (chapter 2). Our analysis pointed out that the current stocking levels and livestock type are causing a degradation of habitat quality in breeding areas, contributing to the steep decline of the little bustard during the 21st century, and making the species more susceptible to other sources of impact, such as linear infrastructures. The improvement of habitat for grassland birds is directly linked to the production of cattle, and will only be possible with changes in the European Common Agricultural Policy and national policies, and with the reinforcement of the attractiveness of the agri-environmental schemes, as indicated by other authors (Traba and Morales, 2019).

3. METHODOLOGICAL CHALLENGES FOR STUDIES ON INTERACTIONS BETWEEN BIRDS AND INFRASTRUCTURES

3.1. TRACKING TECHNOLOGY

Precision tracking technology is now widely used to study the interactions between wildlife and anthropogenic infrastructures and was a valuable method applied in this thesis. In chapter 4 it allowed the identification of the stopover locations and respective habitat use, showing that birds select stopovers avoiding paved roads but not power lines. By collecting a relatively high-frequency data across a large special range, GPS tracking data allowed us to demonstrate that wind turbines are responsible for functional habitat loss for migrating black kites (chapter 5). And in chapter 6, we were able to describe in detail the life cycle of the Iberian imperial eagle during the non-adult phase, which is difficult to study due to the animal's high mobility. In general, such results would not be possible without the use of GPS tracking devices, not only because of the referred high mobility of the species but also due to its wide range and poorly known movements.

Tracking technology also has potential to improve our knowledge of the interactions between wildlife and anthropogenic infrastructures and to test the effects of the available mitigation measures. Studies based on tracking data traditionally infer from occurrence data (presence data), comparing the localizations used by individuals against the available ones (pseudo absences) (Hooten et al., 2017), as we did in chapters 4 and 6. However, such an approach does not take into account the biological function underlying the use of the sampled locations, i.e. it provides detailed spatial data on when and where species occur, but does not inform about why a species is using a certain habitat. Nowadays, it is possible to link locations with animal behaviour, through to the combined use of GPS-trackers and accelerometer sensors. Accelerometers record tri-axial body posture movements, which can then be attributed to observable behaviours by supervised machine-learning algorithms (Brown et al., 2013; Nathan et al., 2012). Studies regarding the effects of infrastructures on wildlife are just starting to include combined location and behavioural data, which can help us to understand the behavioural contexts in which landscape features are selected or avoided. For example, Abrahms et al. (2016) showed that African wild dog (*Lycaon pictus*) response to roads varied markedly with both the animal behaviour and the landscape: they selected roads when travelling and avoided them when resting, a difference that was not evident when all movement data were considered together. These results suggest that unpaved roads enhance landscape permeability for the species and highlights that the conservations strategies targeting this species should be different when considering resting sites and movement corridors.

Major advances in data collection are still expected for future years, as tracking technology evolves. Main expected improvements include the collection of even higher frequency data (with a temporal resolution of seconds), the joint use of different bio-sensors (e.g. temperature-loggers, magnetometers, accelerometers) and the reduction in tag size. Together, they will provide data of higher temporal and spatial resolutions for the study of an increasing number of smaller species (Cagnacci et al., 2010; de Weerd et al., 2015; Guo et al., 2009; Tomkiewicz et al., 2010).

However, the use of tracking technology still poses some major obstacles (Cagnacci et al., 2010; Hebblewhite and Haydon, 2010). GPS tracking devices do not last the full life span of medium/ long-lived species. Also, the high cost of GPS devices limits the sample sizes used in ecological studies, which in turn limits the statistical power of models. The trade-off between the number and cost of each unit (Hebblewhite and Haydon, 2010), and ethical and animal welfare standards may also hamper the tagging of a high number of individuals. Both financial and ethical criteria can contribute to small sample sizes that may hinder robust population-level inferences (Hebblewhite and Haydon, 2010).

3.2. ISOLATING EFFECTS

To fully understand how an individual is affected by an anthropogenic infrastructure it is key to isolate its effect from that of other factors that cause noise in the analysis, such as environmental variables or even the presence of other infrastructures. This is particularly important if the impacts of new developments have to be identified for designing compensatory programs. However, there are several challenges when studying the effects of anthropogenic infrastructures, and adequate study designs are key to obtain satisfactory results.

There is a general consensus that BACI (Before-After Control-Impact) studies are the best option to isolate the exact consequence of infrastructures from other determinants of animal spatial use (Colman et al., 2017; Langston and Pullan, 2003). Such study design assumes that the parameter to monitor is collected before (i.e. before the implementation of the infrastructure) and during the occurrence of an impact (i.e. after the construction), both in areas with impact (i.e. at or near the infrastructure) and control areas (i.e. areas far away from the focal infrastructure that share the ecological conditions of the areas potentially impacted). Nevertheless, BACI designs are not always achievable, because some studies are only performed after the infrastructure is already implemented or because there are no control areas available. Moreover, when studies focus on effects at large spatial scales, it is frequently not possible to obtain a reference dataset without human disturbance. We faced that challenge in chapter 4, when studying little bustard habitat selection at stopover sites and in chapter 5, when identifying the avoidance behaviour of black kites to wind turbines. In both cases we used an IG (Impact Gradient) design that measured the monitored parameter at different distances from the disturbance source (i.e. the infrastructure), and we also controlled for other variables that are known to affect the species habitat selection or movements.

Additionally, anthropogenic infrastructures tend to occur in a clustered pattern, due to planning strategies. Power lines, for example, are preferably installed parallel to pre-existing linear elements, like roads or other aerial cables, to reduce habitat fragmentation and mitigate bird collisions (Bernardino et al., 2018). This arrangement makes it difficult to disentangle the effect of a single infrastructure type, because the cumulative effects of multiple infrastructures (i.e. interaction of elements) can be purely additive (i.e. if the total effect that is equal to the sum of the individual contributions), or synergic (i.e. if the total effect that is greater than the sum of the individual contributions). That is why a land use change caused by a single infrastructure may result in a negligible impact, but the synergy of multiple individual changes over time (from several infrastructure types) may constitute a major impact within a landscape or region (Theobald et al., 1997). In chapter 2 we only found effects of power line density on little bustard numbers, but we do not discard that roads are also having some effect that we were not able to identify. In fact, we hypothesized that the effect of roads might be masked by the one from power lines, as both linear structures were moderately and positively correlated in our dataset.

3.3. DATA COMPATIBILITY AND ACCESSIBILITY

In chapter 3 we faced a major challenge when trying to integrate data from multiple monitoring studies. We collected 156 collision events from great bustard and little bustards in transmission power lines, from 9 different studies, but only a fraction of the data collected in most of the studies were discoverable and accessible to us. Major gaps included the lack of detailed spatial and temporal details; a study reported collision events at 2 km sections rather than power line spans or coordinates, and some studies did not include the date or even the season of the collision events. Additionally, each study had different methodological protocols that conditioned the overall sampling effort (e.g. variable sampling frequency or overall study duration). To deal with the lack of detailed information and to assure compatibility across data, we had to simplify our database and therefore our analysis. Even though we were able to reach interesting results, we don’t know to what extent this may have limited our conclusions.

Data accessibility and sharing is a widespread problem in ecology and is being overcome with increasingly Open Data protocols and databases (Reichman et al., 2011). Even though this can be an option for archiving data from scientific studies focusing on wildlife and human interactions, there is an enormous amount of data collected for non-scientific purposes with a high scientific potential that is generated by the industry. In chapter 3, we were able to collect studies undertaken by governmental organizations, non-governmental agencies and private consultancies, that were produced with different aims (national assessment of transmission power lines impacts, monitoring programs from Environmental Impact Assessment processes and studies of wire-marking effectiveness). Most studies we collected were small-scale, short-term and focused on single projects, i.e. single power lines, so their overall results were relatively local. However, all the studies targeted infrastructures managed by a single entity, as the transmission power line network in Portugal is managed by a single company. Even if this is quite a unique situation, most developers have multiple projects and hence are potentially generating multiple valuable data. Such information should be stored and made accessible by industry, for example through collaborative platforms that already exist in the industry (e.g. CIGRE, WindEurope, National Wind Coordinating Collaborative).

Making data compatible and accessible is particularly important because cumulative anthropogenic effects on wildlife populations are critical but hard to study, and the collection of good sampling sizes is frequently a challenge (see the previous section). Large-scale and multidisciplinary projects that integrate diverse data sets have an enormous potential to enhance our knowledge and help answering the remaining questions about this topic, like cumulative effects of several infrastructure types or population-level impacts.

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