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ORIGINAL ARTICLE

Juvenile dispersal in an uninhabited continent: young Spanish Imperial Eagles in Africa

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Abstract

The Spanish Imperial Eagle (*Aquila adalberti*) disappeared from Africa as a breeding species in the 1960s coincident with a general decline of their populations in the Iberian Peninsula. Because of a combination of successful conservation actions and a general change in human attitudes, the Spanish Imperial Eagle population has been increasing in Iberia from 103 pairs in 1980 to more than 500 breeding pairs in 2018. As a consequence, the number of juveniles that cross the Strait of Gibraltar into Africa has increased recently. Abundance and distribution of potential prey should affect young eagles' behaviour and could be a limiting factor for a potential re-colonization of previous North-African populations. Additionally, determination of temporary settlement areas is crucial from a conservation point of view. Conservation actions in these areas, particularly reduction of juvenile mortality, are a priority to facilitate future reestablishment of breeding populations of the species in North Africa. Here we report on the dispersal movements of juvenile Spanish Imperial Eagles marked with GPS-GSM transmitters in Andalusia (southern Spain), some of which crossed the Strait of Gibraltar into north-western Africa, an area that does not have populations of the eagle's main prey, the European rabbit. We analysed the differences in dispersal patterns and temporary settlement behaviour in the two study areas. We found that dispersal movements were greater, temporary settlement areas were larger, and individuals stayed longer in areas and moved greater distances among them in Africa than in Iberia. We believe that our results are best explained by applying the Marginal Value Theorem, which predicts that individuals will leave a foraging area when the availability of prey drops to similar levels of those of the surrounding environment. We suggest that the increase in the records of the species in Africa could lead to a recolonization of the species in Africa based on birds coming from the "source" Iberian population, but only if the Iberian population continues to increase. We recommend that conservation measures must be established in these temporary settlement areas in Africa.

Keywords *Aquila adalberti* · Spanish imperial eagle · Juvenile dispersal · Temporary settlement · Long-lived species · Movement behaviour · GPS–GSM tracking · Social attraction · Recolonization

Zusammenfassung

Juvenile Dismigration auf einem unbewohnten Erdteil: Junge Spanische Kaiseradler in Afrika.

In den 1960er-Jahren verschwand der Spanische Kaiseradler (*Aquila adalberti*) als Brutvogel aus Afrika, was mit einem generellen Rückgang seiner Populationen auf der Iberischen Halbinsel einherging. Aufgrund einer Kombination aus

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erfolgreichen Schutzmaßnahmen und einem allgemeinen Wandel der menschlichen Einstellung wuchs die Population Spanischer Kaiseradler auf der Iberischen Halbinsel von 103 Brutpaaren im Jahr 1980 auf über 500 Brutpaare im Jahr 2018 an. Infolgedessen stieg die Anzahl der Jungvögel, welche die Straße von Gibraltar in Richtung Afrika überqueren, in neuerer Zeit an. Die Häufigkeit und Verteilung potenzieller Beutetiere sollte das Verhalten der jungen Adler beeinflussen und könnte einen limitierenden Faktor für eine mögliche Wiederbesiedlung der Gebiete ehemaliger nordafrikanischer Populationen darstellen. Darüber hinaus ist aus Sicht des Naturschutzes die Ermittlung vorübergehend genutzter Ansiedlungsgebiete von entscheidender Bedeutung. Schutzmaßnahmen in diesen Bereichen, speziell zur Verringerung der Jungensterblichkeit, sind eine Vorbedingung für eine zukünftige Wiederansiedlung der Art als Brutvogel in Nordafrika. Hier beschreiben wir die Dismigrationsbewegungen juveniler Spanischer Kaiseradler, welche in Andalusien (Südspanien) mit GPSGSM-Sendern ausgestattet wurden, und von denen einige die Straße von Gibraltar nach Nordwestafrika überquerten, ein Gebiet, in dem es keine Wildkaninchenpopulationen gibt, welches die Hauptbeuteart des Adlers ist. Wir analysierten die Unterschiede in den Ausbreitungsmustern und im zeitweiligen Ansiedlungsverhalten zwischen den beiden Studiengebieten. In Afrika gab es stärkere Ausbreitungsbewegungen, die zeitweisen Ansiedlungsbereiche waren größer, Individuen blieben länger in den Gebieten und legten zwischen diesen weitere Strecken zurück als auf der Iberischen Halbinsel. Wir sind der Meinung, dass unsere Ergebnisse sich am besten durch die Anwendung des Grenzertragstheorems (engl.: Marginal Value Theorem) erklären lassen, welches besagt, dass Individuen ein Nahrungsgebiet verlassen, wenn dort die Beuteverfügbarkeit auf ein ähnliches Maß wie im Umland sinkt. Wir vermuten, dass der Anstieg in den Nachweisen der Art in Afrika dort zu einer Wiederbesiedlung durch Vögel aus der iberischen "Quellpopulation" führen könnte, allerdings nur, wenn die iberische Population weiterhin wächst. Wir empfehlen den Ausbau von Schutzmaßnahmen in diesen zeitweiligen afrikanischen Ansiedlungsgebieten.

Introduction

The Spanish Imperial Eagle (*Aquila adalberti*) disappeared from Africa as a breeding species in the 1960s. Shortly thereafter, observations of eagles dispersing across the Strait of Gibraltar from Iberia (González 1991; Ferrer 2001) became sporadic and infrequent (González et al. 2006). However, an increase in the number of young eagles crossing the Strait of Gibraltar into Africa has been reported as their breeding numbers have again increased in Spain. The European wild rabbit (*Oryctolagus cuniculus*) is the main prey for the Spanish Imperial Eagle (Ferrer and Negro 2004) but is not a native species in North Africa (Alves and Hackländer 2008). Ferrer (2001) suggested that the African population of Spanish Imperial Eagles was probably a marginal one that was maintained primarily by surplus birds coming from the Iberian Peninsula where high wild rabbit densities resulted in high eagle densities in the past.

Because of a combination of successful conservation actions (Ferrer and Hiraldo 1991; Ferrer 2001; López-López et al. 2011) and a general change in human attitudes regarding predators, including raptors (Martínez-Abraín et al. 2009), the Spanish Imperial Eagle population has been increasing in Iberia from 103 pairs in 1980 (Ferrer 2001) to more than 500 breeding pairs in 2018 (National Working Group unpublished data). One of these conservation actions was a reintroduction program to recover an historic population of eagles in Cadiz province close to the Strait of Gibraltar, which connected several sub-populations, increasing metapopulation resilience in the region (Madero and Ferrer 2002). Consequently, the number of juveniles that cross the Strait of Gibraltar has increased recently (Ramírez et al. 2016; Bergier et al. 2011, 2012, 2014; Torralvo et al. 2011; Amezian et al. 2015).

According to the Marginal Value Theorem, which can model food searching and patch-departure decisions for foragers when resources are distributed irregularly (Charnov 1976), we should expect differences in dispersal patterns of the juvenile eagles between the Iberian Peninsula and Africa resulting from the marked differences in abundance and spatial distribution of potential prey in the two areas. The recent re-establishment and growth of the Iberian population provides us with the chance to test this possibility in a large eagle with individuals dispersing and temporarily settling in the Iberian Peninsula or Africa and some of them using areas on both continents. In Iberia, the basic prey is the wild rabbit, with a relatively homogeneous distribution in the Iberian Peninsula (Smith and Boyer 2008), whereas in North Africa, prey includes medium-sized rodents including the fat sand rat (*Psammomys obesus*), Barbary ground squirrel (*Atlantoxerus getulus*), Sundevall's jird (*Meriones crassus*), and the lesser Egyptian jerboa (*Jaculus jaculus*) (Ramírez et al. 2016), all of which are common in desert or semi-desert areas in the region (Amori et al. 2016; Aulagnier 2016; Granjon 2016), and whose populations fluctuate in association with seasonal rains. These continental differences in prey provide us with the opportunity to study changes in dispersal patterns in non-breeding areas without adult individuals.

The Marginal Value Theorem applied to the active search of food predicts that individuals will leave food patches or foraging areas when the availability of prey drops to similar levels of those of the surrounding environment (Charnov 1976), a response that was described (Ferrer 1993a) for juveniles of Spanish Imperial Eagles in the Iberian Peninsula. In North Africa, an area without rabbits and with alternative prey with a high local density but a highly heterogeneous distribution of the patches, we predicted that individuals would stay in individual temporary settlement areas longer before switching, that temporary settlement areas would be larger, and that such areas would be farther apart from each other than in Spain. Abundance and distribution of potential prey should affect young eagles' behaviour and could be a limiting factor for a potential re-colonization of previous North-African populations of Spanish Imperial Eagles. Additionally, determination of temporary settlement areas is crucial from a conservation point of view. Conservation actions in these areas, particularly reduction of juvenile mortality, are a priority to facilitate future reestablishment of breeding populations of the species in North Africa.

Methods

Study species

The Spanish Imperial Eagle is a large (2500–3500 g), long-lived bird of prey with delayed maturity of 4–5 years and a typical life span of approximately 22 years (Ferrer 2001). With approximately 500 breeding pairs in 2018 (National Working Group, unpublished data), this Iberian endemic is the most threatened raptor in Europe and one of the rarest large eagles in the world (CMAyOT 2015). The species is sedentary, territorial, and monogamous, with an annual productivity in stable populations of approximately 0.75 chicks per pair (Ferrer and Calderón 1990). Reproduction occurs over an 8-month period from February to October after which juveniles disperse at a mean age of 135 days before settling in their first temporary area at a mean age of 164 days (Ferrer 1993b). After leaving the nest, dispersing young typically move among 3–8 temporary settlement areas and return frequently to the natal population before attempting to breed (Ferrer 1993b). In Iberia, temporary settlement areas are usually open-habitat pasture and open-crop areas away from human disturbance with widely dispersed *Quercus* spp. and high densities of European rabbits (Ferrer and Harte 1997).

Data collection and study area

We equipped 15 eagles with GPS-GSM transmitters at 45–55 days of age: 8 in 2015 (5 females and 3 males) and 7 in 2016 (2 females and 5 males). We used three models of radio-transmitters (Ecotone Duck-4 GSM, 24 g; Ecotone Saker-H LF GSM, 33 g; E-obs GPRS High-Res, 40 g), all of them below 2.5% of body mass of the chicks at fledging (Kenward 2001). Transmitters were programmed to collect location data at hourly intervals. Tagged eagles were monitored from the first flight longer than 20 km away from the nest (Ferrer 1993b) until their second year of life (i.e., 700 days old), except for one bird who either died or whose transmitter failed. We characterized temporary settlements as areas with six or more consecutive overnight stays (half the average duration of a temporary settlement, Ferrer 1993b) and dispersive movements as movements that occurred between settlement areas with more than 20 km between successive roosting sites (Ferrer 1993b).

Statistical analysis and cartography

We analysed the total area used by each young eagle in each one of their settlements, the length of stay in each settlement, and the distances travelled per hour during the dispersive movements in each of the continents. All variables were tested for normality and log transformed if necessary. We used generalized linear mixed models (GLMMs) to conduct our analyses, with these three variables as response variables, sex and study area as fixed factors, and individual as a random factor, to avoid pseudoreplication resulting from repeat observations of the same individual.

We calculate the distance from each settlement area to the nearest settlement area. We used an ANOVA to test whether mean nearest distances among all of the 37 used settlement areas differed between continents. We used a χ^2 goodness of fit test to analyze changes between continents in the proportion of time spent in settlement areas. Finally, we used a nonparametric Mann–Whitney U test to analyze if the number of settlement events or the number of areas used by each individual differed between continents.

Statistical analyses were performed using STATISTICA 13.3 (TIBCO Software Inc., USA). Spatial data, as well as all of the cartography, were processed via ArcMap 10.5.1 (Environmental Systems Research Institute. Redlands, CA, USA).

Ethical note

Our research has been evaluated and approved by The Ethical Committee of the Spanish Council for Scientific Research, which is the oversight authority for such matters in Spain (registration number 20/12/2017/173). The project also was authorized by the Andalusia environmental administration (i.e., Consejería de Medio Ambiente, Junta de Andalucía), which has granted the appropriate licenses for handling and tagging the nestlings.

Results

Dispersal areas used by tagged individuals in the Iberian Peninsula included those from the province of Burgos in the North (42° N) to the Strait of Gibraltar in the south (36° S) and in the east from Valencia coast (1° W) to Cabo de San Vicente in Portugal (9° W), covering an area of 287.28 km^2. In Africa, dispersal areas included 1655.26 km^2 from the Strait of Gibraltar to the south of Mauritania (16° S) and from the Algerian Sahara (0° W) to the coast of Western Sahara (15° W), covering the territory of Morocco, Algeria, Western Sahara and Mauritania. Seven of the 15 eagles tagged with GPS–GSM transmitters from different populations of southern Iberia used both continents during their dispersal, crossing the strait and moving through large areas of northwestern Africa (Fig. 1). We identified five settlement areas in Africa and 32 in the Iberian Peninsula. Means, standard deviations and sample sizes of the studied variables are presented in Table 1. Settlement areas used by dispersing eagles in Africa were 26 times larger than those used in the Iberian Peninsula, but settlement area sizes did not differ among individuals or by sex (Table 2). Dispersing young spent nearly three times as many days in these temporary settlement areas in Africa than in Iberia, but again there was no difference among individuals or by sex (Table 3). Mean distances moved by hour when young eagles were not in a settlement area were more than two times longer in Africa than in Iberia, but distances were also influenced by individual variation (Table 4).

Mean nearest distances among all the used settlement areas were 6.6 times longer in Africa than in the Iberian Peninsula ($F_{1,37} = 18.87$, $P < 0.0001$). For both continents, the mean proportion of time spent in settlement areas was 57% ± 15%, and less time was spent in settlement in Iberia (50% ± 13%) than in Africa (75% ± 14.71, $\chi^2 = 183.24$, $P < 0.0001$).

The number of settlement events averaged 6.62 ± 5.03 events ($n = 106$) overall, and the number of events was higher in Iberia (mean 8.60 ± 5.08 events, $n = 86$) than in Africa (mean 3.33 ± 2.94 events, $n = 20$; $U = 10.50$, $P = 0.0373$). However, the number of areas used by each individual in the two continents did not differ (Iberia: 3.50 ± 2.76 different settlements, $n = 35$; Africa: 2.33 ± 1.75 different settlements, $n = 14$; $U = 23.00$, $P = 0.46$).

Discussion

Juvenile dispersal of Spanish Imperial Eagles was first described using VHF radio-transmitters (Ferrer 1993a). General dispersal behaviour we observed here supports previous findings. As in many other large raptors (Cadahía et al. 2005; Soutullo et al. 2006a, b; Balbontin and Ferrer 2009; Mellone et al. 2011; Soutullo et al. 2013), juvenile dispersal behaviour in the Spanish Imperial Eagle is characterized by an alternation between temporary settlement areas, wandering and exploratory flights and returns to the natal population. During this juvenile dispersal period, bird behaviour is largely determined by the search for food (Ferrer 1993a, b).

As expected by the Marginal Value Theorem (Charnov 1976), the average sizes of temporary settlement areas were larger and the lengths of stays in these areas were longer in Africa than in Iberia. A larger area surveyed for a longer time in a less favourable environment with absence of the usual prey of a specialized predator (González 1991; Ferrer and Negro 2004) and scarcity and irregularity of potential alternative prey (Ramírez et al. 2016) suggest more intensive exploitation of the area. The average number of days in the Iberian settlements (13) was similar to that previously found (12, Ferrer 1993a). In contrast, the average number of days in the temporary settlements of Africa, without European rabbits but with seasonal patches of secondary prey, was 39 days, three times longer than in Iberia. This difference is reasonable if prey capture rates outside settlement areas were lower in Africa than in Iberia. This phenomenon has been described in several other species (Cassini et al. 1990; Patrick et al. 2017), supporting the notion that individuals can shift the proportion of time dedicated to either exploration outside of the settlement area or exploitation of the settlement area, depending on the quality of the patch. On the other hand, settlements in Africa might be larger because there were no adults present, as there were in Iberia. Territorial defense by breeding adults, who chase out floaters from their territory, would limit the size of settlements in areas with high density of adult pairs (Morandini and Ferrer 2017a, b). Because temporary settlements in Africa are likely to have been exploited more thoroughly, the proportion of time spent on exploitation of the settlement was higher there than compared with the Iberian Peninsula, where they spent more time on exploration outside of settlement areas. Thus, tagged individuals remained in settlements a higher percentage of time in Africa (75%) than in Iberia (50%), a result consistent with the 54% of time settled found in another study with juveniles marked with VHF radio-transmitters in the Iberian Peninsula (Ferrer 1993b).

The mean number of temporary settlement events was lower in Africa than in the Iberian Peninsula, but the number of different areas used as settlements was not different. Lower numbers of settlement events in Africa may be due to the difficulty of finding optimal food patches because of the absence of the usual prey and the irregularity of possible alternative prey, small rodents of arid zones that have demographic explosions associated with periods of seasonal rains

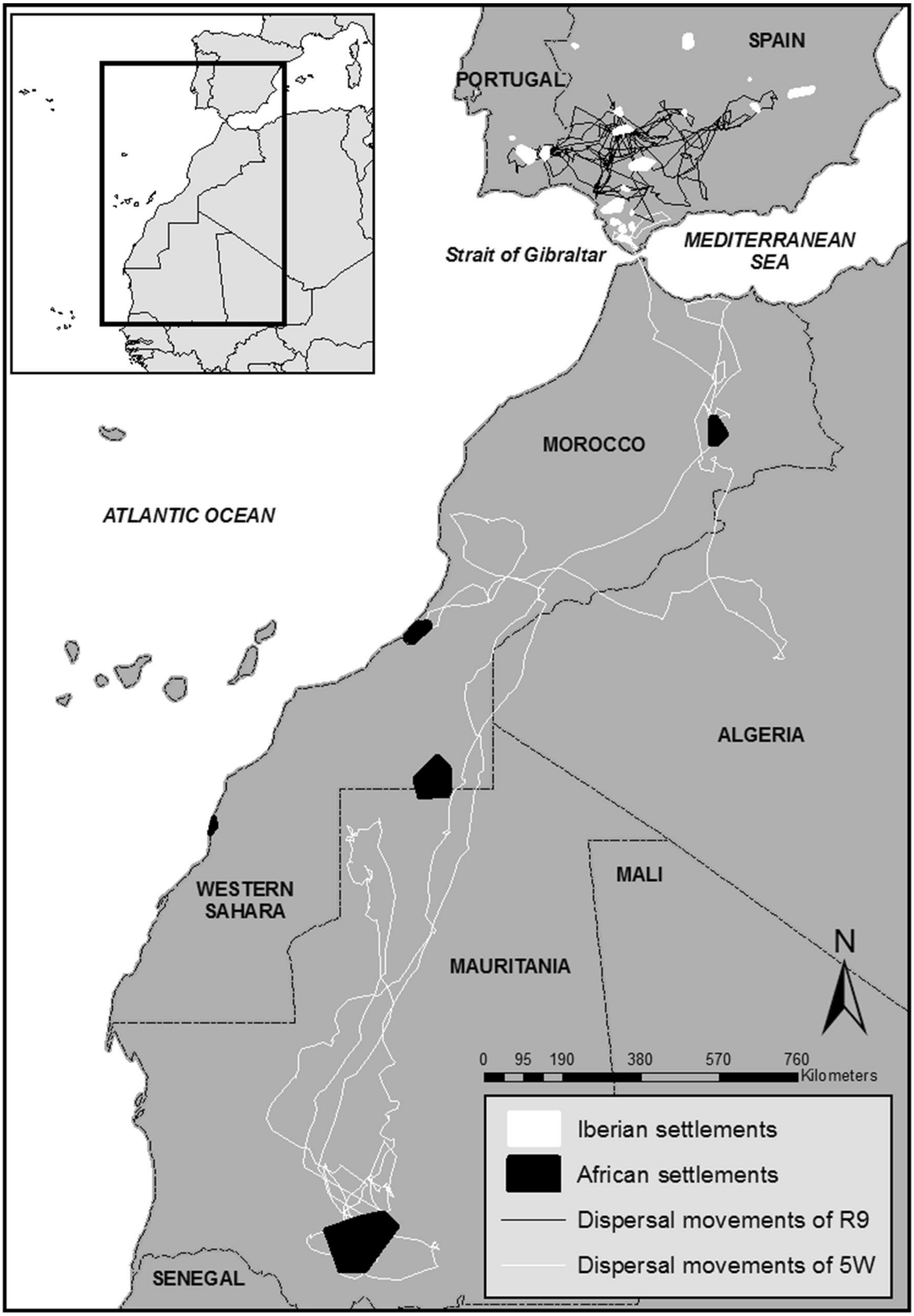

Fig. 1 Map of temporary settlement areas in Iberia and Africa and examples of dispersal movements of two individual birds, one each mainly in Iberia (R9) and Africa (5 W). Note the larger temporary settlement areas and dispersal movements in Africa

Table 1 Means and standard deviations of variables measured in the Iberian Peninsula and Africa

Variable (unit)	Mean ± SD	*N*
Settlement area used surface (km^2)		
Total	317.26 ± 1235.50	103
I. Peninsula	64.17 ± 84.59	87
Africa	1693.41 ± 2819.08	16
Length of the stays (days)		
Total	18.03 ± 24.08	106
I. Peninsula	13.14 ± 13.05	86
Africa	39.05 ± 43.22	20
Nearest distance (km)		
Total	130.26 ± 199.94	37
I. Peninsula	71.50 ± 59.23	32
Africa	473.04 ± 361.66	5
Dispersal distance by hour (km)[a]		
Total	7.80 ± 12.28	6548
I. Peninsula	4.97 ± 9.14	3647
Africa	11.35 ± 14.60	2901
Percent of time in settlement areas		
Total	57% ± 15	13
I. Peninsula	50% ± 13	7
Africa	75% ± 14.7	6
Settlement events		
Total	6.62 ± 5.03	106
I. Peninsula	8.60 ± 5.08	86
Africa	3.33 ± 2.94	20
Number of areas used by each individual		
Total	3.3 ± 2.19	49
I. Peninsula	3.5 ± 2.76	35
Africa	2.33 ± 1.75	14

Highly significant differences between continents were found in all variables measured

[a]Only for individuals that dispersed in both Iberia and Africa

(Morandini et al. 2016; Ramírez et al. 2016). This could induce individuals to prospect more extensively in larger territories and, once they found one of these patches, such patches would be exploited for longer periods, thus leading to lower numbers of settlements. Conversely, the total number of areas used as settlement in both study areas was similar. Thus, although in Iberia monitored individuals had more settlement events than in Africa, they did not necessarily use new zones, so the number of temporary settlement zones per individual did not differ between the two continents. According to the Marginal Value Theorem, when the possibility of capturing prey falls below a certain level, an individual will consider whether or not it is advantageous to move to a new temporary settlement area, but not necessarily different from those previously used. In the study conducted in the Iberian Peninsula, Ferrer (1993b) documented between 3 and 8 different settlements for the individuals studied, and an average of 4.86 settlement events per individual in the period studied.

Temporary settlements were farther apart in Africa than in Iberia, as were distances travelled in dispersive movements outside temporary settlements. The irregularity in the distribution of the alternative prey and their seasonal character may have led the birds to expand the area of dispersion to find food and to accumulate greater distances during exploratory movements and, subsequently, a greater dispersion of the temporary settlements.

Given the coincidental extirpation of Spanish Imperial Eagle populations on both sides of the Gibraltar Strait in the 1960s, and the increasing number of reports of young Spanish Imperial Eagles in Africa in recent years, as the Iberian population continues to increase (Migres Foundation, unpublished data 2017), we suggest that there may be an increased flow of individuals into Africa coming from the "source" Iberian population. In addition, a breeding population eventually may be re-established in north Africa, but only if the Iberian population continues to increase.

Recently, electrocution has been the main cause of juvenile mortality in the species in Iberia (Calderón et al. 1988; Ferrer et al. 1991; Ferrer 2012). Fortunately, this situation has changed by correcting the most dangerous electrical lines (López-López et al. 2011; Ferrer 2012). The death of two of the monitored specimens by electrocution in Africa motivated a subsequent investigation that reported an additional three untagged Spanish Imperial Eagles and other large raptors had been electrocuted in the Guelmim settlement area in Africa (Amezian et al. 2015). We remain concerned that this threat will become an increased problem in North African territories now under rapid development.

Table 2 Results of a generalized linear mixed model with the size of settlement areas used as the response variable, sex and continent as fixed factors, and individual as a random factor

	Effect	df	MS effect	Df error	MS error	*F*	*P*
Sex	Fixed	1	7.32	5.56	3.21	2.281	0.1854
Continent	Fixed	1	129.04	36.99	2.70	47.683	**0.0000**
ID	Random	13	2.91	87.00	2.47	1.1792	0.3080

P values in bold indicate significance at the 0.05 level

Table 3 Results of a generalized linear mixed model, with days of stays in settlement areas as the response variable, sex and continent as fixed factors, and individual as a random factor

	Effect	df	MS effect	Df error	MS error	*F*	*P*
Sex	Fixed	1	1.28	7.04	0.72	1.770	0.2247
Continent	Fixed	1	12.38	30.89	0.49	25.270	**0.0000**
ID	Random	13	0.581	87.00	0.38	1.541	0.1187

P values in bold indicate significance at the 0.05 level

Table 4 Results of a generalized linear mixed model with mean distance moved by hour when young eagles were not in a settlement area as the response variable, sex and continent as fixed factors, and individual as a random factor

	Effect	df	MS Effect	Df Error	MS Error	*F*	*P*
Sex	Fixed	1	5.12	3.06	2.84	1.798	0.2706
Continent	Fixed	1	10.86	4.08	1.21	8.962	**0.0395**
ID	Random	4	1.26	443.00	0.25	4.913	**0.0007**

P values in bold indicate significance at the 0.05 level

Power lines using pylons with dangerous design (Ferrer 2012) would be a limiting factor increasing the sink effect for young eagles, making impossible a potential recolonization. After the present study, we now know the locations of temporary settlement areas for young eagles in Africa, providing us with critical knowledge to inform which power lines must be urgently retrofitted. Additionally, when existing dangerous power lines have been retrofitted and new bylaw regulations require power lines to be constructed using only safe designs, a species reintroduction program could accelerate any eventual successful recolonization (Morandini and Ferrer 2017b).

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