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COLONIZATION PROCESSES IN LONG-LIVED SPECIES: REINTRODUCTIONS AS EXPERIMENTAL APPROACH

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Contents

Introduction

Understanding how density-dependent and independent processes influence demographic parameters, and hence regulate population size, is fundamental within population ecology. As Newton 1979 commented: “Effective conservation of raptors ultimately depends on a thorough understanding of what regulates their numbers”.
Population regulation results from mechanisms that cause demographic density dependence: a negative feedback between population growth rate and population density (Newton, 1998). Identification of these mechanisms, as well as the way they operate, is of fundamental importance to ecology, and particularly for our understanding of colonization processes. To identify and measure these mechanisms, populations that have been reintroduced and monitored since the beginning of the process, constitute a useful source of valuable information (Whitfield et al., 2009).

➢ Colonization processes: hypotheses and predictions

It is widely accepted that small and isolated populations are particularly prone to extinction (Lande, 1993, 1998; Shaffer, 1981). Colonization of a new area constitutes a process where the relationship between density-dependent parameters and the growth of population is especially intense due to the small size and isolation of the population. Even though it is obvious that changes in density-dependent demographic parameters will have a profound influence on the viability of small and isolated populations, surprisingly few studies have studied these parameters in reintroduced populations. In consequence, it seems necessary to consider the influence of density-dependent parameters in the populations’ persistence to optimize the outcome of future reintroduction projects.

Productivity

The viability of a reintroduction project depends on its capacity to establish a self-sustaining population; in this sense, the possibility to produce more young than in an established and saturated population would contribute to the success of the colonization. Productivity has been defined as the number of chicks per number of territorial pairs in the population (Miguel Ferrer, Newton, & Casado, 2008). According to both the habitat heterogeneity and interference hypotheses, higher values for productivity should be recorded in a colonizing population than in an established one because of the greater availability of high quality territories or lower interference expected at low population densities.

BOX: Habitat heterogeneity hypothesis VS. Interference hypothesis

Some authors consider that, in territorial species, density-dependent depression of fecundity can arise from an increased frequency of agonistic encounters and interference, resulting in a hostile social environment that leads to a relatively uniform decrease in productivity among pairs. As densities rise, individuals would have a reduced fecundity but variance among individuals is not expected to change (A. A. Dhondt & Schillemans, 1983; Fretwell & Lucas, 1970; Lack, 1966).

Other authors, however, have proposed that density-dependent depression in fecundity results from habitat heterogeneity (Kadmon, 1993). In a low-density population, individuals will select the best of the available habitat, and the habitats occupied should be of similarly high quality. Variance in fecundity among individuals is expected to be low. But as density increases, a greater proportion of individuals are forced to occupy lower quality habitat. Thus, mean population fecundity decreases and variance in fecundity increases (Andrewartha & Birch, 1954; A. Dhondt, Kempenaers, & Adriaensen, 1992; JL, 1969). These two hypotheses generate the same predictions for the response of mean fecundity in an increasing population; as density increases, mean population fecundity declines. Predictions for the expression of fecundity variance, however, are different. For the "interference" hypothesis, no relationship is expected between density and variance in fecundity. For the "habitat heterogeneity" hypothesis, fecundity variance must increase with density, because at high densities more poor sites (leading to lower fecundity) are occupied; additionally, fecundity within in good sites of the same population is expected to be equal in both low- and high-density situations.

Age of first breeding

Age of first breeding is an important component of lifetime reproduction in raptors, and the proportion of individuals that die without breeding increases each year that breeding is delayed (Newton, 1979). Long- lived raptor species often exhibit prolonged periods of delayed maturity; some of the individual variation in age of first breeding is related to favorable local conditions or to depleted populations leaving territories vacant (Newton, 1976).

Recently, several studies (Miguel Ferrer, Bildstein, Penteriani, Casado, & de Lucas, 2011; Miguel; Ferrer, Otalora, & García-Ruiz, 2004) showed that density-dependent variation in the age of first breeding is critical to the long-term survival of small isolated populations of long-lived species with deferred sexual maturity. This is because density-dependent variation in the age of first breeding buffers population fluctuations and, consequently, increases the persistence of these populations. This buffering effect is such that at low densities, individuals tend to reproduce at younger ages, whereas at higher densities the average age of first breeding increases. Variability in the age of entry into the breeding cohort enables populations to remain closer to carrying capacity, significantly affecting population persistence. This helps to explain the persistence of very small populations of long-lived birds with deferred sexual maturity and density-dependent.

Other authors suggest that high breeding investment in early life may depress survival probability and accelerate senescence (Patrick & Weimerskirch, 2015). However, in long-lived territorial birds, entry in the breeding pool of the population brings a reduction in annual mortality (Miguel; Ferrer et al., 2004). In this situation, to entry in the breeding sector as soon as possible would be advantageous.

In addition, changes in population size and density can determine the availability of potential partners or territories (Kokko, Harris, & Wanless, 2004). In a low-density situation, the habitat heterogeneity hypothesis, suggest high availability of high quality territories. Knowing that the main limiting factor on reproduction is the availability of potential nesting territories (Newton, 1979) in a colonizing process, studied through reintroduction projects, we would expect to see an initial reduction in the age of first breeding, with this age getting later as the population grew.

Sex ratio

Offspring sex ratio adjustment according density is another phenomenon described in saturated and small populations (Miguel Ferrer, Newton, & Pandolfi, 2009; Santoro, Green, Speakman, & Figuerola, 2015).There are two main theoretical frame-works: (1) one postulating that parents should adjust offspring sex ratio depending on predictable sibling cooperation or competition (local mate competition, local resource competition or local resource enhancement) (Morandini & Ferrer, 2015), and (2) one proposing that adaptive sex ratio adjustments depend on the specific conditions of parents (Trivers & Willard, 1973). An increased reproductive effort as a response to decreasing residual reproductive value (Pianka & Parker, 1975) is expected. In consequence, and considering that the relationship between sexual size dimorphism and differential costs has been demonstrated in dimorphic species (Santoro et al., 2015), at low densities, we expect a offspring sex ratio deviated to the cheaper sex and, when densities rise, the sex ratio deviation would swing towards females. When the proportion of immatures in the population is high, the offspring sex ratio of the population will tend to the cheaper sex (Miguel Ferrer et al., 2009). However, to separate density and age of breeders is difficult in declining populations or not monitored colonizing populations, because the proportion of immatures occupying breeding territories is related to the density of those populations.

In the reintroduction project discussed in this thesis, all released individuals were identified and could bel accurately identified and monitored throughout their lives, giving the opportunity to relate offspring sex ratio with the age of breeders, breeding experience and number of breeding pairs in the population. We expected to find a surplus of males during the first stage of the colonization process and of females when the new colonists have reached higher densities.

Dispersal patterns

Dispersal is one of the most important yet least understood phenomena in population biology, ecology and evolution (Gadgil, 1971). Knowledge of the distance moved by animals during dispersal is therefore fundamental to our understanding of many ecological and evolutionary processes, as well as to the design of successful conservation strategies (R Muriel, Morandini, Ferrer, & Balbontín, 2015; Roberto Muriel et al., 2016).

Dispersal can affect population persistence through genetic and demographic linkage within metapopulations (Dale, 2001; Margalida et al., 2013; Wadgymar, Cumming, & Weis, 2015) and through rapidity or form of geographic spread in establishing and introduced populations (Lensink 1997, South &Kenward 2001, Gammon & Maurer 2002). Greenwood & Harvey (1982) suggested that the movement of an animal between its birth site and the site where it first reproduces be termed 'natal dispersal', to distinguish it from 'breeding dispersal', which is the subsequent movement of adults between sites of reproduction. The movements undertaken by juveniles once they become independent from their parents are often denominated 'juvenile dispersal' (Miguel Ferrer, 2001; González et al., 2006).

Movements of individuals of long- lived vertebrates during the 'juvenile dispersal' are especially informative, because it is during this period when mortality rates are highest. In addition,it is during this period that dispersers prospect their environment to gather information on habitat quality essential for movement and settlement decisions,which eventually determine the effective natal dispersal (Clobert, Danchin, Dhondt, & Nichols., 2001).Consequently, estimation of the dispersal distances during juvenile dispersal are critical in designing reintroduction programs.

Mostly of long- lived raptors are attracted by the presence of conspecific showing the called ‘social attraction’. Reintroduction programs typically starts with no breeding pairs in the release area, causing dispersing young to move on and search elsewhere. Consequently, under the social attraction hypothesis we expect an increase in dispersal distances for young without breeding adults in the area. Reintroductions projects present a unique long-term opportunity for the study of dispersal in a colonizing population.

BOX: Competitive displacement hypothesis VS. Wandering hypothesis

In most dispersal studies of birds a typical leptokurtic and skewed distribution has been found (Miguel Ferrer, 1993a, 1993b; Newton, 2010). It has been suggested that such a distribution could be generated by competition among dispersing individuals during territory acquisition (i.e. competitive displacement hypothesis). Those individuals that disperse longer distances, forming the tail of the distribution, are individuals at lower competitive advantage, which would probably be the last to hatch and also take a longer time after fledging to disperse (Waser, 1985). An alternative explanation for variation of dispersal distances was proposed by Ferrer (1993): in the ‘wandering’ hypothesis, a leptokurtic distribution of dispersal distances is also expected but with individuals in better nutritional condition leaving the natal area earlier and moving longer distances, forming therefore the tail of the distribution. In contrast, those young in poorer nutritional condition that hatched later in the season dispersed short distances, remaining closer to their natal nests.

➢ Reintroductions as experiments to study colonization processes

The reintroduction of species to fulfill conservation objectives is a relatively recent activity that has developed as a consequence of increasing global awareness of the need to conserve biological diversity in the face of species extinctions (Philip J Seddon, Griffiths, Soorae, & Armstrong, 2014). Reintroduction, defined by the IUCN (1998, p. 6) as “an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct”, are increasingly considered as an important component of conservation activities, in Europe and globally (D. P. Armstrong & Davidson, 2006; Arts, Fischer, & van der Wal, 2012; Ewen, Soorae, & Canessa, 2014). Because individuals are usually reintroduced into areas with zero or low density, they provide an opportunity to study the dynamics of populations during the colonization process (D. P. Armstrong, Davidson, Perrott, Roygard, & Buchanan, 2005). In the early years many reintroduction projects were purely management manipulations, often doomed to failure due to poor planning, inappropriate founder animals, low sample sizes, and lack of resources. The attitude was largely "let's put some animals out there and see if they survive." Post-release monitoring was negligible or absent so that causes or timing of failures were unknown, as were the processes by which reintroduced populations may have become established (Philip J. Seddon, Armstrong, & Maloney, 2007). However, the prevalence of adequate post-release monitoring increased and well-documented failures as well as successes have increasingly found their way into the scientific literature (Figure 1).

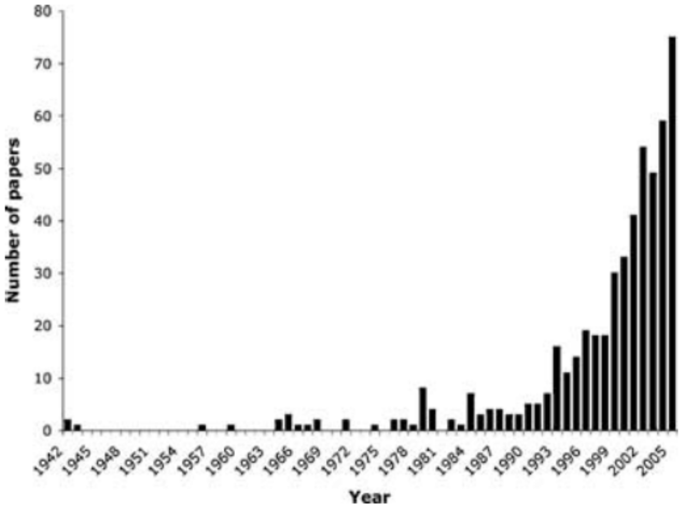

Figure1: Number of reintroduction-related papers published in peer-reviewed journals by year since the first records located up to 2005 (Philip J. Seddon et al., 2007).

Although the situation improved, a recent review suggests that the success rate of translocations is still generally low, with many attempts having resulted in either failure or partial success (Chauvenet, Ewen, Armstrong, Blackburn, & Pettorelli, 2013), and parameters to quantify the success of a reintroduction are still being debated (Robert et al., 2015; P. J. Seddon, 2015) (Table 1).

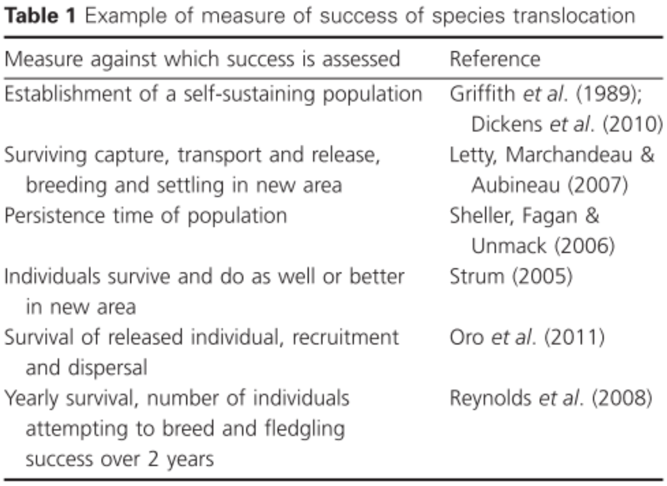

Table 1 Example of measure of success of species translocation

Measure against which success is assessed	Reference
Establishment of a self-sustaining population	Griffith *et al.* (1989); Dickens *et al.* (2010)
Surviving capture, transport and release, breeding and settling in new area	Letty, Marchandeau & Aubineau (2007)
Persistence time of population	Sheller, Fagan & Unmack (2006)
Individuals survive and do as well or better in new area	Strum (2005)
Survival of released individual, recruitment and dispersal	Oro *et al.* (2011)
Yearly survival, number of individuals attempting to breed and fledgling success over 2 years	Reynolds *et al.* (2008)

Identification of parameters involved in the colonization of a new area could prove useful both to improve future conservation actions and to limit the definition of reintroductions success. In addition, reintroductions provide better opportunities to highlight fundamental insights into population ecology (D. Armstrong & Seddon, 2008; Philip J. Seddon et al., 2007) compared with natural colonizations because:

(1) Reintroductions represent the controlled expansion of a population into an effectively novel environment, initially from a limited number of simulated ‘natal’ sites;
(2) A successfully reintroduced population permits the study of population processes over a wide range of population abundance and competitive influence; all individuals are of known origin; and
(3) Individuals can be more readily marked and therefore followed over their lifespans; and long-term detailed monitoring programs are often incorporated.

- **Long lived raptors as models for study.**

Raptors constitute a good study models to investigate the demography of colonizing populations. Raptors include some of the most extreme examples among birds of low reproductive rates, long deferred maturity and great longevity; and they can be studied over long periods of years. Moreover, most species are territorial, so it is easy to judge how filled is a habitat at any one time.

Most of large raptors show social attraction behavior: the tendency to breed inside the limit of other existing populations. This behavior limits the tendency of populations’ to expand to areas far from other existing populations and, in consequence, the typical growth of these expanding populations is around the peripheral limits of the already occupied areas. The location of nests is relatively easy and to monitor individuals it is possible to ring both chicks and adults. Also, large raptors are big enough to carry radio emitters that permit the detailed study of their dispersal movements. Given sufficient funding, all these factors combine to allow the detailed study of their expanding populations over long periods of years.

Osprey (*Pandion haliaetus*)

The osprey is a widespread fish-eating raptor, with breeding dispersion ranging from solitary to loosely colonial (Poole, 1989). Breeding individuals defend their nest site, but not their feeding places (Poole, 1989). In many raptors, territoriality is the main source of density dependence (Newton, 1998), although in the Osprey territory is mainly limited to the nest site. Although osprey populations are large and show stabilized or increasing trends in central and northern Europe, the situation is currently different in the Mediterranean basin, where there are few, small and isolated populations (Monti et al., 2014; Saurola, 1997). The species was extirpated from mainland Spain after 1981, when the last pair bred in the province of Alicante (Urios, Escobar, Pardo, & Gómez, 1991), after a continuous decline since at least the 1960s.

To accelerate the return of the Osprey to the Iberian Peninsula, a reintroduction program was commenced in 2003 in the region of Andalusia (Casado & Ferrer, 2005). Between 2003 and 2013, 180 young Ospreys were released, by means of hacking, at two locations: a reservoir in the province of Cádiz and a coastal marshland in the province of Huelva. In 2009, the first breeding pair successfully reared three chicks in the Odiel Marshes, the first breeding in mainland Spain for about 27 years. The present reintroduced population at the two sites together reached 21 territorial pairs in 2016.

Spanish Imperial eagle (*Aquila adalberti*)

The Spanish Imperial Eagle is a large bird of prey (2500-3500 g.)(Miguel Ferrer & de Le Court, 1992) with a low reproductive rate and an immaturity period of 4-5 years (Miguel Ferrer & Calderón, 1990). Before the reintroduction project, the Spanish Imperial eagle population at Doñana was apparently isolated from other breeding populations of the same species, the nearest of which was 300 Km away.

The Spanish Imperial eagle reintroduction started in 2002, and during the next 10 years 92 young were released in the province of Cádiz. In 2009, the first territorial pair became established in Piletas-Fte Rey (Cádiz) and in 2010 the first breeding pair reared two chicks in Ahijones Altos. Between 2010 and 2016, 34 chicks were hatched in the province of Cádiz, establishing a new population that reached at least 4 breeding pairs in 2017.

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Aims

The main objective of this thesis is to understand the mechanisms, including the adaptive behavioral strategies, that allow even a small population to survive for a longer time than predicted by simple theoretical models, as historical records of real populations suggest. With the reintroductions of Spanish Imperial eagle and Osprey in southern Spain as models for study, we investigated the parameters involved in making possible colonization of new areas by species with slow demography, and assessed the effectiveness of reintroductions as a means of recovering species.

To achieve this overall goal, the following specific objectives were pursued:

1. To determine the real possibilities and effectiveness of reintroductions, compared with natural colonizations.

2. To establish the success of colonizations in human dominated landscapes. Because most natural colonizations and reintroductions in Europe are taking place in such landscapes, it is important to assess their viability.

3. To describe the behavior of individuals in reintroduced populations and find how it compares with the behavior of individuals in established and high-density populations.

4. To investigate mechanisms that facilitate the colonization of a new area by species with slow demography and their consequences in the growth of reintroduced populations.

5. To propose management criteria to optimize the development of future reintroduced populations.

These aims are developed in 4 chapters presented as 9 scientific papers, some of which have already been published.

Supervisor's Report

Dr. Miguel Ferrer and Dr. Ian Newton, directores de la tesis doctoral titulada **COLONIZATION PROCESSES IN LONG-LIVED SPECIES: REINTRODUCTIONS AS EXPERIMENTAL APPROACH** certifican que la disertación presentada, ha sido llevada a cabo por Virginia Aguilar Clapés- Sagañoles (Virginia Moradini) en su totalidad y es apta para ser presentada bajo la modalidad de compendio de artículos.

Los artículos presentados son los siguientes:

- Capítulo I:

Predators' expansions to human dominated landscapes: Spanish Imperial eagle in southern Spain as a case of study. Morandini V. (2017)

Biodiversity and Conservation (2016): en revisión. Impact factor (2016): 2.258

Natural expansion versus translocation in a previously human- persecuted bird of prey. Morandini V., de Benito E., Newton I and Ferrer M. (2017).

Ecology and Evolution 2017; 00:1–7. https://doi.org/10.1002/ece3.2896

Impact factor(2015):2.537

- Capítulo II:

Floater interference reflects territory quality in the Spanish Imperial Eagle Aquila adalberti: a test of a density-dependent mechanism. Ferrer M., Morandini V. and Newton I. (2015)

Ibis 2015; 157(4): 849-859. Impact factor(2015): 1.804

Juvenile dispersal distances, competition, philopatry and social attraction: an experiment with Spanish imperial eagles. Morandini V. and Ferrer M. (2017).

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Journal of Avian Biology (2017): accepted. Impact factor (2015):2.192

- Capítulo III:

Density-dependent parameters of reintroduced populations: age of first breeding and the overestimation of extinction risks. Morandini V., Dietz S. and Ferrer M. (2017). In prep.

Sex specific dispersal and sex ratio adjustment as a strategy to optimize colonization processes Biological Conservation (2017): submitted. Impact factor (2015): 3.985

- Capítulo IV:

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PLoS ONE 12 (4): e0174186. https://doi.org/10.1371/journal. pone.0174186. Impact factor(2016):3.54

Chapter 1: The end of the human-predators war in Europe.

During the previous two centuries, many predators have been so heavily persecuted by people that they have suffered substantial population declines and geographic range contractions, as they have disappeared altogether from most of their former range. Their habitats and distributions have generally been greatly fragmented (Chapron et al., 2014; Ripple et al., 2014). In order to protect wildlife, special natural reserves for wildlife were set aside in the past, with the aim of separating nature from people. (Chapron et al., 2014). However, in modern times, our relationship with nature has changed dramatically and the direct historical war against wildlife seems to be ending in southern Europe (Martínez-Abraín, Crespo, Jiménez, Gómez, & Oro, 2009) and, in consequence, large predators are expanding their range, re-occupying parts of their former range. An alternative model, "allowing people and predators together" (coexistence model), following a landscape-scale conservation approach, is taking hold, allowing wildlife to expand beyond the limits of protected areas. In Europe, as in many other parts of the world, we are increasingly managing a complex socio-ecological system in which wildlife as well as humans are an integral component of landscapes (Sutherland et al., 2010).

It seems that this change in human attitude has brought an increasing desire to restore wildlife from where was extirpated in the past. In fact, the increase of reintroduction programs and conservation actions to preserve large predators' habitat clearly reflects the rising cultural value attached to them.

It is expected, therefore, that the number of reintroductions will increase in Europe in the coming years and that this will be done largely in human dominated landscapes. Thus, assessing the utility of reintroductions in recovering previously exterminated species in human dominated landscapes becomes a necessary step underpinning this process.

This thesis starts with the study of the expansion of a previously persecuted bird of prey, the Spanish Imperial eagle, in southern Spain.

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Chapron, G., Jhon, D. C. L., Manuela, von A., Huber, D., Andrén, H., López-bao, J. V., … Boitani, L. (2014). Recovery of large carnivores in Europe ' s modern human-dominated landscapes. *Science*, *346*(6216), 1517–1520.

Martínez-Abraín, A., Crespo, J., Jiménez, J., Gómez, J. A., & Oro, D. (2009). Is the historical war against wildlife over in southern Europe? *Animal Conservation*, *12*(3), 204–208. http://doi.org/10.1111/j.1469-1795.2009.00239.x

Ripple, W. J., Estes, J. a, Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 1241484. http://doi.org/10.1126/science.1241484

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Predators’ expansions to human dominated landscapes: Spanish Imperial eagle in southern Spain as a case of study.

Morandini, V. (2017)

Biodiversity and Conservation, under review

Predators' expansions to human dominated landscapes: Spanish Imperial eagle in southern Spain as a case of study.

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Abstract:

Change in human attitude toward top predators is allowing an increase in distribution of previously human persecuted species. The separation model that kept wildlife in protected areas with the objective to protect wildlife from ourselves, is changing to the coexistence model as the human persecution decrease. Now a day, in Europe many recent conservation actions are related to biodiversity in human dominated landscapes. Here I analyze a Spanish Imperial eagle population in southern Spain and nighttime lights as a value of human activity from 2001 to 2015.

Results show a decrease in the distance to nighttime lights over the studied period. Moreover, I found higher productivity values in territories closer to human activity. I concluded that with a change in human attitude, the availability of territory for the species is increasing and, without a direct human persecution, this new area could represent a high quality habitat for the species.

Those changes will have potential influence in the selection of available habitat for species, with direct consequences in future reintroduction projects. For that, I suggest revising the habitat selection criteria for species previously human persecuted.

***Keywords**: human attitudes, nighttime lights, human activity, reintroductions, territory quality.*

Introduction

During the previous two centuries, many predator species have experienced substantial population declines, geographic range contractions, and fragmentation of habitat distribution (Ripple et al., 2014). Killing by people remains the greatest threat to the persistence of many top predators throughout the world including tropical areas (A. Benítez-López et al., 2017). However the direct war against wildlife seems to be waning in Europe (Martínez-Abraín, Crespo, Jiménez, Gómez, & Oro, 2009). As some authors suggested, European and North American predators expansion, extinction and persistence patterns are more adequately explained by management policy and its enforcement than by human population density (Chapron et al., 2014; Linnell, Swenson, & Andersen, 2001).

European and North American experience clearly shows that predators and their prey can persist at high human densities (Linnell et al., 2001; Martell, Englund, & Tordoff, 2002; Rutz, 2008). In this context, the separation model "keeping people and predators apart" is changing to "allowing people and predators together" (coexistence model; Chapron *et al.*, 2014). In fact, visitors to Europe from outside the continent are sometimes surprised to learn that most wildlife persist in intensively managed private land and that many recent conservation actions are related to biodiversity on farmland (Boitani & Sutherland, 2015).

There have been previous attempts to quantify the impact of human activities on wildlife (Ana Benítez-López, Alkemade, & Verweij, 2010; M de Lucas, Janss, & Ferrer, 2007; Manuela De Lucas, Janss, & Ferrer, 2005; Miguel Ferrer, de La Riva, & Castroviejo, 1991; L. M. González, Arroyo, Margalida, Sánchez, & Oria, 2006; Hernández-Pliego, de Lucas, Muñoz, & Ferrer, 2015; Marques et al., 2014). And consequently, a many studies focused on impact mitigation of human infrastructures on wildlife (Manuela de Lucas, Ferrer, & Janss, 2012; López-López, Ferrer, Madero, Casado, & McGrady, 2011; Negro & Ferrer, 1995; Soutullo, López-López, & Urios, 2008).

Even though human activities are still affecting wildlife (Ana Benítez-López et al., 2010), I suggest that a change in human attitudes towards large predators is allowing them to expand out from their past refuges (Chapron et al., 2014; Morandini, de Benito, Newton, & Ferrer, 2017) pushing the population boundaries closer to human activities and infrastructures. This recolonization process is allowing species to recolonize areas where they were previously extirpated and now, with a lessening of human persecution, could represent high quality areas for these species.

Location and intensity of nocturnal lighting is one of the clearest signs of human activity that can be measured from space (Elvidge et al., 1999, 2009). Images of the Earth at night are therefore an extremely useful tool for research involving human communities and their interaction with the environment. In contrast with models that analyze human activity by human infrastructures, the analysis of nightlight lead to discriminate the real use of human constructions excluding for example abandoned areas.

The present distribution of Spanish Imperial eagles (*Aquila adalberti*) distribution in Andalusia is the result of direct human persecution in the past (Morandini et al., 2017). In the present study, we selected an expanding Spanish Imperial eagle population and analyzed productivity, parental age and distance to human activities represented as nighttime lights. The aim of this study was to analyze whether proximity to human activities continue to limit the expansion of predator distributions when direct human persecution has mostly disappeared and human attitudes toward birds of prey species has changed.

Material and methods

Species

During the study period, work was focused on a population located mainly in the Sierra Morena in the north limit of Andalusia (≈38°22′N 3°50′W). Andalusia occupies a large part of the southern Iberian Peninsula and has a wide altitudinal range (0–2,000 m.a.s.l.), with a dry- humid Mediterranean climate (annual rainfall: 300–2,000 mm, average annual temperature: 9–19°C). The landscape consistes of a mosaic of Mediterranean forests in hilly and mountainous areas. The Spanish imperial eagle *Aquila adalberti*, a globally threatened bird of prey (Vulnerable in the IUCN Red List, BirdLife International 2008), and its current breeding population has been estimated at around 500 breeding pairs (National Working Group, unpublished data 2016) located entirely in the Iberian Peninsula. The species is a large (2,500–3,500 g) long- lived raptor, monogamous, sedentary and territorial, with a low annual productivity averaging 0.75 chicks/pair (Ferrer & Calderón, 1990).

We considered as a breeding event when a pair showed breeding behavior (nest construction, defense, incubation, etc.). All nests were monitored from the beginning of the breeding season (January–February, during courtship and nest site selection; Ferrer, 2001) until the last chick left the natal territory, and data on breeding, distance to nearest neighbour's nest (NND), and the pair's plumage state were recorded. We refer to all pairs with at least one member in subadult plumage as "immature pairs." Productivity was calculated as the number of fledglings per nest. To allow for annual variation in reproductive performance, we adjusted productivity (number of fledglings) for year effects by subtracting annual means from the raw data. Corrected data are referred to as relative values (Ferrer & Bisson, 2003; Horváth et al., 2014; Penteriani, Balbontin, & Ferrer, 2003).

Nighttime lights

We calculated the night light impact from high resolution satellite imagery (NOAA National Geophysical Data Center 2012). The files are cloud-free composites made using all the available archived DMSP-OLS smooth resolution data for calendar years. The annual average brightness level is represented in units of 6 bit digital numbers (DN) spanning the range 0 to 63. Area where DN values equal 63 (saturated light pixels) occur in the center of cities which are not suitable nest habitat for Spanish Imperial eagles. The data are available in http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html.

We focused our study around low thresholds (DN <6), because higher thresholds eliminates large areas of less developed land and attenuates smaller lights while fragmenting larger agglomerations connected with dimmer regions (Small, Elvidge, Balk, & Montgomery, 2011),. With the values of brightness, I have make a map with the limits of the nighttime light and the location of the Spanish Imperial eagles nests (Figure 1) and measured distances from each nest to the nighttime light limit every year.

Statistical analysis

I analyzed differences in breeding parameters and distances to nearest neighbor nest and night-lights using STATISTICA 13. The studied population increased from 11 territories in 2001 to 91 in 2015 and 745 breeding attempts registered during the study period. We conducted a GLMM analysis with standardized productivity per year as dependent variable, distances from each nest to the nighttime light limit and distance to the nearest nest as covariables, and age of parents as a fixed factor. To remove the effect of territory quality, I compared productivity between immature and adult pairs present in the same territory with a nonparametric Wilcoxon signed- rank test for pooled data for the 54 territories occupied in different years by adult- immature pairs.

I tested for differences in distances from nests to nighttime lights, between age classes and studied period (ANOVA). For that, I separated the study in two different periods, 2001-2007 and 2008-2015.

Results

The population increased from 11 to 87 breeding pairs during the studied period. New territories tended to appear around the peripheral limits of existing breeding pairs. Near neighbor distances varied from 6.6 km to 7 km and non-significant differences in NND were recorded between the two periods (ANOVA. Study period: F (1.729) =0.533, P=0.47).

The percentage of immature breeding pairs in the population varied according the period of the study; from 31% in 2001-2007 to 60% in 2008-2015.Productivity changed from 1.18 to 1.11 and variance of productivity decreased from 1.15 to 0.99.

Productivity was related to proximity to human activities, age of parents and territory identity, (Table 1). More productive nests and with younger parents were closer to nighttime lights.

No differences were found in productivity between adult and immature pairs in the same territory (sign test. N = 54, Z = 1.497, p = .134) suggesting that territory identity is related with breeding pairs age. Nest distance to nighttime lights decreased over the studied period being significantly different between the first (Mean 4.9 km; SD+- 182.85 m) and the second period (Mean 4.4 km; SD+- 129.43 m), (ANOVA Study period: F (1, 729) =5.4508, p= 0.019).

Results show that young pairs tend to breed closer to human infrastructures (ANOVA Parental age: F (1, 729) =6.8777, p=0.008) but with higher NND than adults pairs (ANOVA Parental age: F (1.729) =14.34, p= 0.0001).

Discussion

With a change in our approach to wildlife and the reduction of direct human persecution in Europe (Martínez-Abraín et al., 2009; Whitfield, 2004) the recolonization of past distribution areas is now a reality (Chapron et al., 2014). This increase in number and distribution of predators (Evans et al., 2009; Morandini et al., 2017) leads to the inevitable sharing of human dominated landscapes.

The main distribution of the Spanish Imperial eagle was determined by past human persecution (Morandini et al., 2017). Conservation measures, as electrocution mitigation (López-López et al., 2011) or a decrease in shooting and poisoning, enable the recovery of the species. Our studied population growth from 11 to 87 breeding pairs in fifteen years. As the Spanish Imperial eagle show strong philopatric behavior (Miguel Ferrer, Morandini, & Newton, 2015) the natural tendency is to breed close to other existing pairs. However, the possibility to occupy an existing territory is related with the age of individuals (Miguel Ferrer & Bisson, 2003; Miguel Ferrer et al., 2015; Penteriani, Balbontin, & Ferrer, 2003). Thus an adult individual has higher chance to occupy a previously occupied nest or territories closer to other nest. In this sense, results of this study show how NND is related with parental age, with higher NND in younger pairs is reflected in a non-significant increase in the NND over the years. This tendency suggests that the increase in the number of breeding pairs was accompanied by an expansion of the occupied area and not with a saturation of the existing populations. Also, the increase in the percentage of young pairs in the population and the decrease of the productivity variance suggest the expansion of population into available and high quality territories (Miguel Ferrer & Donazar, 1996; Miguel; Ferrer, Otalora, & García-Ruiz, 2004). This expansion means that the occupation of human dominated landscapes from the past refuges areas where the species was relegated by human persecution (Horváth et al., 2014; Morandini et al., 2017). As the NND increased, the distance to human dominated landscapes decreased, but that decrease was not matched with a decrease in productivity. Territories closer to human activity were significantly more productive than nests further away.

These results suggest that past refuges areas were not necessarily in the best habitat for the species and were probably the only places where the species was not persecuted. As other studies suggest these past habitats seem to be occupied mainly because their inaccessibility for humans (Luis Mariano González, Bustamante, & Hiraldo, 1992).

The fact that nowadays such species are recolonizing their past distribution areas and can persist in these novel ecosystems, encourages their reintroduction even to human dominated landscapes with the appropriate conservation measures. Is necessary to revise the criteria of habitat selection for species that suffered from human persecution in the past and where now human attitudes have changed and persecution has decreased. Consequently, the enlarge of the available habitat for the species creates new opportunities to reintroduce species to more distant locations than the main habitat occupied by previously persecuted species (Morandini et al., 2017).

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Figure 1: Distribution of studied Spanish Imperial eagles nests and nighttime lights during the studied period (2001-2015). Nighttime light is represented with grey colors and nests with black spots. Dark grey represents DN values equals to 21 and light grey represents DN values of 5.

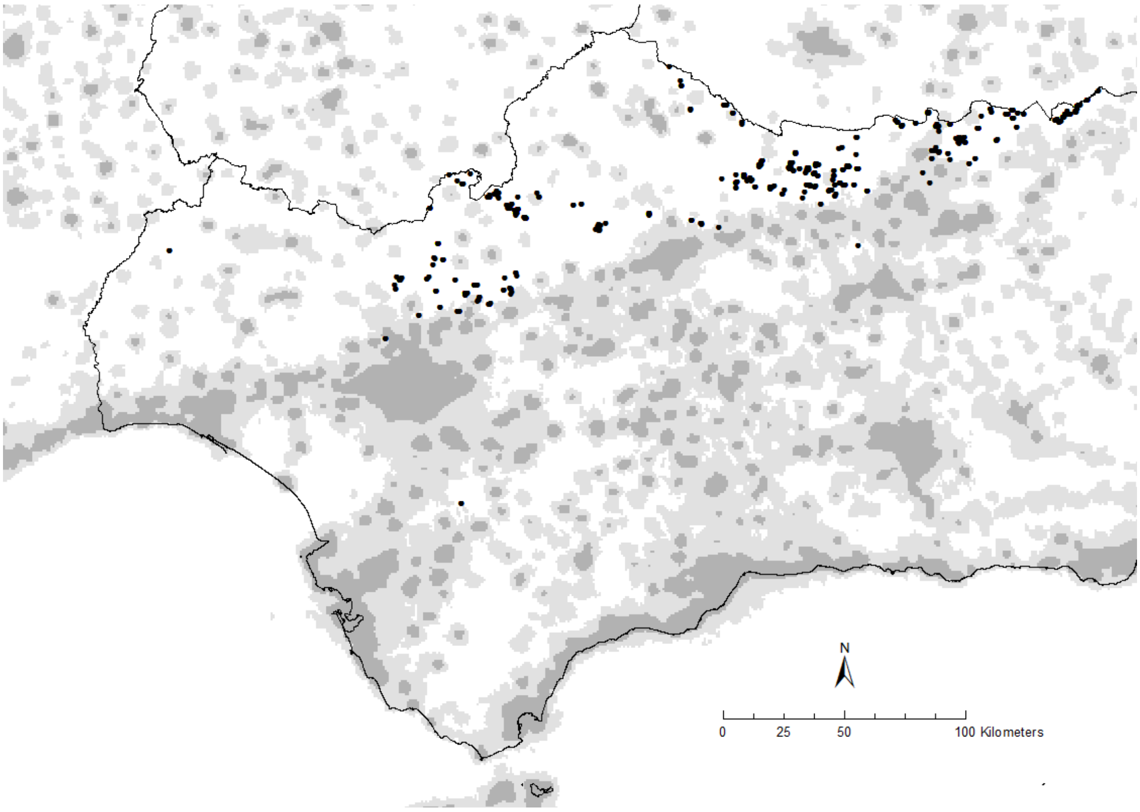

Figure 2: Number of Spanish Imperial eagles breeding pairs (11 in 2001 and 87 in 2015) and distances in meters from nests to nighttime lights. Number of breeding pairs is represented with a dotted line and distances nest-nighttime light with a continuous line.

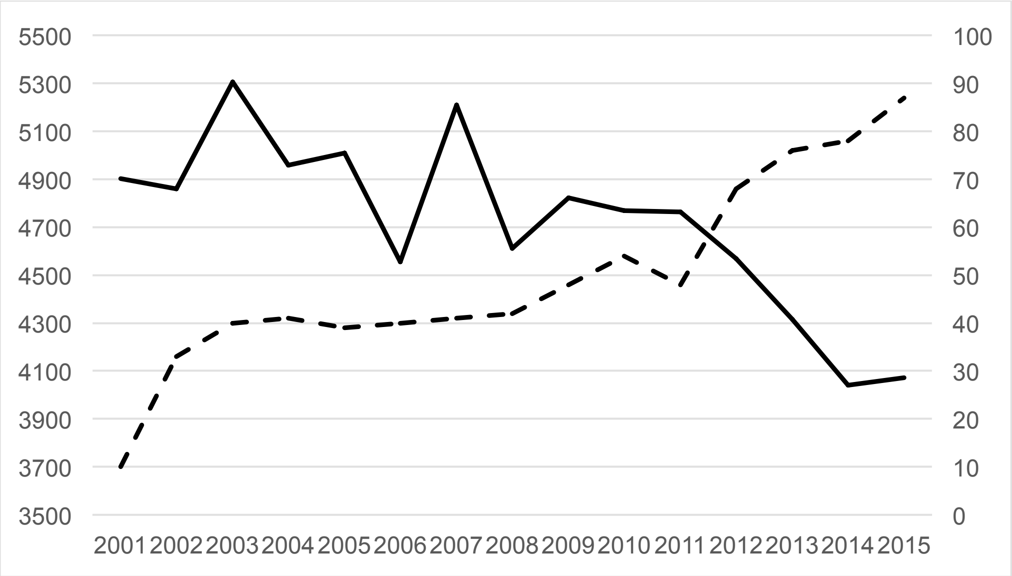

Table 1: Results of the generalized linear mixed model of factors influencing relative productivity in Spanish Imperial eagle breeding pairs, including Age of breeding pairs as a fixed effect, distances nests-nighttime lights and near neighbor distance (NND) as covariates and territory identity as a random factor. Significant terms were found in distances nests-nighttime lights, age of pair and territory.

MS Type: I	df Error computed using Satterthwaite method * Tests assume that entangled fixed effects are 0						
	Effect (F/R)	df Effect	MS Effect	df Error	MS Error	F	p
Distances nests-nighttime lights	*Fixed	1	8.23393	99.0569	1.643376	5.01037	0.027434
NND	*Fixed	1	0.34212	139.2776	1.391576	0.24585	0.620795
Age of pair	Fixed	1	42.86141	74.4746	1.143693	37.47633	0.000000
Territory	Random	92	1.70752	14.3490	0.697535	2.44794	0.029462

Natural expansion versus translocation in a previously human- persecuted bird of prey

Morandini, V., de Benito, E., Newton, I. and Ferrer M. (2017) Ecology and Evolution; 00:1–7. https://doi.org/10.1002/ece3.2896

Natural expansion versus translocation in a previously human-persecuted bird of prey

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Abstract:

Abstract Many threatened species in Europe have been expanding their distributions during recent decades owing to protection measures that overcome historical human activity that has limited their distributions. Range expansion has come about via two processes, natural expansion from existing range and reintroductions to new ranges. Reintroductions may prove to be a better way to establish populations because individuals are less subject to competitive relationships lowering breeding success than individuals expanding from existing populations. Whether this is true, however, remains uncertain. We compared success of breeding pairs of an expanding and a reintroduced population of spanish imperial eagles monitored for over 15 years in the south of Spain. We found significant differences in productivity between breeding pairs of each population. Newly established territories in reintroduction areas were almost three times more productive than new territories established as individuals expanded out from an existing population. We conclude that among these eagle populations reintroduced to new areas may fare as well or better than individuals expanding out form existing populations.

Keywords: *Aquila adalberti, human disturbance, natal dispersal, refuges areas, reintroduction*

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ORIGINAL RESEARCH

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Natural expansion versus translocation in a previously human-persecuted bird of prey

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Abstract

Many threatened species in Europe have been expanding their distributions during recent decades owing to protection measures that overcome historical human activity that has limited their distributions. Range expansion has come about via two processes, natural expansion from existing range and reintroductions to new ranges. Reintroductions may prove to be a better way to establish populations because individuals are less subject to competitive relationships lowering breeding success than individuals expanding from existing populations. Whether this is true, however, remains uncertain. We compared success of breeding pairs of an expanding and a reintroduced population of spanish imperial eagles monitored for over 15 years in the south of Spain. We found significant differences in productivity between breeding pairs of each population. Newly established territories in reintroduction areas were almost three times more productive than new territories established as individuals expanded out from an existing population. We conclude that among these eagle populations reintroduced to new areas may fare as well or better than individuals expanding out form existing populations.

KEYWORDS
Aquila adalberti, human disturbance, natal dispersal, refuges areas, reintroduction

1 | INTRODUCTION

Habitat loss and persecution has caused large predators to be largely confined to landscape locations that are subject to minimal human activity (Brown, McMorran, & Price, 2011; Chapron et al., 2014; Seddon, Griffiths, Soorae, & Armstrong, 2014). Changing human attitudes toward predators over recent decades (Pereira & Navarro, 2015) has led to growing concern over their fate to the extent that there are now widespread decreases in human persecution. Consequently, populations of predators are able to expand their ranges to recolonize areas from which they were previously extirpated (Chapron et al., 2014; Horváth et al., 2014). It also created opportunity to reintroduce predators to more distant locations that offer suitable habitat both (reinforcements and reintroductions) and outside of the historically indigenous range (assisted colonization) (Seddon et al., 2014). Natural range expansions and recolonization of vacant range are common in many species (Caniglia, Fabbri, Galaverni, Milanesi, & Randi, 2014; Gadenne, Cornulier, Eraud, Barbraud, & Barbraud, 2014; Kojola et al., 2006; Martin, Koeslag, Curtis, & Amar, 2014). Reintroductions involve the release of individuals into suitable vacant habitat where the species may or may not have been extirpated (Seddon, Armstrong, & Maloney, 2007).

It has been proposed, however, that individuals undergoing natural range expansion are constrained by density-dependent reductions in mean productivity because they may be forced into poorer-quality habitat by individuals holding established territories (Ferrer & Bisson, 2003; Ferrer & Donazar, 1996; Ferrer, Newton, & Casado, 2006, 2008; Korpimaki, 1988; Newton, 1998; Sergio & Newton, 2003). This comes about because in a low-density population, individuals entering the breeding population are able to select optimal territories of high quality. As density increases, and the best territories become occupied, more and more individuals are forced to occupy poorer territories, where their reproductive success is lower. As the overall population increases, therefore, the mean breeding success (young per pair) falls. But, when individuals are released in a new area, lack of competition may allow individuals to occupy high-quality territories allowing individuals to achieve a mean productivity higher than in the original population, and perhaps also breed at a younger age.

In well-established populations, with greater competition, older individuals have more chance of occupying vacancies than young ones (Ferrer, Newton, & Pandolfi, 2009; Ferrer & Penteriani, 2003), and are more likely to occupy the better territories, so good reproduction is expected from adult pairs (Carrete, Sanchez-zapata, Martinez, Sanchez, & Calvo, 2002; Carrete, Sánchez-Zapata, Tella, Gil- Sánchez, & Moleón, 2006; Ferrer & Bisson, 2003). However, in low-density situations, with young pairs occupying high-quality territories, little difference in productivity between young and adult breeding pairs is expected (Ferrer & Bisson, 2003). In a natural colonization, with empty high-quality habitat outside the old population boundaries, high productivity values are also expected for young pairs. These boundaries are promoted in philopatric species because of the tendency of individuals to return to the natal population to breed (Ferrer, 1993a). Expansion to areas just outside the boundaries of an existing population allows immature pairs to establish territories and start breeding at younger age than if they stayed within the existing population (Ferrer, Newton, & Muriel, 2013; Ferrer, Otalora, & GarcÍa-Ruiz, 2004; González et al., 2006).

Here, we compared two different means of colonization in the Spanish Imperial eagle in order to test potential demographic differences: a natural expansion of a past restricted breeding population into new territories that have not been occupied for at least 30 years and a reintroduced population reintroduced into a new distant area that has not been occupied for at least 30 years.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

The Spanish imperial eagle is one of the rarest eagles in the world (Vulnerable in the IUCN Red List, BirdLife International 2008), with around 430 breeding pairs in 2014 (National Working Group, unpublished data 2014), located entirely in the Iberian Peninsula. The species is a large (2,500–3,500 g) long-lived raptor, monogamous, sedentary and territorial, with a low annual productivity averaging 0.75 chicks/pair (Ferrer & Calderón, 1990). Reproduction usually lasts 8 months from February, when laying starts, until October when the latest juveniles leave the natal area (Ferrer, 2001). Independent juveniles disperse on “exploratory” movements (Ferrer, 1993a), using different temporary settlement areas (Ferrer, 1993b) but making periodic returns to their natal area where they are likely subsequently to breed. Individuals normally recruit to the breeding population at around 4–5 years old (but see Ferrer et al., 2004). Temporary settlement typically occurs in open lands that have high prey densities (especially wild rabbit *Oryctolagus cuniculus*), low human disturbance, and no other medium-large breeding raptors (Ferrer & Harte, 1997).

Spanish imperial eagles can be divided into two easily distinguishable plumage classes: (1) subadult, with tawny-colored plumage or dark patches over a tawny base, present until 4–5 years of age; and (2) adult, predominantly dark brown with characteristic white markings appearing from the age of 5 years (Ferrer & Calderón, 1990). The two age-groups can be easily distinguished in the field.

The monitored nests were in Andalusia occupied a large part of the southern Iberian Peninsula and had a wide altitudinal range (0–2,000 m.a.s.l.), with a dry-humid Mediterranean climate (annual rainfall: 300–2,000 mm, average annual temperature: 9–19°C). The landscape consisted of a mosaic of Mediterranean forests, scrublands, and grasslands in hilly and mountainous areas, crops in lowlands and coastal wetlands.

The fragmented distribution of existing populations of the Spanish Imperial eagle in Andalusia is the result of direct human persecution in the past (Mariano González et al., 2008), and the natural slow expansion of these populations into neighboring areas is more or less restricted to the edges of these refuges sites, regardless the quality of habitat available.

In the reintroduction project, the release site (in neighboring Cádiz Province) was selected for reasons of habitat suitability and potential connectivity with other Spanish Imperial eagle populations (González, Bustamante, & Hiraldo, 1992; Madero & Ferrer, 2002; Muriel, Ferrer, Casado, Madero, & Calabiug, 2011). It was situated 85 km away from the nearest established population in the Coto Donana (24 times the near neighbor distance in a high-density population). The reintroduction project started in 2002 and continued until 2015, with a total of 87 chicks released by hacking being Sierra Morena the donor population.

2.2 | Data analysis

During the study period, work was focused on two populations (see Figure 1), one occurring naturally in the Sierra Morena in the north limit of Andalusia (≈38°22′N 3°50′W) and the other reintroduced in Cádiz (≈36°20′N 5°48′W). Territorial pairs present in both populations were studied from 2001 to 2015. The data were derived from a total of 112 different territories and represented 763 breeding events. We considered a breeding event when a pair showed breeding behavior (nest construction, defense, incubation, etc.). All nests were monitored from the beginning of the breeding season (January–February, during courtship and nest site selection; Ferrer, 2001) until the last chick left the natal territory, and data on breeding, distance to nearest neighboring nest (NND), and the pair’s plumage state were recorded. We refer to all pairs with at least one member in subadult plumage as “immature pairs.” Productivity was calculated as the number of fledglings per nest. To allow for annual variation in reproductive performance, we adjusted productivity (number of fledglings) for year effects by subtracting annual means from the raw data. Corrected data are referred to as relative values (Ferrer & Bisson, 2003; Horváth et al., 2014; Penteriani, Balbontin, & Ferrer, 2003). Also, as in other studies

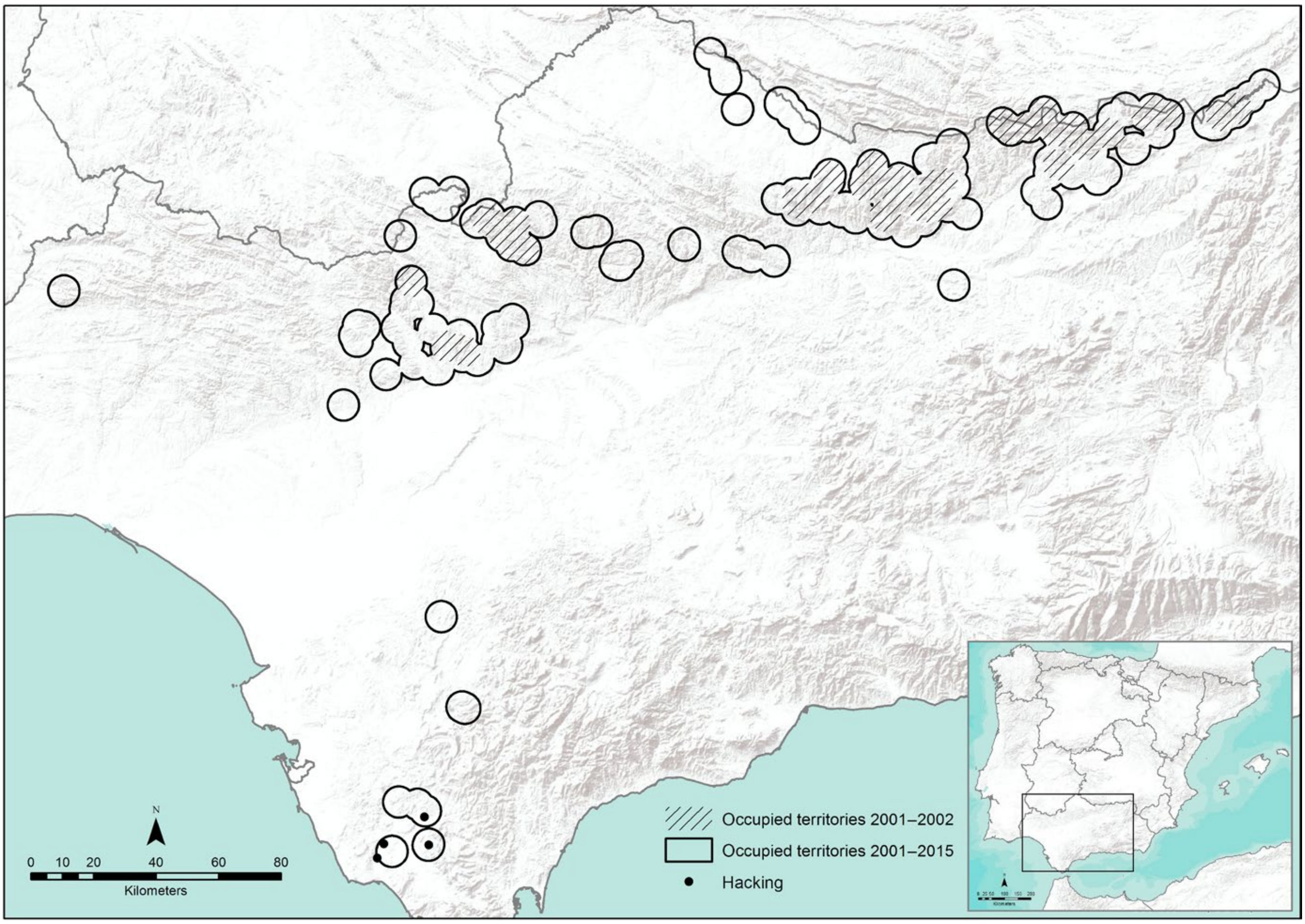

FIGURE 1 Distribution of Spanish Imperial eagle nests in Andalusia during the study period (2001–2015). Occupied territories during 2001–2002 are represented with shading lines. The expansion of the population is represented with a circle. The release points in the reintroduction area are the black spots in the Cádiz Province

of raptors, territory quality was estimated by frequency of occupancy (Ferrer & Donazar, 1996; Newton, 1991; Sergio & Newton, 2003).

We distinguished between colonized territories and old territories inside the existing population accounting for both the location of the territory (with colonized territories established at locations in the external ring of nests in the existing population Ferrer, Belliure, Minguez, Casado, & Bildstein, 2014) and the NND. We used NND recorded in the Doñana population during 1993, a period of high density, with the maximum number of territorial pairs ever registered in the Doñana National Park. The mean neighbor nest distance was 3,464 m, ranging between 1,800 and 9,250 m (Ferrer, 1990). Consequently, we considered a peripheral area of 9,250 m around the existing population, considering as colonized territories all those with NND values higher than 9,250 m.

We distinguished between two different colonization types: (1) territories which appeared without human intervention in the peripheral limits of the Sierra Morena population (natural colonization, Sierra Morena) and (2) territories which appeared in the reintroduction area and with at least one member coming from the reintroduction project.

Finally, as other studies showed, body condition of nestling imperial eagles is closely related to hatching date (Ferrer, 1994; Muriel, Ferrer, Balbontín, Cabrera, & Calabuig, 2015). We tested for differences in nutritional conditions by analyzing differences in hatching dates between chicks from reintroduced and natural territories. For the analysis of the hatching dates, only nests from 2012 to 2015 (*N* = 216) had reliable hatching dates, expressed in relation to the earliest hatching recorded in the 3 years as Day 1 (Ferrer, 1994).

2.3 | Statistical analysis

We calculated occupancy as the frequency of occupation of one territory from the first time that it was occupied to 2015. Also we excluded of this analysis territories with less of 3 years of occupation data. In order to check occupancy as measure of quality of territories, a Spearman correlation between occupancy and productivity (mean young per nesting attempt) was conducted.

To avoid potential pseudo-replication due to the high potential for strong site-fidelity and pair-fidelity in this long-lived species, a generalized linear mixed model (GLMM) was conducted with territories as a random effect. In this case, relative productivity was considered as the dependent variable over the years.

To remove any effect of age, we used a GLMM using only data from adult–adult pairs. To remove the effect of territory quality, we

TABLE 1 Results of the generalized linear mixed model of factors influencing relative productivity, including age of pair and type of population as a fixed effects and territory identity as a random factor

	Effect	*df* effect	MS effect	*df* error	MS error	F	*p*
1. Age of pair	Fixed	1	26.565	74.077	1.268	20.948	<.0001
2. Type of population	Fixed	1	10.713	75.605	2.182	4.908	.029
3. Territory identity	Random	96	1.833	14.011	0.692	2.646	.021
1 × 2	Fixed	1	0.124	31.271	0.727	0.170	.682
1 × 3	Random	46	0.741	523.000	0.811	0.913	.637

Significant terms were found in age of pairs, type of populations, and territory identity. Type of population: (1) existing population and (2) colonizing population (includes natural colonization and reintroduction).

compared productivity parameters between immature and adult pairs present in the same territory with a nonparametric Wilcoxon signed-rank test for pooled data for the 54 territories occupied in different years by adult-immature pairs.

We used GLMM to test for differences in productivity among colonized and existing territories with territories as a random effect, and age of pair (adult plumage or immature plumage) and colonized or old territories as fixed factors. We tested differences between colonized territories from Sierra Morena and colonized territories from the reintroduction area. Knowing that the reintroduced population so far has no adult pairs occupying territories during our study period, a GLMM for colonized territories (both, natural and assisted) occupied only by immature pairs was used. Finally, hatching dates of chicks from the reintroduced and natural populations were compared.

3 | RESULTS

The number of breeding pairs of Spanish Imperial eagles in the south of Spain increased from 11 in 2001 to 91 in 2015. Annual population growth rate was calculated for the entire study period for each population as $\lambda = 1.59$ for the reintroduced population (one pair from the first territorial pair after the reintroduction project in 2010 to four pairs in 2015) and as $\lambda = 1.17$ for the naturally expanding population (10 pairs in 2001 and 87 pairs in 2015). Natural colonized territories appeared from the beginning of the study period with four territories with NNDs of more than 9,250 m and outside the external ring of nests of the existing population in 2001.

Occupancy varies from 100% (territory occupied every year since the first time it had been occupied) to 6.7% (territory occupied in only one breeding season during 2001–2015). Variation in territory occupancy was positively correlated with variation in mean standardized productivity (Spearman rank order correlations $N = 81$, Spearman $R = .368$, $p = .0007$). In other words, the most frequently occupied territories showed the highest average annual breeding success.

Analyzing all territories, differences in standardized productivity among territories were related to age of the pair and territory identity, pairs composed only by adult birds showed higher productivity than immature pairs (GLMM; age of pairs: $F = 27.99$, $df = 1$, $p < .001$; territory: $F = 2.14$, $df = 101$, $p = .023$). The highest value for relative productivity was found in territory number 4 (in the expanding population), occupied by an adult pair in 2001 and with a relative productivity of 2.56. The lowest value for relative productivity was found in territories 92 and 3 (both in the nucleus of the existing population), occupied by a young pair and an adult pair, respectively, with a relative productivity of −1.6 during 2001 and 2003.

To remove the effect of age class, we conducted analyses considering only data from adult–adult pairs. Again, productivity differed significantly among territories (GLMM; $N = 523$, territory: $F = 2.373$, $df = 82$, $p < .001$). Also, no differences were found in productivity between adult and immature pairs in the same territory (sign test. $N = 54$, $Z = 1.497$, $p = .134$). Significant differences in relative productivity between old territories and colonized ones (including both natural and assisted colonization) were found, resulting from the effect of age of the pair and territory identity, with both effects highly significant (Table 1). New colonized territories showed higher productivity levels than old ones (mean old territories: −0.049; colonized territories: 0.205).

Analysis of only colonized territories (natural and reintroduced) and comparison only of immature pairs (there were no adult pairs in the reintroduced population) revealed significant differences among territories and between the two colonization types (Table 2). Territories which appeared by reintroductions were 2.11 times more productive (mean relative productivity = 0.582) than those of natural colonization in the peripheral limits of the Sierra Morena population (mean relative productivity = −0.266).

TABLE 2 Results of the generalized linear mixed model of factors influencing relative productivity in immature pairs, including colonization type (reintroduction or natural colonization) as a fixed effect and territory identity as a random factor

	Effect	*df* effect	MS effect	*df* error	MS error	F	*p*
Colonization type	Fixed	1	7.259	17.871	1.563	4.641	.045
Territory identity	Random	24	1.392	45.000	0.812	1.714	.058

Colonization type emerged as a significant effect.

Finally, in immature breeding pairs, chicks from the reintroduced population show significant earlier hatching dates than chicks from all natural territories (GLMM; type of population: $F = 44.823$, $df = 1$, $p < .005$).

4 | DISCUSSION

During the twentieth century, most raptor populations in Europe declined, and their geographical ranges were reduced mainly by human persecution (Whitfield, 2004). However, nowadays most raptor species are increasing in both numbers and distributions (Ferrer et al., 2013; González et al., 2006; Horváth et al., 2014), and many species have been subject to reintroduction programs aimed to re-establish them in former range. The present distribution of the Spanish Imperial eagle is mainly the result of past human persecution, so the current population mainly occupies remote and inaccessible areas that do not necessarily hold the best habitat for the species (Ferrer, Negro, Casado, Muriel, & Madero, 2007; González, Bustamante, & Hiraldo, 1990; González et al., 1992).

The Spanish Imperial eagle range expansion during the last decade was facilitated by a reduction of the number of electrocuted birds due to mitigation measures implemented on power poles (López-López, Ferrer, Madero, Casado, & McGrady, 2011). This population growth was associated with the establishment of new territories in places that had not been occupied for at least 30 years (González et al., 1992; Horváth et al., 2014). It was to improve the species recovery that the reintroduction program started in Cádiz Province in 2002.

In a natural colonization, breeding pairs prefer to settle near existing ones and productivity is limited by the habitat quality present in those areas. In contrast, translocations are not relegated to areas surrounding existing populations and the selection of good habitats for the species is the main criteria in the choice of a release site (Armstrong & Seddon, 2008). For this reason, new territories limited to areas surrounding existing populations show lower productivity than territories in release areas selected by habitat quality values and without already established populations (Table 2). Immature pairs, whose productivity is highly dependent on the quality of the territory (Balbontín & Ferrer, 2008; Ferrer & Bisson, 2003; Ferrer et al., 2008), showed significantly higher productivity in the reintroduction area. Difference between productivity in Sierra Morena and Cádiz could be promoted only by differences in habitat quality being all the occupied territories in Cádiz territories of high quality for the specie. An alternatively explanation for the differences in productivity between natural and assisted colonization would be differences in quality of founder individuals of the reintroduction program. Genetic differences depending on the donor population would affect productivity. In our case, we can discard any genetic differences that could affect the productivity of breeding pairs because released individuals in the reintroduction area were translocated from the Sierra Morena population (Muriel et al., 2011).

As all breeding pairs in the Cádiz population contained at least one reintroduced individual fed ad libitum during the release process (Muriel et al., 2015), we cannot separate the effect of good physical condition in their first stage of life from the territory quality effect. If the higher productivity of the Cádiz population breeding pair was a consequence only of the ad libitum feeding of chicks, we expected a decrease in productivity in future breeding pairs without a reintroduced member. Nevertheless, body condition of nestling imperial eagles is closely related to hatching date (Ferrer, 1994; Muriel et al., 2015), with earlier hatching dates indicating better nutritional conditions. Muriel et al. (2015) established that released individuals in the reintroduction program were mainly later hatched birds in the season due to the extraction protocol during the program. Consequently, it seems that the idea of a priori better-quality released birds could be discarded. Furthermore, significant differences in chick hatching dates between natural and reintroduced colonized populations support the idea of better territory quality in the reintroduction area.

As previous studies showed, the Spanish imperial eagle is a long-lived species with slow turnover, strong philopatric behavior, and conspecific attraction (Ferrer, 1993a; González, 1989; Muriel, Morandini, Ferrer, & Balbontín, 2016). With these characteristics, reflected in a tendency to breed close to existing populations, areas without the presence of conspecifics or far away from established populations have little chance of being occupied. The main strategy of individuals trying to enter in a breeding population is to look for vacancies in the natal area during the beginning of the breeding season (Ferrer, Morandini, & Newton, 2015), as the presence of other breeding pairs apparently signals suitable habitat (Kivela et al., 2014).

The probability of getting a vacant territory inside an existing population is related to the time spent searching for vacancies (Ferrer & Penteriani, 2003), as well as experience and competitive ability (Balkiz et al., 2010), and knowledge of the locations and qualities of territories (Kokko, Harris, & Wanless, 2004). For these reasons, young individuals are less likely to find and fill vacancies in the natal area than older individuals, and breeding dispersal outside the population limits gives more chance of finding a potential territory. In fact, as our results show, during the process of population expansion, the number of immature pairs increases in territories with higher NND values (Ferrer et al., 2004, 2009, 2013; González et al., 1992; Horváth et al., 2014; Margalida et al., 2008), suggesting that immature pairs tend to establish territories far from existing nests. Where immature individuals are able to occupy high-quality territories, values of productivity do not differ from adults in high-quality territories, so productivity is not correlated only with the age of breeding pairs (Ferrer & Bisson, 2003; Ferrer et al., 2013; Horváth et al., 2014). We found no differences in productivity depending on age of breeding pairs in high-quality territories. Our results confirm the importance of territory quality to productivity and the ability of young pairs to reproduce as well as adult pairs when they have the opportunity to occupy high-quality territories (Ferrer & Bisson, 2003).

As other authors suggested, we found that occupancy of territories was related to productivity (Sergio & Newton, 2003). Expanding population processes show again that quality of territory has a major influence on the productivity of breeding pairs (Ferrer & Bisson, 2003; Ferrer & Donazar, 1996; Ferrer et al., 2013). The presence of empty habitat adjacent to existing population perimeters allows immature pairs to settle near their natal population (Horváth et al., 2014; Kivela et al., 2014), but reintroduction projects allow the occupation of vacant high-quality habitat not limited by the existing population's distribution.

Territory quality seems to be a major driver of productivity (Osborne & Seddon, 2012) and even past refuges served well for the protection of target species in the era of human persecution. Now with a changing human attitude, the best habitats for the species may be empty and far away from existing population nuclei. Yet efforts to restore populations in their indigenous range tend to select release sites based on current habitat use under the assumption that the present location of the species represents optimal habitat. This could lead to a serious mismatch whereby suboptimal sites are chosen for reintroduction attempts, which subsequently fail to result in population establishment, growth, and persistence. The assessment of high-quality habitat is a key step before starting a reintroduction project.

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CONFLICT OF INTEREST

None declared.

DATA ACCESSIBILITY

All Spanish Imperial eagle data used in this manuscript (productivity, nest location, individual plumage) are available from Consejería de Medio Ambiente (Junta de Andalucía).

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Chapter 2: Differential behavior between colonizing and established population.

Dispersal and fecundity can affect population persistence through genetic and demographic linkage within metapopulations (Dale, 2001; Wadgymar, Cumming, & Weis, 2015) and through rapidity or form of geographic spread in naturally-establishing and introduced populations (Chapron et al., 2014; Monti et al., 2014). Studies on large birds with delayed sexual maturity show a notable tendency of juveniles to return to their natal population (Ferrer, 1993; Lindberg, Sedinger, Derksen, & Rockwell, 1998; López-López, Zuberogoitia, Alcántara, & Gil, 2013; Stiebens et al., 2013). These returns have been interpreted under two non-mutually exclusive hypotheses. First, according to some authors, juvenile birds may show a natural tendency to return to the natal area for breeding, called philopatric behavior(Greenwood & Harvey, 1982). In this way, juveniles would be preferably selecting familiar areas as breeding territories where reproduction is possible for sure. Second, juveniles may show a tendency to look for areas with breeding pairs of the same species as reliable indirect cues of intrinsic habitat quality for reproduction, known as conspecific attraction (Muller, Stamps, Krishnan, & Willits, 1997; Ray, Gilpin, & Smith, 1991). Philopatry (and the associated local experience) and conspecific attraction have been viewed as strategies favoring less costly dispersal patterns in terms of juvenile survival and post-settlement fecundity (Stamps, 2006).

Philopatry and social attraction cannot be studied independently in natural populations, however, because juveniles always know both their natal area and their own parents, so the effect of any one factor cannot be studied separately from the other. In this sense, reintroduction provides a useful way of testing separately predictions of the different hypotheses about juvenile dispersal movements. Typically, juveniles are released in an area without breeders so the influence of the philopatry and local experience can be assessed without the confounding influence of social attraction.

The aim of this chapter is to assess dispersal mechanisms in established populations and to study factors that outline differential behavior in colonizing populations.

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Floater interference reflects territory quality in the Spanish Imperial Eagle Aquila adalberti: a test of a density-dependent mechanism

Ferrer M., Morandini M. and Newton I. (2015) Ibis 157, 849–859

Floater interference reflects territory quality in the Spanish Imperial Eagle Aquila adalberti: a test of a density-dependent mechanism

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Abstract:

We report on an 11-year study of floater interference in a population of Spanish Imperial Eagles Aquila adalberti. We analysed changes over the years in the productivity of 15 territories to test predictions of two hypotheses of density-dependent productivity in relation to the presence of floaters (birds without territories). According to the ‘interference’ hypothesis, the frequency of intrusion by floaters increases with density, resulting in a decrease in productivity. Thus, in a high-density population a negative relationship between floater intrusions and productivity of the territory is expected. In contrast, under the ‘habitat heterogeneity’ hypothesis, as density increases a higher proportion of individuals is forced to occupy lower quality habitats. Support of this hypothesis requires that floaters detect differences in quality among territories and preferentially visit the better quality territories. Consequently, a positive relationship between floater intrusions and productivity is expected. Results showed that floaters tended to visit their natal area at the beginning of the breeding season. Among floater Eagles, males made significantly more intrusions per day than did females, but females stayed in the natal population for longer each year than males. Floater intrusions and productivity were highly positively correlated, supporting the ‘habitat heterogeneity’ hypothesis; individuals were apparently able to assess the quality of a territory and, at the frequencies observed, their interference with the breeding pair had no obvious negative effect on productivity.

Keywords: *density dependence, Do~nana National Park, floater, habitat heterogeneity, interference, population dynamics, productivity, Spanish Imperial Eagle*

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Floater interference reflects territory quality in the Spanish Imperial Eagle *Aquila adalberti*: a test of a density-dependent mechanism

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We report on an 11-year study of floater interference in a population of Spanish Imperial Eagles *Aquila adalberti*. We analysed changes over the years in the productivity of 15 territories to test predictions of two hypotheses of density-dependent productivity in relation to the presence of floaters (birds without territories). According to the 'interference' hypothesis, the frequency of intrusion by floaters increases with density, resulting in a decrease in productivity. Thus, in a high-density population a negative relationship between floater intrusions and productivity of the territory is expected. In contrast, under the 'habitat heterogeneity' hypothesis, as density increases a higher proportion of individuals is forced to occupy lower quality habitats. Support of this hypothesis requires that floaters detect differences in quality among territories and preferentially visit the better quality territories. Consequently, a positive relationship between floater intrusions and productivity is expected. Results showed that floaters tended to visit their natal area at the beginning of the breeding season. Among floater Eagles, males made significantly more intrusions per day than did females, but females stayed in the natal population for longer each year than males. Floater intrusions and productivity were highly positively correlated, supporting the 'habitat heterogeneity' hypothesis; individuals were apparently able to assess the quality of a territory and, at the frequencies observed, their interference with the breeding pair had no obvious negative effect on productivity.

Keywords: density dependence, Doñana National Park, floater, habitat heterogeneity, interference, population dynamics, productivity, Spanish Imperial Eagle.

The proximate mechanisms by which density can affect demographic parameters, mainly productivity, have been debated (Lack 1966, Fretwell & Lucas 1970, Dhondt & Schillemans 1983, Sinclair 1989, Newton 1991, 1998, Ferrer & Donazar 1996, Ferrer *et al.* 2006, Ferrer & Penteriani 2008). Two main hypotheses have been proposed to explain how density-dependent productivity arises. Some authors suggest that in territorial species, density-dependent depression of productivity can arise from an increased frequency of agonistic encounters and floater interference, resulting in a hostile social environment that leads to a general decrease in reproductive success. As the frequency of intrusions and interference increases, individuals show reduced productivity (Lack 1966, Fretwell & Lucas 1970, Dhondt & Schillemans 1983, Fernandez *et al.* 1998, Newton 1998, Sillett *et al.* 2004). Other authors, however, have proposed that density-dependent depression in mean productivity is the result of habitat heterogeneity (Korpimaki 1988, Kadmon 1993, Ferrer & Donazar 1996, Newton 1998, Ferrer & Bisson 2003, Sergio & Newton 2003, Penteriani *et al.* 2004, Casado *et al.* 2008, Tanferna *et al.* 2013). In a low-density population, individuals entering the breeding population select optimal territories of high quality. As density increases, a higher proportion of individuals are forced to occupy poorer quality territories, where their reproductive success is lower. Thus, while productivity in the better territories is main-

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tained, mean population productivity in the breeding population as a whole decreases (Andrewartha & Birch 1954, Brown 1969, Rosenzweig 1991, Dhondt *et al.* 1992, Sutherland 1996, Rodenhouse *et al.* 1997, Newton 1998, Gill *et al.* 2001, Sutherland & Norris 2002, Casado *et al.* 2008).

The existence of important differences in quality among territories, according to the habitat heterogeneity hypothesis, suggests that when populations reach saturation level, competition for optimal territories must be intense. In this situation, and assuming that floaters are able to adequately assess the quality of the site (Kokko *et al.* 2004, Stamps 2006), a positive relationship between prospecting/intrusion frequency by floaters and territory productivity would be expected. However, according to the interference hypothesis, a high frequency of floaters in the territory would depress productivity, reducing the breeding success of pairs experiencing the most intrusions (Lack 1966, Dhondt & Schillemans 1983, Fernandez *et al.* 1998, Newton 1998, Sillett *et al.* 2004). Thus, a negative relationship between intrusion frequency by floaters and territory productivity would be expected (Sillett *et al.* 2004). Study of this relationship could help to distinguish between the interference and habitat heterogeneity hypotheses as mechanisms of density-dependent reproductive success.

Here, we report an 11-year study of floater interference and territory productivity in the Spanish Imperial Eagle *Aquila adalberti* population at Doñana National Park in Spain during 1986–96. In this paper, a floater is defined as an individual without a territory, usually a young individual which has not bred previously, but which is likely to compete with established territorial individuals to take over a territory (and mate). The floaters in this study are probably gathering information for possible later attempts to enter the breeding population, and probably do not represent a serious threat to occupying adults. They are, nevertheless, intruders and so their potential effects on territory holders by way of disruption are relevant to the hypotheses being tested.

Floaters use different temporary settlement areas away from breeding territory. Each settlement area was used intensively for a variable but short period, and each individual used the same areas (between three and eight) in rotation at least during the first 3 years of life, returning occasionally to the natal population (Ferrer 1993). During this period, more than 41.3% of floaters were radiotagged and their individual returns to the natal population in the Doñana National Park were monitored. We recorded all the intrusions that these floaters made in different territories, inside the natal population, and the productivity of those territories. The aim of this study was to analyse the relationship between frequency of floater intrusions and breeding output, thereby testing predictions of these two hypotheses of density-dependent productivity. Throughout the study period, the breeding population remained close to its limit in the area (mean number of territorial pairs per year 14.44, sd = 1.6, maximum number of territorial pairs = 16; Ferrer & Donazar 1996).

METHODS

Study area

The study was conducted in Doñana National Park (37°N, 6°30′W) in southwestern Spain (Fig. 1). The data used in this study were collected during 1986–96 inclusive. Three habitat types are present in the area: (1) Mediterranean scrubland, formed by the shrubs *Halimium* spp., *Cistus libanotis* and *Erica* spp., with scattered Cork Oaks *Quercus suber* and small Stone Pine *Pinus pinea* woods; (2) marsh, comprising principally *Scirpus* spp., which remains flooded during winter and dry during summer; and (3) coastal sand dunes, characterized by *Ammophila arenaria*, *Corema album* and *Juniperus phoenicia*. The climate is Mediterranean type with Atlantic influence. A more detailed description of this area is presented in Rogers and Myers (1980).

The Spanish Imperial Eagle is a large (2500–3500 g), sedentary and territorial bird of prey, with a low reproductive rate, which does not acquire adult plumage until 4–5 years of age (Ferrer & Calderón 1990). During most of the study period (1986–93), the population at Doñana National Park consisted of 15–16 breeding pairs at a high density (occupying 20 000 ha of available habitat inside the National Park with a mean territory size of 1200 ha, range = 980–1870 ha; Ferrer 2001). After 1993, the population declined from 15 to 10 occupied territories due to a decrease in a major prey species, wild Rabbit *Oryctolagus cuniculus*, and an associated increase in adult mortality (Ferrer *et al.* 2003, 2013a, Ferrer & Penteriani 2008). Eagle territories were exclusive and were vigorously defended throughout the year (Ferrer 1993). Nests were located in Cork Oaks and Stone Pines not far

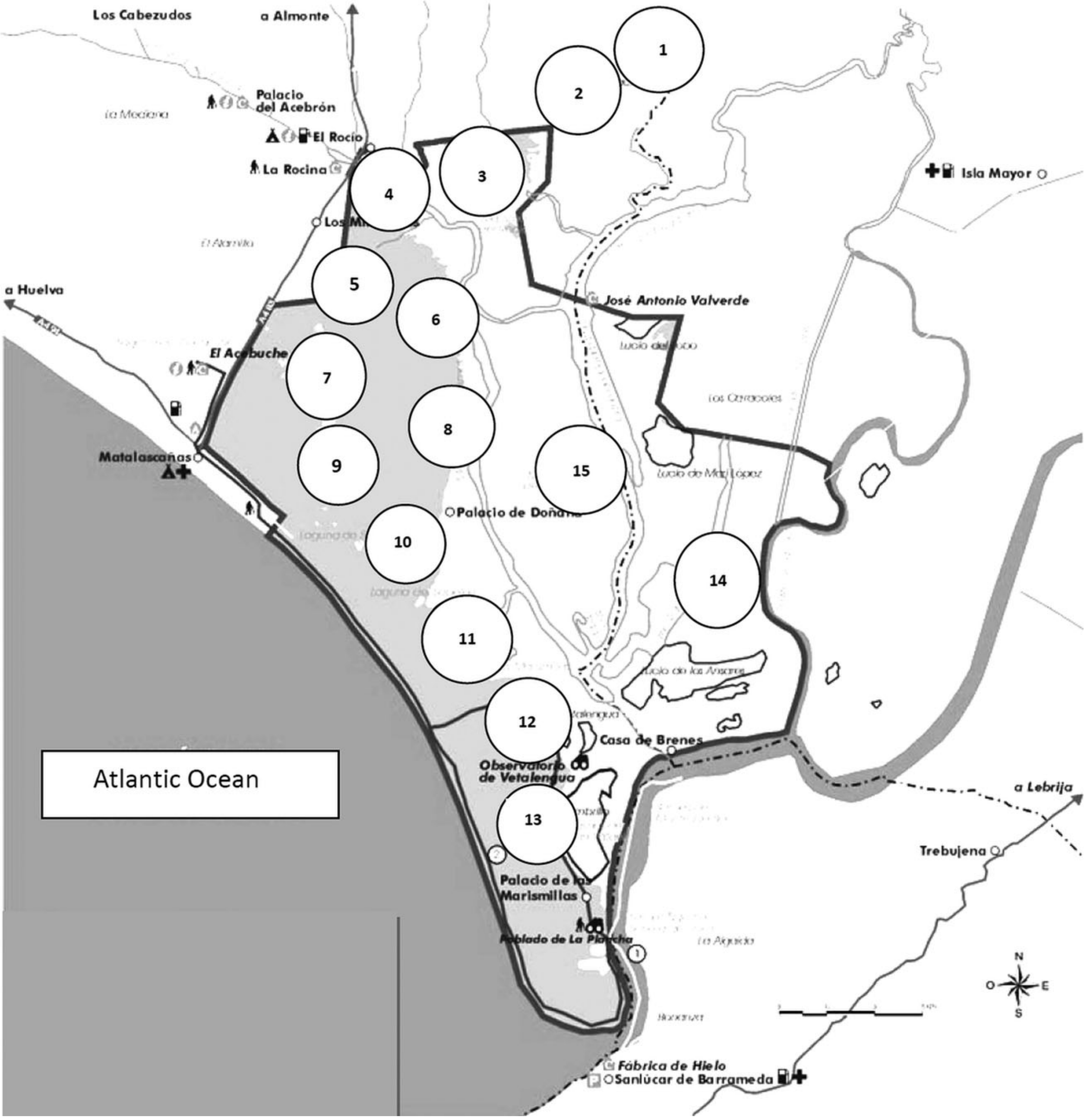

Figure 1. Distribution of territories inside the Doñana National Park population.

from the marshland. The Spanish Imperial Eagle population at Doñana is well separated from other breeding populations, the nearest of which is 300 km away. Consequently, the probability of floaters coming from other populations is low (Ferrer & Calderón 1990, Ferrer *et al.* 2003). Evidence for density dependence in this species, and specifically in this population, has been published previously (Ferrer & Donazar 1996, Ferrer *et al.* 2004, Penteriani *et al.* 2006).

Data collection

The entire National Park area was surveyed at the beginning of each breeding season (January–February, during the courtship and nest-site selection period) to determine whether pairs were present on territories. The sedentary behaviour and the tendency to call repeatedly helped detection of a pair on territory. Hatching date was determined according to observation of incubation behaviour. Clutch size and the number of nestlings and fledglings were recorded while visiting nests. Visits were made by two or three people, one of whom climbed up to the nest at each visit.

Brood size is defined as the number of hatchlings. We considered fledging to have occurred when the nestlings reached at least 50 days of age (the age of ringing) and productivity was measured as the number of chicks produced. Mortality during the last period in the nest is very low (Ferrer 2001) and first flights occur when nestlings are around 65–72 days old. We ascertained the number of territorial pairs, the number that started reproduction and their productivity annually over an 11-year period.

In addition, 50 young Eagles were equipped with solar-powered radiotransmitters (type HSPB 1400 3XA; Wildlife Materials Inc., Carbondale, IL, USA) during 1986–96 inclusive. During this 11-year period, 121 young were produced by this population, so that 41.3% of the young were tagged. Transmitters were fixed by a harness to the back of the nestlings at the end of the nestling period (50–60 days of age) (Kenward 1987). The weight of the transmitter and harness together ranged from 28 to 37 g, approximately 1% of the bird's weight, well under the recommended limit of 3% in avian research (ringing and transmitters permit numbers: 660143; CONV-1300256).

Of the 50 fledglings, 28 were males and 22 females, as determined by forewing length (Ferrer & De le Court 1992). Of the 50 young Eagles, 24 survived for at least 6 months, 17 for at least 1 year and 12 for at least 2 years.

Two teams were used to track the young Eagles during their returns to the natal population (Ferrer 1993). One team made observations from a vehicle, equipped with a non-directional antenna with a magnetic base fixed to the roof; triangulation was done using a directional antenna when a radiotagged Eagle was detected. This team also made direct observations of individuals when possible. The second team was located in a 35-m-high tower in the middle of the natal population, and attempted to locate every young bird at least once a day. When a young Eagle was detected, both the vehicle and the tower teams recorded its position and (if flying) the flight direction every half hour. A total of 13 743 locations of the 50 radiotagged young inside the natal population were obtained.

To assess whether floaters intrude into occupied nesting territories, we considered a circle around each nest with a radius of 1950 m as representing a circular territory of 1200 ha, the mean territory size for this population (Ferrer 2001). Every time a floater was located by triangulation or by direct observation inside this circular territory, it was counted as an intrusion. Because nest positions changed from year to year, we fixed the territory circles separately each year. In cases when an adult pair did not breed or build up a nest, we used the location of the last active nest in this territory as the centre of the circle. Only records of young birds older than 200 days of age were considered floater intrusions because until this age returns of young to their natal nest were still frequent and parents sometimes fed their young to this age (Ferrer 2001). We used this method to remove any possibility that returns were not prior to young birds' dispersal and were not due to returns after excursions.

Data analysis

We fitted generalized linear mixed models (GLMMs) to investigate variation in productivity among nests in relation to the number of intrusions made by floaters. This approach is suited to examining data measured repeatedly on the same individuals at different times (high pseudoreplication). We considered productivity as the response variable, individual as random effect and nests as a fixed effect, with number of intrusions as a covariate. Due to annual variation in reproduction, we adjusted clutch size, brood size, and productivity for year effects by subtracting annual means from the raw data. Corrected data are referred to as relative values. Effects were tested by means of the *F*-ratio. Errors were computed using the Satter thwaite method.

We tested the monthly distribution of intrusions using the chi-square test for homogeneity. We corrected for the potential effect of floaters visiting their own natal nests more frequently, which would result in a spurious correlation among floater intrusions and productivity because the most productive nests produce more floaters. First, differences between numbers of intrusions in their own natal territory against other territories were tested using a chi-square test for homogeneity. For this, we compared for all floaters the number of visits made to their natal territory with the number of visits made to other territories. Then we compared this distribution against a distribution generated on the assumption that probability of visits was equal across territories, so that expected frequency of visits to the natal territory was total visits divided by number of territories in the population, with the remainder of total visits being expected visits to other territories. Additionally, we removed all visits by floaters to their natal territories and checked whether the relationship between productivity and intrusions remained or changed.

To assess possible differences between sexes in the duration of returns to the natal population, we used a GLM with duration in days of the returns as the response variable, with normal error distribution and log-link function and sex as an explanatory factor. A GLM with a Poisson distribution and log-link was used to assess differences between sexes in the number of territories visited per day. Similarly, a GLM with a Poisson distribution and log-link function was used to analyse differences among territories in the number of intruders and frequency of intrusions. Finally, we tested the relationship between productivity and intrusions per territory with linear analysis using the *F*-ratio to assess whether the slope of the relationship was significantly different from zero. Variances of the linear models were tested for homogeneity using Cochran's C statistic. For these analyses, mean values for the entire study period were used to avoid the effect of a different number of radiotagged floaters per year. Statistical significance was assumed at $P < 0.05$ and analyses were conducted using the STATISTICA 8.0 package (Statsoft Inc., Tulsa, OK, USA).

RESULTS

A total of 825 intrusions by 50 individual floaters into territories of their natal population were recorded during the 11-year period. Analysing floater intrusions into their own natal territory vs. other territories revealed no significant bias toward their own territory ($\chi^2_1 = 0.25$, $P = 0.6186$). The mean number of recorded intrusions per territory per year was 5 (sd 6.7), with the highest record in Territory 2 (8.63 intrusions per year) and the lowest in Territory 6 (1.62 intrusions per year). During the study period the mean number of radiotagged floaters of all ages in the study area was 9 per year (sd 2.7), with a minimum of 6 in 1987 and a maximum of 14 in 1989.

According to GLMM analysis, territories and intrusions showed a very significant effect on relative productivity (Table 1), with a positive relationship between intrusions and productivity. Interaction between both factors was non-significant. No effect of the random factor 'individual' was found, allowing us to use the mean number of intrusions per nest as the response variable in the following analyses.

Figure 2 shows the monthly distribution of recorded intrusions during the study period. This seasonal distribution was clearly non-homogeneous ($\chi^2_{11} = 1336.21$, $P < 0.001$), with 74% occurring during 3 months, November–January (the time of nest building), and the rest during February–April (the time of egg-laying/incubation). No intrusions were recorded in May–October. Hence, we assume that intruders could not see nestlings in the nests.

The mean period that floaters were present in the study area was 3.5 days (sd 2.69), during which time they visited several nests. Each time we were able to see an encounter ($n = 54$), the floater was aggressively expelled by the owners when detected. Typically, when floaters enter the territory, the owner starts to call and fly towards the floater, which always tries to escape. Usually it was the male of the territory that started the aggression ($n = 49$), sometimes the pair together ($n = 28$) and only occasionally was the attack conducted by the female alone ($n = 5$). In all these female attacks, the intruder was a female floater. Floaters of different sexes differed in the duration of their returns, females staying longer (3.7 days) than males (2.7 days; GLM normal distribution and log-link, Wald statistic 27.91, $P < 0.001$).

Table 1. Results of the GLMM of factors influencing relative productivity, including territory as a fixed effect, individual identity as a random factor, and number of intrusions as a covariate. Significant terms were found in territory and intrusions but not in individuals or the interaction of territory and individuals.

	Effect	df	*F*	*P*
Intrusions	Covariate	1	41.251	< 0.001
Territory	Fixed	14	15.954	< 0.001
Individual	Random	49	0.988	0.500
Territory*Individual	Random	280	0.638	0.998

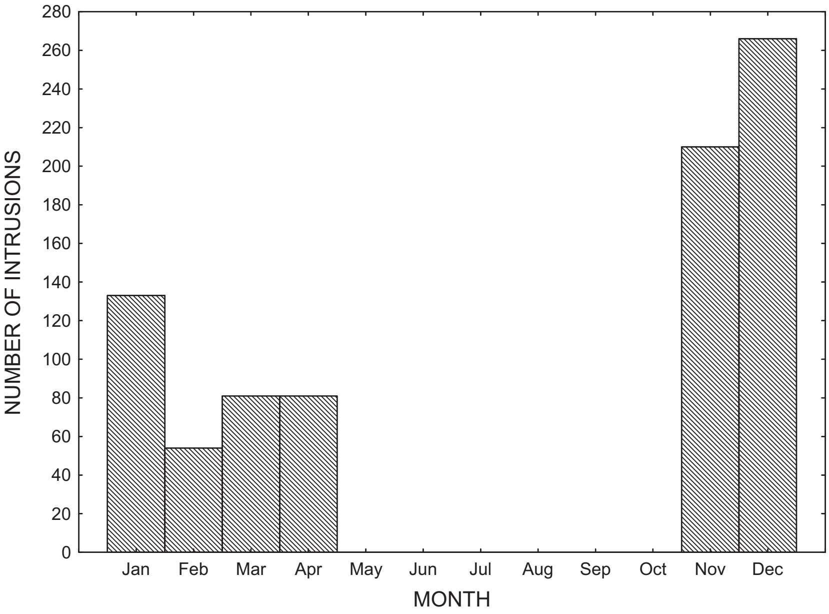

Figure 2. Non-homogeneous monthly distribution of recorded intrusions during the study period (χ^2_{11} = 1336.21, $P < 0.001$), with 74% occurring during November–January (the time of nest-building/egg-laying), and the rest during February–April (the time of egg-laying/incubation).

However, males visited more territories per day (0.64 territories per day) compared with females (0.26 territories per day; GLM Poisson distribution and log-link, Wald statistic 63.78, $P < 0.001$).

Territories differed significantly both in the frequency of detected intrusions (GLM Poisson distribution and log-link function, Wald statistic 126.37, $P < 0.001$) and in the number of individual intruders involved (GLM Poisson distribution and log-link function, Wald statistic 64.07, $P < 0.001$). The two measures were highly positively correlated ($r = 0.905$, $P < 0.001$), showing that those territories receiving a higher frequency of intrusions were also visited by more individual floaters.

Using mean values for each territory, a highly significant positive relationship was found between the frequency of intrusions and the mean annual productivity ($r = 0.866$, $n = 28$, $P < 0.001$, Fig. 3). Even when all the visits of individual floaters to their own natal territories were removed from the analysis (64 cases, sample size 761 intrusions) to avoid any potential effect of young Eagles visiting their own nest more frequently, the relationship between intrusions and productivity remained highly significant ($r = 0.852$, $n = 28$, $P < 0.001$). Mean frequency of recorded intrusions varied from 0.9 in territories with no fledglings, 6.5 in territories with one fledgling, 13.3 in territories with two fledglings and 14.0 in territories with three fledglings. Removing from the analyses territories in years with zero productivity did not change this relationship ($r = 0.6843$, $n = 28$, $P = 0.0049$).

The same positive relationship was found between intrusions and brood size ($r = 0.7882$, $n = 28$, $P < 0.001$) and clutch size ($r = 0.796$, $n = 28$, $P < 0.001$), showing that those territories with more intrusions had higher clutch and brood sizes that those territories with a lower frequency of intrusions. No relationship between intrusions and hatching rate was found ($r = -0.008$, $n = 28$, $P = 0.975$) but there was a positive relationship between the survival rate of nestlings and number of intrusions ($r = 0.497$, $n = 28$, $P = 0.050$). Finally, a significant negative relationship was found between hatching date and intrusion frequency ($r = -0.594$, $n = 28$, $P = 0.019$), territories with early nests being visited more often than territories with late nests.

DISCUSSION

The number of floater interferences correlated positively with habitat quality, as measured by breeding success. According to the 'interference'

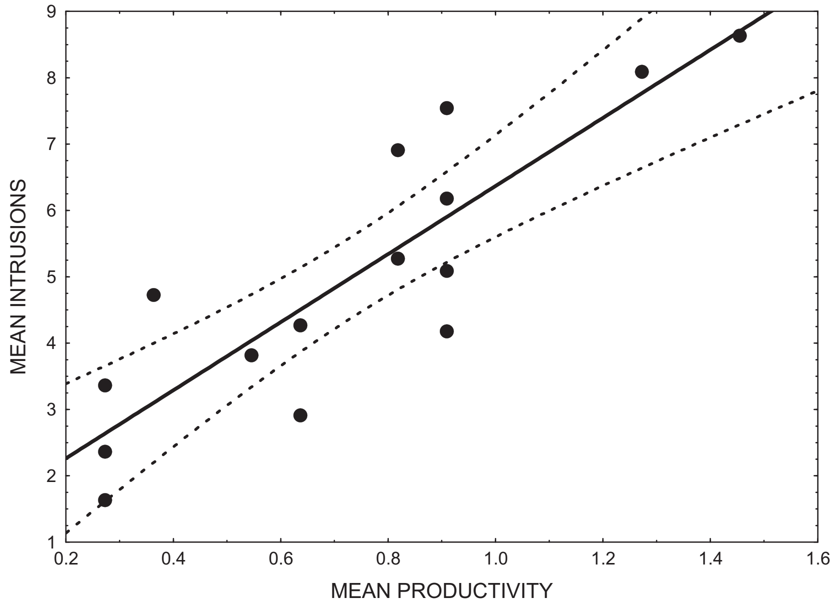

Figure 3. Relationship between mean frequency of intrusions and the mean annual productivity for each territory, measured as the number of fledglings produced ($r = 0.866$, $P < 0.001$, 95% confidence interval limits).

hypothesis, as density increases, the frequency of floater intrusion increases, resulting in a decrease in productivity. In contrast, our results show that floater intrusions and productivity were highly positively correlated, supporting the 'habitat heterogeneity' hypothesis, where floaters must be able to distinguish differences in quality among territories.

Seasonal trend in intrusions

There was a clear trend for intrusions to be concentrated in some months of the year, coinciding with the beginning of the breeding cycle (Calderón *et al.* 1987). In the Spanish Imperial Eagle, the breeding cycle lasts about 8 months, from the beginning of February, when laying starts, to the beginning of October, when the last chicks become independent of their parents (Ferrer 2001). Copulation takes place from the end of January to the end of April, peaking in early March, and laying occurs between mid-February and the end of March. This timing suggests that intruders were not using the number of eggs or young in the nest as a measure of territory quality, but rather other features of the territory.

Maximum intrusions per month occurred during December, followed by November and January. Thus, floaters visited the nests most frequently just at the beginning of the breeding cycle when, if they found a vacancy, they would be able to breed that year. The absence of intrusions during a large part of the year supports the idea that the concentration of visits in November–January was a strategy that enabled them to be in the right place at the right time. Alternatively, floaters may be avoiding territories that have nestlings because aggression by owners could be more dangerous. Floaters spent around 30% of their time in returns to their natal population (Ferrer 1993), but intrusions into territories were concentrated only in certain months. The mean time that the floaters spent in the natal population during these returns was significantly shorter than the period they spent in temporary settlement areas outside the natal population area (Ferrer 1993).

Returns to the natal population could be interpreted in two ways. First, the natal population could be used as another area of temporary settlement, in which the average stay is shorter due to expulsion by territory owners, but the frequency of returns is higher due to a high motivation to settle there (perhaps because of the chance of obtaining a meal in this area of high prey density). An alternative possibility is that the returns could be used by the floaters to explore the possibility of pair formation with a territorial bird that had lost its mate. Pairs with one member or both in non-adult plumage are frequently found in sedentary long-lived birds (Newton 1980, Steenhof *et al.* 1983, Ferrer & Calderón 1990, Ferrer *et al.* 2011), with important consequences for population dynamics (Ferrer *et al.* 2004). In a situation of high adult mortality, young floaters may have more opportunities for establishment in the reproductive population (Ferrer *et al.* 2003). One way to detect vacancies is to check the breeding population frequently. The trend toward concentrated returns in November–January could be interpreted in this way because these months mark the beginning of copulation, a high intensity of territorial displays and the beginning of nest-site selection (Ferrer 2001).

Sex differences

Returns to the natal population lasted longer in females than males, on average, but males made significantly more intrusions per day. Apparently males conducted a more active search for potential vacancies, and as a result experienced more aggressive interactions with the territory owners. This finding fitted the fact that male Spanish Imperial Eagles are more active than females in nest-building and territory defence (Ferrer 2001), as in some other raptors (Newton 1980). The relatively longer stay of the females could be a consequence of their reduced aggressive interactions with territory owners. Furthermore, some extra-pair copulations of female floaters with already paired males were reported (Penteriani & Ferrer 2004), suggesting again a different strategy between the sexes in floater Eagles. Another explanation would be that male floaters visit more territories because they are more likely to be chased from a territory than are female floaters (so they do not stay as long and move to another territory) because territorial males are more active in attacking intruders and they are more likely to attack intruding males than females.

Productivity and intrusions

In highly productive territories, a greater frequency of intrusions was recorded, as well as a higher number of different intruders, compared with low-productivity territories. This relationship held with clutch size and brood size. Furthermore, a negative relationship was found between the number of intrusions and laying date, in that early nests were visited more than later ones. Overall, it emerged that floaters visited high-quality territories more often than low-quality ones, but that, at the levels recorded, this high frequency of intrusions had no obvious effects on the productivity of those territories.

The habitat heterogeneity hypothesis assumes that individuals are able to discriminate adequately between territories of different quality. However, this basic assumption has seldom been tested (Kokko *et al.* 2004, Stamps 2006, Ferrer *et al.* 2013b). Individuals usually have to rely on proximate cues of quality when choosing habitats, with the number of chicks in the nests being one of the clearest (Kokko *et al.* 2004). This critical assumption of correct assessment of the quality of a site must be fulfilled, otherwise occupations would be random with respect to territory quality. Our data suggest that birds can assess the quality of territories with limited experience, before they actually nest in them. High-quality Eagle territories were nine times more frequently visited, on average, and by up to five times more different floaters, than were low-quality territories. This strongly implied that individual Eagles, too young to have bred, knew which were the best territories in the area. It seems clear that floaters are actively prospecting high-quality territories even if they are still so young that opportunities for pairing are low (Whitfield *et al.* 2009a).

In territorial birds such as raptors, territory quality is likely to differ greatly among pairs (Högstedt 1980, Newton 1980, 1991, Ferrer & Donazar 1996, Penteriani 2002). In some sedentary long-lived species, such as the Spanish Imperial Eagle, age of first breeding is density-dependent (Ferrer *et al.* 2004) and is often correlated with territorial quality, with birds in non-adult plumage usually occupying low-quality territories (Newton *et al.* 1981, Steenhof *et al.* 1983). Variability in the age of entry into the breeding cohort enables populations to remain closer to carrying capacity, significantly affecting population persistence (Ferrer *et al.* 2004, 2011). For this mechanism to work, young birds able to enter the breeding population need to be able to assess the degree to which that population is saturated so that they can search for and fill vacancies as soon as they become available. Continual searching is evident among young birds of sedentary populations, which continually move between their temporary settlement areas and central breeding sites until they find a breeding vacancy and enter the reproductive cohort (Ferrer 1993, 2001, Ferrer *et al.* 2004).

Unexpectedly, the observed frequency of breeding individuals in non-adult plumage, taken as a surrogate measure of floater entrance into the territorial population, was inversely correlated with the frequency of intrusions. Less productive territories showed the highest frequency of immature breeders (Ferrer & Bisson 2003). This could be because the floaters themselves consist of birds of different ages, and in a competitive situation, the older individuals (some perhaps in adult plumage) end up filling vacancies in the best territories, while younger birds are relegated to filling vacancies in poorer territories, or remaining as floaters. Given the annual survival of adult Spanish Imperial Eagles on territory, no more than one or two vacancies would be expected to appear at this site each year.

Nevertheless, floater Eagles tended to visit their natal population during certain months coincident with the beginning of the breeding cycle. Any vacancy in other months (i.e. the majority of the year) would be first detected by neighbouring territorial Eagles rather than by floaters, and a territorial adult in a poor territory may take the opportunity to move to a vacant better territory, leaving its mate behind. These kinds of movements by established adults have been reported in the Spanish Imperial Eagle (Ferrer & Bisson 2003, Penteriani *et al.* 2003) and in other similar species (e.g. White-tailed Eagle *Haliaeetus albicilla*; Whitfield *et al.* 2009a,b). As it seems clear that eagles know where good territories are, vacancies may last longer in poor-quality territories, facilitating their occupation by younger floaters (Ferrer & Penteriani 2003).

In many bird species, territory quality is one of the main factors affecting reproductive success, especially at the population level in high-density populations (Newton 1991, Dhondt *et al.* 1992, Ferrer & Donazar 1996). Although habitat heterogeneity in natural landscapes has often been documented (Wiens 1976, Turner 1989, Kotliar & Wiens 1990, Rodenhouse *et al.* 1997, 1999), few studies have tested how different turnover rates (e.g. mortality, migration, frequency and duration of vacancies) associated with differences in territory quality could affect mating processes within populations (but see Newton 1991, Ferrer & Penteriani 2003, Sergio *et al.* 2007).

Our results do not support the interference hypothesis and show, contrary to the predictions of the hypothesis, a positive relationship between intrusions and productivity. Nevertheless, we have to remember that our analysis is only about floater intrusions. We cannot discard the possibility that intrusions of owners of neighbouring territories would have any effect on productivity. Our results support one of the expectations under the hypothesis of habitat heterogeneity, because rates of floater intrusions and annual territory productivity were highly positively correlated, showing that floaters can detect the quality of the territories and prefer to visit those of high quality. These findings were made in a breeding population in which all or most territories were occupied for most of the study period, and in which floaters occurred at a particular range of densities. The situation might change if breeding numbers declined, so that vacancies were always available, or if floater numbers and intrusions increased to such a level that they could impinge on nest success or adult survival, as recorded, for example, in Golden Eagle *Aquila chrysaetos* (Jenny 1992, Haller 1996) and Bald Eagle *Haliaeetus leucocephalus* (Bowman *et al.* 1995). Our results in this paper also demonstrate that intrusion frequency could be used as another measure of territory quality, and that individual birds can assess territory quality on what would seem to be relatively little evidence.

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Natal philopatry: local experience or social attraction? An experiment with Spanish Imperial eagles.

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Natal philopatry: local experience or social attraction? An experiment with Spanish Imperial eagles.

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Abstract:

We investigate juvenile dispersal in a territorial long-lived species with deferred maturity, the Spanish imperial eagle (*Aquila adalberti*). Here we used a reintroduction program as an experimental approach to test separately predictions of the different hypotheses about natal philopatry: social attraction and local experience. We determined maximum juvenile dispersal distances of 90 young eagles in three different scenarios: (i) 31 translocated young released without adults in the area, (ii) 29 tranlocated young released with established adults breeding in the area, and (iii) 30 wild non manipulated individuals. Mean maximum dispersal distances for all the juvenile eagles was 174.4 Km. No differences between sexes were found but highly significant differences among the three scenarios, with longer distances in young released without adults in the area (232.7 Km) and similar distances in the other two scenarios (released young with adults mean distance= 154.2 Km; wild young mean distance= 132.9 Km) were found. Our results showed that social attraction determined the juvenile dispersal strategies of a territorial long-lived species.

Keywords: *Aquila adalberti, dispersal, hacking, long-lived species, movement behavior, philopatry, radio-tracking, Spanish imperial eagle, social attraction translocation*

Introduction

Juvenile dispersal is a fundamental process affecting genetic flow, distribution, population dynamics and persistence of species (Hanski & Gilpin, 1997; Dieckmann et al. 1999;, Clobert et al., 2001). Nowadays most of the published information on juvenile dispersal behavior of birds is based on the continuous following of tagged individuals (Ferrer, 1993a; 1993b; Sternalski et al., 2008, Muriel et al., 2015, Muriel et al., 2016). A long-term database of this kind allows us to better understand the behavioral decisions, importance and factors involved in the period prior to settlement, known as juvenile dispersal (Whitfield et al., 2009a, b). Due to the usual high mortality during juvenile dispersal, dispersal decisions must be under high selective pressure due to the costs associated with dispersal and settlement, and the resulting fitness (Stamps, 2001; Bowler & Benton, 2005). The model species we study here is a typical large raptor with around 84% of first year mortality (Ferrer &Calderon, 1990), and consequently different strategies during dispersal movements would be under strong selection.

Typically, in birds with deferred sexual maturity, individuals frequently tend to return to breed in their natal populations (e.g., Ferrer, 1993a; Sternalski et al., 2008; Ferrer et al., 2015). This widespread behavior, called natal philopatry has been interpreted under two mutually exclusive hypotheses. First, according to some authors, juvenile birds may show a natural tendency to return to the natal area for breeding because they would be preferably selecting familiar areas as future breeding territories where reproduction is possible for sure (Greenwood, 1980, 1982; Shields, 1982). This is the “local experience” hypothesis. Second, juveniles may also show a tendency to look for areas with breeding pairs of the same species as reliable indirect cues of intrinsic habitat quality for reproduction, known as social (or conspecific) attraction hypothesis (Ray et al., 1991; Muller et al., 1997; Fletcher 2006). According the social attraction hypothesis, juveniles should increase dispersal distances when they failed to find adults of their same species during their movements.

Philopatry (and associated local experience) and social attraction can be considered as strategies that may lead to higher fitness benefits in terms of juvenile survival and post-settlement fecundity (Stamps, 1988; Danchin et al., 2001; Doliguez et al., 2003; Fletcher 2006). These two strategies, however, cannot be studied separately in natural populations because juveniles always know both their natal area and their own parents, so it is impossible to separate the effect of one factor from the effect of the other.

In the present study, we investigate juvenile dispersal in a territorial long-lived species with deferred maturity, the Spanish imperial eagle (*Aquila adalberti*). Here we used a reintroduction program (Muriel et al., 2011) as an experimental approach to test separately predictions of the different hypotheses about juvenile dispersal movements. We examine the ontogeny of the movement behavior of radio-tagged juvenile eagles throughout their first two years of life under three different scenarios: (1) tranlocated young released without adults in the area, (2) tranlocated young released with established adults breeding in the area, and (3) wild non manipulated individuals. In the first two scenarios, *ad libitum* food was provided during six weeks before release, potentially improving the nutritional condition of the young. In the wild young, no supplementary food was provided.

According to the social attraction hypothesis, we expect longer dispersal distances in young eagles released without adults in the area, and no differences in maximum dispersal distance in the other two scenarios (wild young and released young with adults breeding in the area). In contrast, under a local experience context, shorter distances would be expected in released young without adults who would defend their territory and eject any young from the area

Methods

Study species

The Spanish imperial eagle is a large (2500-3500 g) raptor breeding only in the Iberian Peninsula with a conservation status of “vulnerable” (IUCN Red List, BirdLife International 2008). With around 500 breeding pairs in 2015 (National Working Group, unpublished data 2015) this species is one of the rarest eagles in the world. It is long-lived (21-23 years), with a mean annual productivity of 0.75 chicks/pair, sedentary and territorial, (Ferrer & Calderon, 1990). The reproductive cycle lasts around 8 months (from February to October), and independent juveniles show long distance dispersal behavior (Ferrer, 1993a), including exploratory movements, temporary settlement, and visits to other breeding populations. The age of first breeding is around 4-5 years old on average (Ferrer et al., 2015). Temporary settlement areas usually contain high prey densities (wild rabbit), and few or no other large breeding eagles (Ferrer & Harte, 1997).

Study area and data collection

In total, 105 birds hatched in 14 non-consecutive years, from 1986 to 2013, were studied. Those young were from the population of Doñana National Park (1049.7 km^2; 36º56'N, 6º30'W), a reinforcement project in the same area, and a reintroduction project in the province of Cadiz (≈36º20'N 5º48'W, around 87 km from Doñana National Park), in southern Spain. Data from wild birds were taken during the years 1986-2010, young released without adults in the area in the period 2002-2009 and young released with adults in the area in 2005-2013. We conducted a monitoring programme over a large area of the southern Iberian Peninsula, a mixture of dry-humid Mediterranean forest, scrubland and wetlands (for a more detailed description see Muriel et al., 2015). Hatching dates of the young were accurately known due to previous checks of the nests. Mean hatching date for all the young was 25 April ± 8 days.

The Spanish imperial eagle reintroduction program in the province of Cadiz started in 2002 (Muriel et al., 2011). Between 2002 and 2013, young eagles were translocated when 47.8 ± 6.1 days old to the hacking facilities in three nearby locations, and released after 28.8 ± 6.2 days. Young were fed *ad libitum* until the last young left the release area (for more details see Muriel et al. 2011). As previously known, young eagles do not learn any special flight skill from their parents during the dependence period (Ferrer 1993a), so no differences in dispersal abilities between wild and translocated young would be expected due to parental influence.

All nestlings were ringed and equipped with backpack radio-transmitters when they were 45-70 days old. Radio-transmitters (three models: TW-3, Biotrack Ltd., UK; HSPB 14003, Wildlife Materials Inc., USA; and 5/XOB 17-04, Wagener Telemetrieanlagen, Germany) did not exceed a maximum of 2.5% of the body mass of the young at fledging (Kenward, 2001). Between 2006 and 2013, sex of young was determined by means of the forearm measurement (Ferrer & De le Court, 1992) as well as molecular methods (Fridolfsson & Ellegren, 1999) using blood samples.

Dispersal monitoring

Juveniles were radio-tracked from the beginning of dispersal to the end of their second year of life (i.e., 700 days old) or until transmitter failure/loss. We considered the beginning of dispersal as the first day the individual was located over 6.5 km from the natal population (mean inter-nest distance; González, 1991), i.e. from any active nest belonging to the natal population in the case of non-manipulated juveniles, or from the hacking site for translocated individuals. At least two simultaneous teams tracked birds by car using portable receivers (models Stabo, GFT, Germany; and R1000, Communication Specialist Inc., USA), non-directional antennas and three-element Yagi antennas. Searches were conducted at least 5 days per week by each team, using high observational points regularly distributed over the dispersal area. We always tried to locate the bird visually; otherwise location by triangulations was carried out. Occasionally, search from light-aircraft was also performed within a minimum radius of 150 km around the Doñana population and hacking sites to look for non-located individuals. In total, we devoted 3150 days for the field work and searched an area of 44,243 km2 (kernel 95% of spotting sites used). As previously known, young eagles reached their maximum dispersal distance (Dmax) from their natal nest within two years of their departure (Ferrer, 1993b). Consequently, in the present study we only considered those juveniles that we were able to track for more than 700 days after dispersal. The final data set for Dmax analyses included 90 young eagles (50 males and 40 females); 31 tranlocated young released without adults in the area (all of them in Cadiz), 29 tranlocated young released with adults breeding in the area (14 in Doñana and 15 in Cadiz), and 30 wild non-manipulated individuals (20 in Doñana and 10 in Cadiz).

Statistical analysis

We explored variations in the maximum dispersal distances (Dmax) among the three scenarios considered (released young with and without adults and wild young). We fitted a GLM model with normal distribution to analyze Dmax including 'scenarios' and 'sex' and first order interactions as factors. We also investigated potential differences between the two populations (Doñana and Cádiz) selecting the two common scenarios they share; i.e. wild young and released young with adults in the area. In order to check if the leptokurtic distribution of one of the scenarios can affect the analysis, we conducted the a test for comparison of medians. All tests were two-tailed with statistical significance at $P < 0.05$. Data were analyzed using STATISTICA 8.0 (Statsoft Inc., USA).

Ethical note

The research project was approved by The Ethical Committee of the Spanish Council for Scientific Research, which is the representative authority in Spain. After ethical evaluation, the research program was authorized by the Andalusia environmental administration (i.e. Consejería de Medio Ambiente, Junta de Andalucía) which provided the licenses for the manipulation of nestlings.

Results

Mean maximum dispersal distances for all the juvenile eagles was 174.39 Km (*N*=90, SD=84.78 Km). A GLM was conducted with Dmax as the response variable, and with sex and the three scenarios as factors (Table 1). No differences between sexes were found (males mean distance= 177.59 Km, *N*=50; SD=87,13; females mean distance= 168.95 Km, *N*=40, SD=81,89) but highly significant differences emerged among the three scenarios, with longer distances in young released without adults in the area (232.71 Km, *N*=31, SD=81,58) and similar distances in the other two scenarios (released young with adults mean distance= 154.24 Km, *N*=29, SD=64,56; wild young mean distance= 132.92 Km, *N*=30, SD=71,71) were found (Fig 1). No significant differences between Doñana and Cádiz populations were found (GLM, Wald statistic=0.03, *P*=0.854), excluding from the analysis those young released without adults in the area that was only possible in Cádiz. Also, we conducted a GLM with Dmax as the response variable and with sex and the three scenarios as factors but using only data from the Cadiz population. Again, highly significant differences among scenarios were found (Wald statistic=18.11, *P*=0.0003), with longer distances in young released without adults in the area (232.71 Km) and similar distances in young released in the presence of adults (150.54 Km) and wild young (141.07 Km).

No differences in significance with the previous results were found, when using medians to compare dispersal distances of the three scenarios (Kruskal-Wallis test: H (2, N= 90) =25,81258 p =,0000) (table2).

Discussion

All juvenile eagles dispersed, including released young without adults in the area, despite the ‘favorable’ conditions of the release area, where the parent-offspring conflicts (Trivers, 1974) are not possible in the absence of territorial adults and in the presence of *ad libitum* food. These findings strongly support the existence of an important inherent component in the dispersal process. Some benefits must be obtained from dispersal, sufficient to outweigh any potential costs (e.g. mortality) associated with moving through an unknown environment (Ferrer, 1993b; Muriel et al., 2015, 2016).

Significant differences in Dmax were found among scenarios, with close to double the mean distances in young released in the area lacking adults than in the other two situations with adults present. The differences cannot be attributed to differences between releaseareas (Doñana and Cádiz), because they held in the Cádiz area alone. No differences between populations were found when comparing dispersal distances of wild young and of released young with adults in the area. We showed that social attraction has a critical role in influencing maximum dispersal distances, as was apparent in the area lacking adults, where young eagles almost doubled their normal distances compared with wild young (232 km versus 132 km). Such differences were also significant when compared with those of released young with breeders in the area (232 Km versus 154 km), showing that the increases in Dmax were not related to management or *ad libitum* food.

Expectations under the local experience hypothesis were shorter Dmax in released young without adults who would defend their territory and reject any young in the area. Results demonstrated the opposite. Consequently, it seems that familiarity with the natal area is not the driver of Dmax but the attraction of breeders. In other words, philopatric behavior could result largely from social attraction.

It is important, however, to point out that our results are based on maximum juvenile dispersal distances (Dmax), and not on eagles settled at breeding territories (natal dispersal distances). Nevertheless, there are studies on similar species showing a positive relationship between Dmax and natal dispersal (Whitfield et al., 2009a, b), demonstrating that early juvenile dispersal behaviour and selection of a subsequent breeding site are associated with one another

Another potential problem with our data is that they were based fundamentally on active efforts to relocate VHF (radio) tagged birds. Consequently, there was a possibility that some of the longer distant dispersers may have escaped detection. However, according our results, it seems that this potential bias would have more effect on differences between sexes than among scenarios.

The effect of social attraction on dispersal may entail important consequences on metapopulation dynamics and population management. Social attraction can favor the aggregation of individuals into previously existing populations and thus limit the colonization of empty habitat patches (Stamps, 1988; Hanski & Gilpin, 1997; Muller et al., 1997). Such an effect may constrain colonization from relatively isolated populations and reduce gene flow with distant populations, resulting in lower viability of those peripheral nuclei and decreasing metapopulation stability (e.g., Ray et al., 1991; Serrano & Tella, 2003). Most of the endangered species that suffer human persecution in the past would be in such a situation, with large areas showing suitable habitat but constrained by the social attraction that limits their ability to colonize it (Morandini et al., 2017). Conservation strategies should ensure metapopulation structures with balanced distances among populations to increase inter-patch connectivity and avoid the effective isolation of peripheral nuclei.

This positive density-dependent immigration process could be also expected in reintroductions where other breeding populations occur within the dispersal range, and may affect the establishment and growth of an incipient restored population (Milhoub et al., 2011; Muriel et al., 2015). Hence, the behavioral and spatial strategies under such a social attraction scenario may slow down the initial settlement phase of reintroductions. However, this mechanism may differ according to the translocation status, relative population densities and breeding prospects (Milhoub et al., 2011). For instance, pre-existing populations can enhance growth rates of incipient reintroduced populations by increasing immigration. In fact, the first settled pairs of Spanish imperial eagle in the release area were composed by translocated and non-reintroduced individuals (Muriel et al., 2011).

According to our results, social attraction and the spatial structure of dispersal areas should be taken into account in habitat and population viability analyses when planning reintroductions. Selection of reintroduction sites relatively close to former existing populations may enhance immigration of released young whereas breeding nuclei may hinder the establishment but enhance the growth of the incipient population.

Release and post-release methods can also be adjusted to encourage earlier settlement in such reintroduction contexts. Although the release of adults has shown more rapid settlement in colonial bird species (Sarrazin & Legendre, 2000; Le Gouard et al., 2008), this approach may not be viable in endangered territorial species with small effective populations, such as the Spanish imperial eagle. An alternative would be the modification of conspecific cueing in the release area to make it more attractive for translocated juveniles. For instance, the use of captive adult birds from recovery centers during the first years of releases might decrease Dmax, increase return rates and earlier settlement, which in turn would accelerate the establishment phase.

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Table 1. Results of a GLM with maximum dispersal distance (Dmax) as respond variable, sex and the three scenarios as factors was conducted. No significant differences between sexes were found but highly significant differences among the three scenarios.

	df	**Wald Statistic**	***P***
Intercept	1	11298.28	<0.001
Sex	1	0.15	0.701
Scenarios	2	31.60	<0.001
Sex* Scenarios	2	0.33	0.849

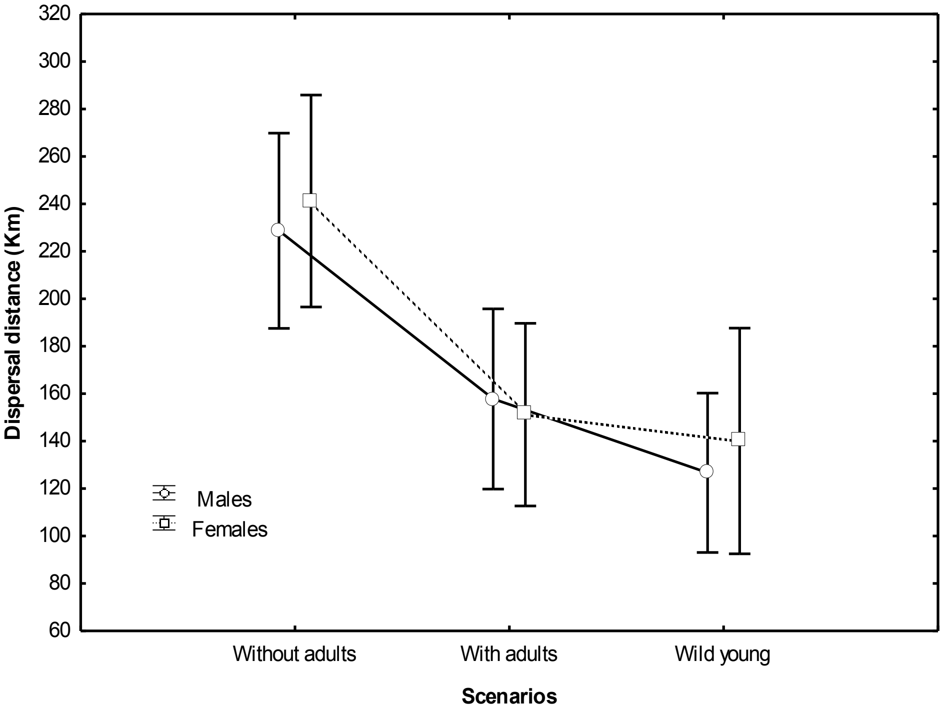
Table 2: Results of comparing medians of the three different scenarios analyzed.

Multiple Comparisons z' values; Dmax nor (dismax 2) Independent (grouping) variable: clase
Kruskal-Wallis test: H (2, N= 90) =25,81258 p =,0000

	1 - R:64,129	**2 - R:40,310**	**3 - R:31,267**
1		3,529155	4,911612
2	3,529155		1,329313
3	4,911612	1,329313	

**1= hacking no adults; 2= k¡hacking adults; 3= wild birds*

Fig 1. Differences in mean dispersal distances among scenarios, with longer distances in young released without adults in the area (232.71 Km, *N*=31) and similar distances in the other two scenarios (released young with adults mean distance= 154.24 Km, *N*=29; wild young mean distance= 132.92 Km, *N*=30). No differences between sexes were found (males mean distance= 177.59 Km, *N*=50; females mean distance= 168.95 Km, *N*=40, bars = 95% confidence interval).



The distribution of juvenile dispersal distances: an experiment with Spanish imperial eagles

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The distribution of juvenile dispersal distances: an experiment with Spanish imperial eagles

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Abstract:

We investigated the distribution of juvenile dispersal distances of a territorial long-lived species with deferred maturity, the Spanish imperial eagle (*Aquila adalberti*). Here we used a reintroduction program as an experimental approach to test predictions of different hypotheses about the distribution of juvenile dispersal distances: competition and wandering behavior. We determined maximal juvenile dispersal distances of 59 young eagles; (i) 30 wild non-manipulated individuals, and (ii) 29 tranlocated young under an *ad libitum* feeding program, released with adults breeding in the area. The competitive displacement hypothesis predicts a leptokurtic distribution of distances in wild non-manipulated young as well as in released young. Under the 'wandering' hypothesis, however, a leptokurtic distribution is expected in wild young, but a normal distribution would be expected in young released (with adults in the release area), owing to a general improvement in the nutritional status of released young that have been fed *ad libitum,* as is usual in reintroduction programs. Additionally, a negative relationship between hatching date and dispersal distances is expected in wild young but no relationship in released young under *ad libitum* feeding. Mean maximum dispersal distances for all the juvenile eagles was 142.8 Km. No differences between sexes were found, nor between populations or between wild and reintroduced young. Wild young distances were not normally distributed, being closer to a Poisson distribution. In contrast, released young with adults (under *ad libitum* feeding) showed a normal distribution. Wild birds showed a significant negative relationship between dispersal distance and hatching date, with young that hatched late in the season dispersing shorter distances. However, released young under *ad libitum* feeding showed no significant relationship between hatching date and dispersal distance. These results support the "wandering" hypothesis as the main driver of the distribution of dispersal distances.

Keywords: *nutritional conditions, competitive hypothesis, wandering hypothesis, Aquila adalberti.*

Introduction

Juvenile dispersal is a fundamental process affecting genetic flow, distribution, population dynamics and persistence of species (Hanski and Gilpin 1997, Dieckmann et al. 1999, Clobert et al. 2001,). Nowadays most of the published information on juvenile dispersal behavior of birds is based on the continuous following of tagged individuals (Ferrer 1993a, 1993b, Sternalski et al. 2008, Muriel et al. 2015, Muriel et al. 2016). A long-term database of this kind allows us to better understand the behavioral decisions, importance and factors involved in the period prior to settlement, known as juvenile dispersal. Due to the usual high mortality during juvenile dispersal, dispersal decisions must be under high selective pressure due to the costs associated with dispersal and settlement, and the resulting fitness (Stamps 2001, Bowler and Benton 2005).

In most studies of bird dispersal, a leptokurtic distribution of distances has been found (e.g. Buechner, 1987; Miller and Carroll,1989; Rodgers and Klenner, 1990; Ferrer, 1993b, Newton 2008), with most of the individuals relatively close to the natal nest and few of them dispersing large distances, forming the tail of the distribution. Two main hypotheses trying to explain this form of distribution of dispersal distances have been proposed. Some authors had suggested that this distribution could arise due to competition among dispersing individuals (i.e. competitive displacement hypothesis), with individuals at lower competitive advantage moving longer distances. Those individuals that form the tail of the distribution, are supposed to be later nestlings in the season raised under poor nutritional conditions and taking longer to disperse (Murray, 1967; Waser, 1985). An alternative explanation is the ‘wandering’ hypothesis (Ferrer 1993b). In this hypothesis, a skewed distribution of dispersal distances is again expected but with juveniles that are hatched early in the season, with better nutritional status, dispersing longer distances, and young that hatched later remaining closer to the natal area.

In the present study, we investigate juvenile dispersal in a territorial long-lived species with deferred maturity, the Spanish imperial eagle (*Aquila adalberti*). We used a reintroduction program (Muriel et al. 2011) as an experimental approach to test separately predictions of the different hypotheses about the distribution of dispersal distances. We examined the ontogeny of the movement behavior of radio tagged juvenile eagles throughout their first two years of life under two scenarios: (i) wild non-anipulated individuals, and (ii) tranlocated young released with adults breeding in the area. In the second scenario, *ad libitum* food was provided during six weeks before release, potentially improving the nutritional condition of the young. In the wild young, no supplementary food was provided.

According to the competitive displacement hypothesis, we expect a leptokurtic distribution of distances in wild non-manipulated young as well as in released young. The long-distance dispersers are expected to be those individuals born late in the season; consequently a positive relationship between hatching date and dispersal distance is again predicted in both scenarios.

In contrast, under the ‘wandering’ hypothesis, a leptokurtic distribution is expected in wild young but a decrease in leptokurtosis, showing a quasinormal distribution, would be expected in the release scenario (with adults in the release area) due to a general improvement of the nutritional status of released young that have been fed *ad libitum* during their growth. Additionally, a negative relationship between hatching date an dispersal distances is expected in wild young but no relationship in released young under *ad libitum* feeding.

Methods

Study species

The Spanish imperial eagle is a large (2500-3500 g) raptor which breeds only in the Iberian Peninsula with a conservation status of “vulnerable” (IUCN Red List, Birdlife International 2008). With around 500 breeding pairs in 2015 (National Working Group, unpublished data 2015) it is one of the rarest eagles in the world. The species is long-lived (21-23 years), with a mean annual productivity of 0.75 chicks/pair, sedentary and territorial, (Ferrer and Calderon 1990). The reproductive cycle lasts around 8 months (from February to October), and independent juveniles show long distance dispersal (Ferrer 1993a), including exploratory movements, temporary settlement, and visits to breeding populations, possibly to gather information on breeding prospects. The age of first breeding is around 4-5 years on average (Ferrer et al. 2015). Temporary settlements areas typically have high prey density (wild rabbit), but few or no other large breeding eagles (Ferrer and Harte 1997).

Study area and data collection

In total, 65 birds hatched in 14 non-consecutive years (1986 to 2013) were studied. These young were from the population of Doñana National Park (1049.7 km^2; 36º56'N, 6º30'W), from a reinforcement project in the same area, and from a reintroduction project in the province of Cadiz (≈36º20'N 5º48'W, around 87 km apart from Doñana National Park), in southern Spain. We conducted a monitoring programme over a large area in southern Iberian, a mixture of dry-humid Mediterranean forest, scrubland and wetlands (for a more detailed description see Muriel et al. 2015). Hatching dates of the young were accurately known due to previous checks of the nests. Mean hatching date for all the young was 25 April ± 8 days.

In the Spanish imperial eagle reintroduction program in the province of Cadiz between 2002 and 2013 (Muriel et al. 2011), young eagles were translocated when 47.8 ± 6.1 days old to the hacking facilities in three nearby locations, and released after 28.8 ± 6.2 days. Young were fed *ad libitum* until the last young left the release area (for more details see Muriel et al. 2011).

All nestlings were ringed and equipped with backpack radio-transmitters when they were 45-70 days old. Radio-transmitters (three models: TW-3, Biotrack Ltd., UK; HSPB 14003, Wildlife Materials Inc., USA; and 5/XOB 17-04, Wagener Telemetrieanlagen, Germany) did not exceed a maximum of 2.5% of the body mass of the young at fledging (Kenward 2001). Sex of young was determined by means of the forearm measurement (Ferrer and De le Court 1992) as well as molecular methods (Fridolfsson and Ellegren 1999) using blood samples collected between 2006 and 2013.

Dispersal monitoring

Radio-tagged juveniles were radio-tracked from the beginning dispersal to the end of their second year of life (i.e., 700 days old) or longer (until transmitter failure/loss). We considered the beginning of dispersal as the first day the individual was located over 6.5 km from the natal population (mean inter-nest distance; González, 1991), i.e. from any active nest belonging to the natal population in the case of non-manipulated juveniles, or from the hacking site for translocated individuals. At least two simultaneous teams tracked birds by car using portable receivers (models Stabo, GFT, Germany; and R1000, Communication Specialist Inc., USA), non-directional antennas and three-element Yagi antennas. Searches were conducted at least 5 days per week by each team, using high observatiol points regularly distributed over the dispersal area. We always tried to locate the bird visually; otherwise by triangulation. Occasionally, search from light-aircraft was also performed within a minimum radius of 150 km around the Doñana population and hacking sites to look for non-located individuals. In total, we devoted 3150 days for the field work and searched an area of 44,243 km^2 (kernel 95% of spotting sites used). As previously known, young eagles reached their maximum dispersal distance (Dmax) from their natal nest within two years of their departure (Ferrer, 1993b). Consequently, in the present study we only considered those juveniles that we were able to track for more than 700 days after dispersal. The final data set for Dmax analyses included 59 young eagles (29 males and 30 females); 29 tranlocated young released with adults breeding in the area (14 in Doñana and 15 in Cadiz), and 30 wild non-manipulated individuals (20 in Doñana and 10 in Cadiz). Data from wild birds were taken in the 1986-2010 period and young released with adults in the area in the 2005-2013 period.

Statistical analysis

We explored variations in the maximum dispersal distances (Dmax) among the two scenarios considered (wild young and released young with adults). Variable hatching day was log transformed to meet normality. We fitted a GLM model with normal distribution and log link function to analyze Dmax including “scenarios”, “sex” and “population” as factors. We also investigated potential differences between the two populations. To account for differences in competitive conditions among the young, we used hatching day as a proxy of nutritional status as a highly significant relationship between them have been published for this species and population (Ferrer 1993b, Muriel et al. 2015). All tests were two-tailed with statistical significance at $P< 0.05$. Data were analyzed using STATISTICA 8.0 (Statsoft Inc., USA).

Ethical note

The research project was approved by The Ethical Committee of the Spanish Council for Scientific Research, which is the representative authority in Spain with this function. After ethical evaluation, the research program was authorized by the Andalusia environmental administration (i.e. Consejería de Medio Ambiente, Junta de Andalucía) which provided the licenses for the manipulation of nestlings.

Results

Mean maximum dispersal distances for all the juvenile eagles was 142.8 Km (n=59, SD=68.45). No differences between sexes were found (GLM; Wald statistic=0.09, P=0.925), nor between Doñana and Cádiz populations (GLM; Wald statistic=0.05, P=0.943), or between wild and reintroduced young (GLM; Wald statistic=1.26, P=0.261, Table 1). Distributions of dispersal distances for the two scenarios are show in Fig 1. Wild young distances were not normally distributed (Shapiro-Wilk test=0.830; P=0.0003), being closer to a Poisson distribution (Fig 1). In contrast, released young with adults (under *ad libitum* feeding) showed a normal distribution (Shapiro-Wilk test=0.951; P=0.216).

The relationship between hatching date and dispersal distances is show in Fig 2. Wild birds showed a negative significant relationship, with shorter dispersal distances in young that hatched late in the season (r=-0.461; P=0.012). However, released young under *ad libitum* feeding (young released with adults in the area), showed no significant relationship between these variables (r=-0.108; P=0.658).

Discussion

Competitive displacement hypothesis predicted a leptokurtic distribution of dispersal distances in both scenarios, but only in wild young were the distances was close to a Poisson distribution, whereas dispersal distances in released young under feeding program were more normally distributed. Furthermore, according to the competitive hypothesis, the relationship between hatching date and distance of dispersal must be positive, with older nestlings dispersing further. However, wild young showed the opposite pattern, with a highly significant negative relationship, with older nestling dispersing shorter distances. This strong relationship disappeared in released young which showed no influence of hatching day on dispersal distance after the *ad libitum* feeding program.

These results give support to the ‘wandering’ hypothesis and reject the competition hypothesis. Mean dispersal distances were similar in both scenarios but distribution of Dmax changed from pronounced leptokurtic and positively skewed distribution to a normal distribution. These findings support the idea of a general improvement in nutritional conditions, affecting dispersal through the *ad libitum* feeding program. Analyses of Dmax and hatching dates demonstrated that leptokurtic distributions disappeared when nutritional conditions are generally improved by *ad libitum* feeding. In the wild young, without any supplementation, Dmax was significantly related to hatching date, with young that hatched early in the season, with a better nutritional condition (Ferrer 1994), dispersing longer distances. Therefore, our results showed how the wandering hypothesis determined the distribution of dispersal distances in a territorial long-lived species, such as the Spanish imperial eagle.

The effect of nutritional conditions on dispersal distances may entail important consequences on metapopulation dynamics and population management. Small populations of endangered raptors are usually under conservation programs sometimes including supplementary feeding (Ferrer and Penteriani 2007, Ferrer et al. 2014). A general improvement of nutritional status and specially a decrease in the natural variance of body condition in a population would affect the distribution of dispersal distances and hence the immigration-emigration ratio.

This nutritional-dependent emigration process should be expected in those reintroductions where other breeding populations occur within the dispersal range, and may affect the establishment and growth of an incipient restored population (Milhoub et al. 2011, Muriel et al. 2015). For instance, pre-existing populations can decreases the growth rate of incipient reintroduced population by increasing immigration. Due to a general improvement of the nutritional status of released young that have been fed *ad libitum* as is usual in reintroduction programs, a higher proportion of dispersing birds would contact the existing population. However, this effect may differ according to the translocation status, relative population densities and breeding prospects (Milhoub et al. 2011).

It is important to point out, however, that our results are based on maximum juvenile dispersal distances (Dmax), and not on eagles settled at breeding territories (natal dispersal distances). Nevertheless, there are studies on similar species showing a positive relationship between Dmax and natal dispersal (Whitfield et al. 2009a, b), demonstrating that early juvenile dispersal behaviour and selection of a subsequent breeding site are associated with one another. Another potential problem with our data is that they were based fundamentally on active efforts to relocate VHF (radio) tagged birds. Consequently, there was a possibility that some of the longer distant dispersers may have escaped detection. However, according to our results, it seems that this potential bias would have more influence on the differences between sexes than between scenarios.

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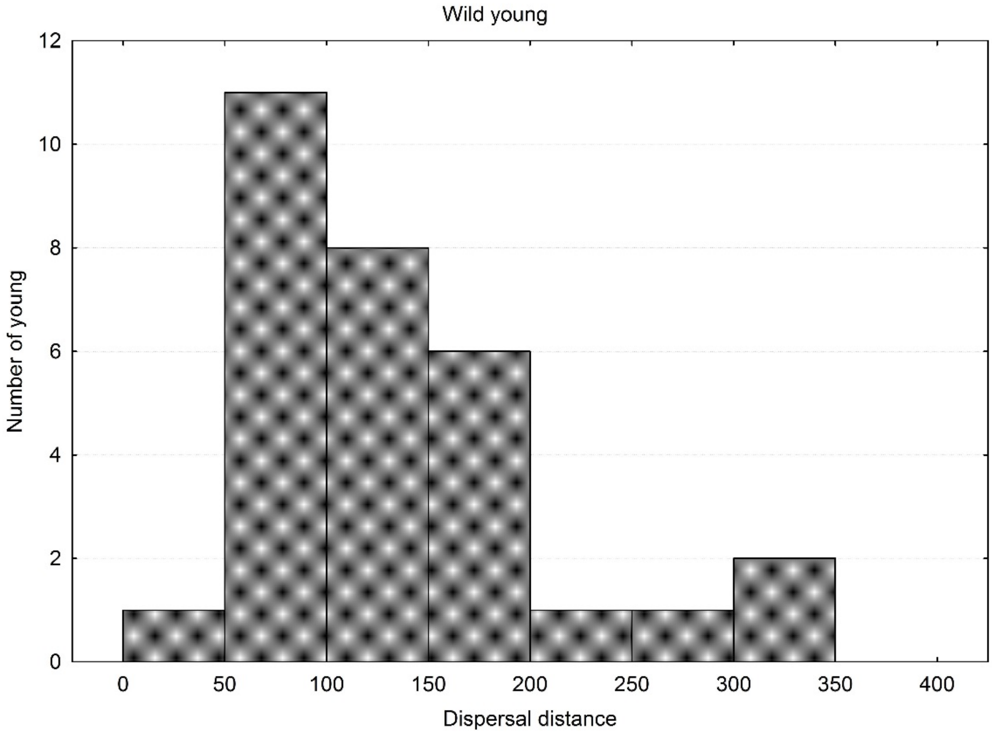
Table 1. Mean, sample size, SD and confident limits of maximum dispersal distances (Dmax) of juvenile Spanish imperial eagles in the first two years of life. No differences by sexes, scenarios or populations were found.

	Dmax Km	**N**	**Std.Dev.**	**-95,00 - Cnf.Lmt**	**+95,00 - Cnf.Lmt**
Males	140.61	29	63.80	116.41	164.87
Females	144.88	30	73.70	117.35	172.40
Reintroduced Young	152.98	29	64.56	128.42	177.53
Wild Young	132.92	30	71.71	106.14	159.70
Doñana	141.07	34	66.37	117.91	164.23
Cádiz	145.10	25	72.51	115.17	175.03
Total	142.78	59	68.45	124.94	160.62

Fig 1. Distributions of dispersal distances in the two scenarios. Released young in the presence of adults (under *ad libitum* feeding) showed a normal distribution of distances (Shapiro-Wilk test=0.967; P=0.114), whereas wild young showed a non- normal distribution of distances (Shapiro-Wilk test=0.830; P=0.0003), more closely approaching a Poisson pattern.



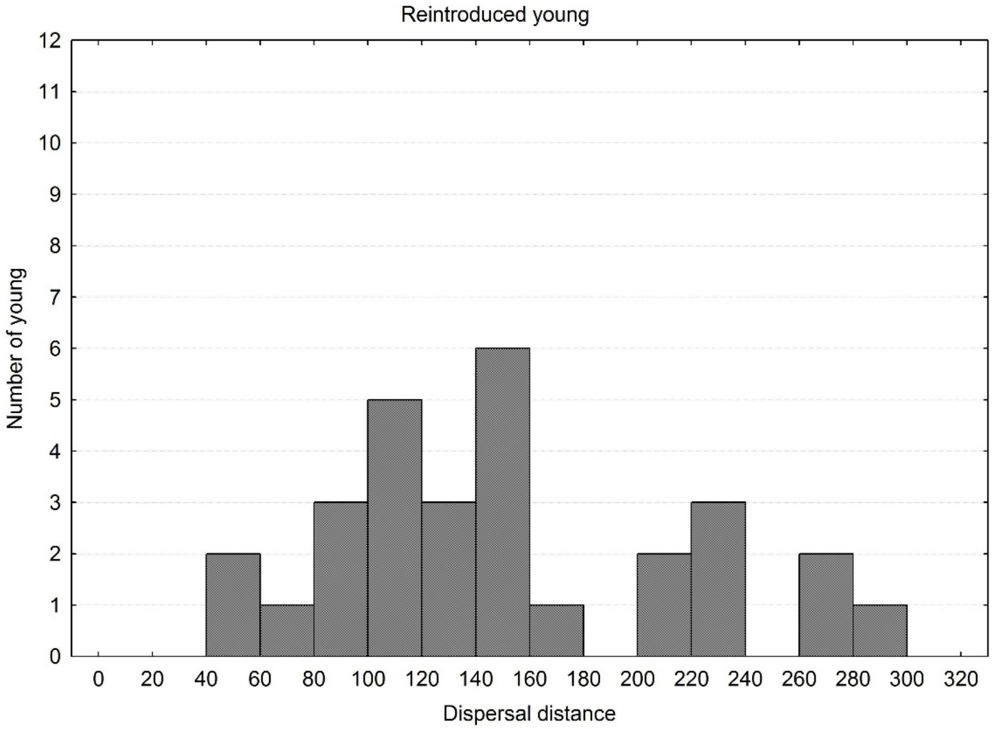
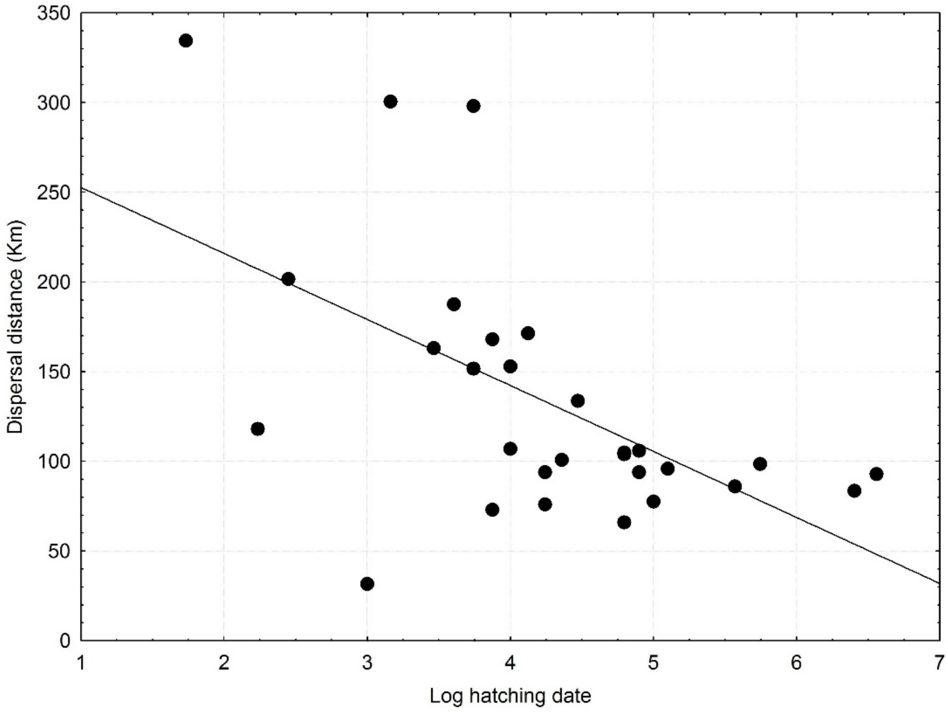
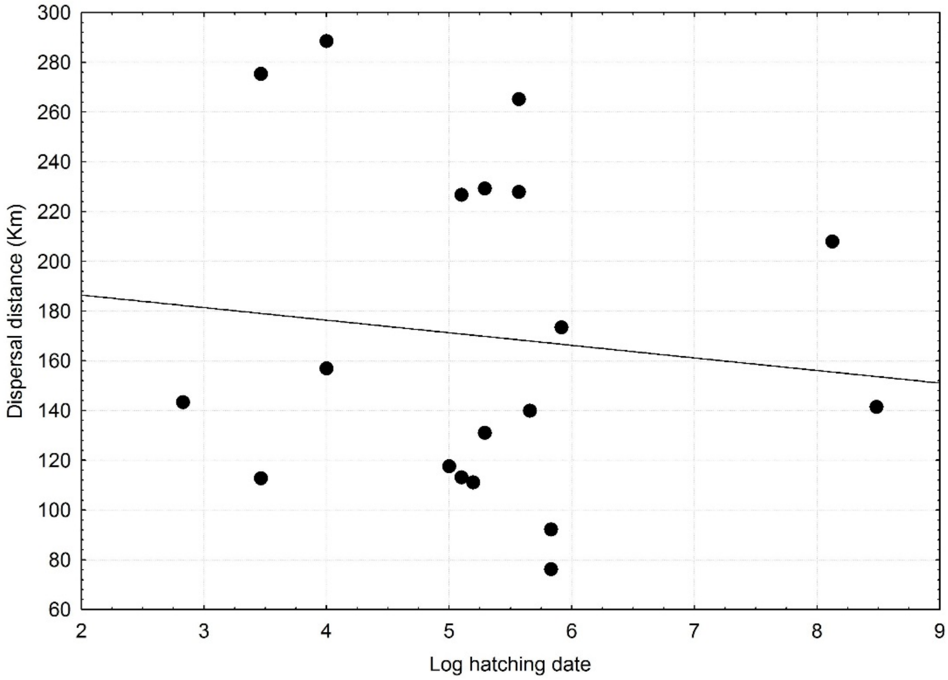


Fig 2.Relationship between hatching dates and dispersal distances. Wild birds, showed a significant negative relationship, with shorter dispersal distances in young that hatched late in the season (r=-0.567; P=0.001). However, released young with *ad libitum* food showed no significant relationship between hatching date and dispersal distance (r=-0.108; P=0.658).


Dispersal distance (Km)
0
50
100
150
200
250
300
350
1
2
3
4
5
6
7
Log hatching date


Dispersal distance (Km)
60
80
100
120
140
160
180
200
220
240
260
280
300
2
3
4
5
6
7
8
9
Log hatching date

Chapter 3: How is a colonization process possible?

Understanding the factors that influence the persistence of small populations continues to be one of the primary challenges confronting conservation biology (Miguel Ferrer, Newton, & Muriel, 2013; Penteriani, Otalora, & Ferrer, 2005; Reynolds, Weiser, Jamieson, & Hatfield, 2013; Seddon, 1999). The influence of the mean intrinsic growth rate of the population (“r”) could be very important in the persistence of populations, especially in the range of small r. This explains the lower time to extinction for the same population size in large animals, with a very modest r, than for small animals with higher mean growth rates (Goodman, 1987). In this sense, long-lived species with deferred maturity, low fecundity and high juvenile mortality rates are defined as bad colonizers. Consequently, we usually assume that species with low r values have a very low capacity to respond to stochastic variation. However, there might be buffer mechanisms that allow even a small population to survive for a longer time than predicted by simple theoretical models, as historical records of real populations suggest (Meriggi & Mazzoni della Stella, 2004; Monti et al., 2014; Whitfield et al., 2009).

The ability to modify demographic parameters that affect the mean intrinsic persistence of small populations according to the density of populations, could play a key role in determining the success of colonization processes (Miguel; Ferrer, Otalora, & García-Ruiz, 2004), including reintroductions.

In this chapter, we compared changes in demographic parameters, such as productivity, age of first breeding and offspring sex ratio, between established and stable, and reintroduced and increasing populations, assessing the ability to colonize a new area according to flourish according to changes in demography.

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Density-dependent parameters of reintroduced populations: age of first breeding and the overestimation of extinction risks

Morandini V., Dietz S., Newton I. and Ferrer M. (2017). In prep.

Density-dependent parameters of reintroduced populations: age of first breeding and the overestimation of extinction risks

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Abstract:

The present biodiversity crisis has led to an increasing number of reintroduction programs, and it seems that this conservation tool is going to be more used in the future, especially in the face of climate change. Many fundamental questions in population ecology centre on the mechanism whereby populations escape extinction. Population Viability Analyses is the most common procedure to analyzed extinction risk. In the use of PVA to model the trajectories of reintroduced populations, demographic values are sometimes taken from other existing wild populations or even from individuals in captivity. No allowance is made in viability models for density dependent effects on demographic parameters such as reproductive and mortality rates. However, density-dependent variation in age of first breeding has a buffer effect on population fluctuations and in consequence on population persistence.
We simulated populations' viability of Spanish Imperial eagle (*Aquila adalberti*) and Osprey (*Pandion halietus*) using both data of established populations and data from reintroduced populations in southern Spain.

Our results show that, populations of long-lived birds resulting from reintroductions or colonizations of new areas increase at maximum rate only when the age of first breeding is reduced. To ignore this variation in PVA means that we are seriously limiting the potential of the model population to respond to fluctuations in density, decreasing its resilience and viability.

Keywords: *reintroductions, age of first breeding, productivity, PVA, Spanish Imperial eagle, Aquila adalberti, Osprey, Pandion haliaetus.*

Introduction:

Computer simulation models are often used to estimate the probability of extinction, time to extinction, population trajectory and loss of genetic variability in small populations (Bustamante 1998; Ferrer, Newton & Pandolfi 2009; Converse, Moore & Armstrong 2013). For recently reintroduced populations, such models can also provide estimates of population growth rates and future population sizes, probabilities of short-term establishment or longer-term persistence, as well as exploring the impacts of different management actions. The assumptions used in such models can influence the estimates of population viability obtained, and can therefore affect management decisions (Bustamante 1998). In the use of PVA to model the trajectories of reintroduced populations (Bustamante 1998; Ferrer *et al.* 2014b; Morandini & Ferrer 2017), demographic values are sometimes taken from other existing wild populations or even from individuals in captivity (Bustamante 1998; Margalida *et al.* 2015). Birds with a medium to high body mass often exhibit deferred sexual maturity and a long period of immaturity, although for many sedentary bird species participation of non-adult individuals in reproduction has been documented (see Ferrer et al. 2004 and references there in). The frequency of individuals in immature plumage in breeding populations is variable and density dependent (Ferrer et al. 2004). Fixing the age of first breeding in the usual values of a medium to high density population means that we are seriously limiting the potential of the model population to respond to fluctuations in density, decreasing its resilience and viability.

However, no allowance is made in viability models for density dependent effects on demographic parameters such as reproductive and mortality rates.

The aim of this paper is to show what difference taking account of density dependent changes in demographic rates makes to the projected rates of increase and other measures of population in two raptors species, namely the Osprey *Pandion haliaetus* and the Spanish Imperial Eagle *Aquila heliaca*. In both these species, demographic measures are available for this purpose from both recently-reintroduced and long-established populations.

Material and methods:

Study species

The Osprey breeds in all continents except Antarctica, being resident in some areas and migratory in others (Poole 1989). It is a specialist fish-eating raptor with a breeding dispersion ranging from solitary to loosely colonial (Poole 1989). Over the years, it has suffered heavily from various human impacts, becoming extinct over large areas due to human persecution in the late 19th and early 20th centuries (Poole 1989; Saurola 1997). In mainland Spain, after a continuing decline in the number of breeding pairs at least from the 1960s, the last pair bred in the province of Alicante in 1981 (Urios et al. 1991).

Data used here came from an Osprey reintroduction program in 182 in which juveniles (76 males, 64 females) were released by hacking in southern Spain from 2002 to 2012. All these released birds were ringed as nestlings with metal rings and PVC colour rings, so individuals could be readily identified. The first nesting attempt occurred in 2005 (Muriel *et al.* 2006) and the first successful nest was in 2009 (Muriel *et al.* 2010). By the end of the 2016 nesting season, we had documented 92 nesting attempts, of which 51 (55%) started incubation and 44 (48%) were successful. During 2009-2016, 78 wild-fledged chicks were produced by this new population. As in other studied Osprey populations (Monti *et al.* 2014), mean natal dispersal distance was greater in females (315 km) than in males (19.3 km) (Morandini et al. in prep.). In total, 41% of territorial adults came from the release program.

The Spanish imperial eagle is one of the rarest eagles in the world (Vulnerable in the IUCN Red List, BirdLife International 2008), with around 500 breeding pairs in 2016 (National Working Group, unpublished data 2016), breeding entirely in the Iberian Peninsula. The species is a large (2500-3500 g) long-lived raptor, monogamous, sedentary and territorial (Ferrer & Calderón 1990). Spanish imperial eagles can be divided into two easily distinguishable plumage classes: (1) subadult, with tawny-colored plumage or dark patches over a tawny base, present until 4–5 years of age; and (2) adult, predominantly dark brown with characteristic white markings appearing from the age of 5 years (Ferrer and Calderón, 1990). The two age groups can be easily distinguished in the field.

The fragmented distribution of existing populations of the Spanish Imperial eagle in Andalusia is the result of direct human persecution in the past (Mariano González et al., 2008). The natural slow expansion of these populations into neighboring areas has been restricted to the edges of these refuges, regardless the quality of habitat available there or elsewhere (Morandini et al. 2017).

A reintroduction project started in 2003 in southern Spain (Cádiz province) in order to establish a new population and thereby connect fragmented populations isolated by distance (Muriel *et al.* 2011). All of the released eagles were ringed as nestlings with metal and PVC colour rings. The first breeding pair became established in 2010, and by 2016, the reintroduced population had reached 4 breeding pairs (Morandini *et al.* 2017). Over this period, we documented a total of 24 nesting attempts, of which 20 (83%) started the incubation and 19 (79%) bred successfully, producing a total of 27 chicks. In total, 76% of territorial males and the 50% of females come from the release program.

Simulations

We used the Vortex simulation software (Vortex, version 10.00; Lacy et al., 2005) to simulate growth of a reintroduced population for both species. In VORTEX, a Monte Carlo simulation of demographic events, population processes are modelled as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. We used stochastic rather than deterministic models because the studied populations were small and could be much affected by demographic, environmental or sexual stochasticity.

Base scenario

We used previously published estimates of demographic parameters for both species (Table 1).

A new population could be considered successful when the probability of extinction during twice the life-span period for the species (Spanish imperial eagle: 22 years, osprey: 20 years) is less than 0.001 ($p<0.001$) and population growth was positive ($r>0.00$; Morandini & Ferrer 2017). We performed 1000 replicates of each scenario during twice the life-span for each species (44 years in the Spanish imperial eagle and 40 years in the Osprey), assuming a monogamous breeding system and breeding by 100% of adults.

In order to replicate reintroduced populations, we started the model with 0 individuals and started the releases in the first year of simulation, assuming the release of 20 young every year for 5 years (Ferrer *et al.* 2014a; Morandini & Ferrer 2017) and a sex ratio of 1:1.The model included the following additional assumptions. (1) Mortality was status-dependent, with three mortality rates. Juveniles in their first year had the highest mortality; thereafter, we assumed that mortality rates were independent of age, but higher in non-territorial than in territorial individuals (Ferrer *et al.* 2004) (Table 1). (2)

There was no cost of early reproduction with respect to survival of breeders or chick condition (Ferrer & Bisson 2003; Ferrer *et al.* 2004).

We parameterized the base demographic model, and then evaluated model sensitivity to deviation in specific parameters by systematically increasing the age of first reproduction and the mean annual productivity in steps of 20% to see how this influenced the predictions (Ferrer & Calderón 1990; Ferrer *et al.* 2004). We conducted several simulations with different combinations of age of first reproduction (from the youngest age recorded in our reintroduced population to one year older than the oldest age of first reproduction recorded (Poole 1989)) and with different combinations of productivity (productivity recorded in stable populations, +20%, +40%, +60% and +80%).

Comparison scenarios

Three different sets of simulations for both species were conducted using VORTEX: (1) in the base model, we simulated a reintroduction considering published demographic data of the species in established populations (Table1). (2) In the next simulations, we evaluated model sensitivity to changes in specific parameters (age of first reproduction and productivity) by successively increasing proportionally the base values of the parameters by 20%. (3) Finally, we included simultaneously values of age of first reproduction and productivity taken from the reintroduced populations.

Statistical analyses

Statistical significance was set at $P< 0.05$, and analyses were conducted using the Statistica 10.0 package (Statsoft Inc., Tulsa, OK, USA). When data were not normally distributed, they were log-transformed prior to parametric testing. A generalized linear mixed model (GLMM) was conducted with age of first breeding as a random effect. Stochastic “r” of simulations was considered as the dependent variable over the years and productivity as a covariate. We tested for differences in the extinction probability among the different assumed measures of age of first breeding and productivity using a Spearman rank test.

Results

The mean age of first breeding recorded in real reintroduced populations was lower than the average for both species in established populations, and productivity values were higher (Table 2-3). Probability of persistence was clearly affected by age of first breeding and productivity (Table 4). Significant differences in probability of persistence were found changing only the age of first breeding (Table 5).

Significant positive correlations were found between extinction probability of simulated populations and age of first reproduction (Spearman Rank Order Correlations; N=18, Spearman R= 0.800, t(N-2)= 5.333, p= 0.000) but not with productivity values (Spearman Rank Order Correlations; N=18, Spearman R= -0.090, t(N-2)= -0.364, p= 0.720).

At the end of a period equivalent to twice the maximum lifetime, extinction probability was less than 0.01 only when the age of first reproduction was as low as3 2 years old (Figure 1). Fixing the age of first reproduction at 5 and increasing the productivity values proportionally to the decrease of age of first reproductions (20%, 40%, 60% and 80%), extinction probability varies from 0.9070 to 0.7210 for Ospreys and from 0.7210 to 0.3520 for Spanish imperial eagles (Figure 2). Populations with breeding parameters of real reintroduced populations (changing both age of first reproduction and productivity) achieve extinction probabilities < 0.001 (Table 4) over the simulated period.

Discussion:

In long lived raptors, recruitment is the main factor limiting successful colonization of a new area. The decrease in the age of first reproduction reported from reintroduction projects (Sarrazin *et al.* 1996; Monti *et al.* 2014; Morandini *et al.* 2017) acts as a buffer against extinction in small and colonizing populations (Ferrer *et al.* 2004). In fact, our results demonstrate that changes in age of first breeding have dramatic consequences for the growth rate and persistence probability of populations.

In long-lived territorial raptors, entry to the breeding sector has been found to bring about a reduction in the probability of mortality. Previously published studies (Ferrer 2001; Ferrer *et al.* 2004; Penteriani *et al.* 2005; Monti *et al.* 2014) showed that the immature annual survival increases by 20% and 30% after the age of first entry to the breeding population. Decreasing the minimum age of first breeding affects population growth rate in two ways: individuals can contribute with offspring to the population at an earlier age and can live longer once they gain a territory (Ferrer *et al.* 2004).

As other studies have found (Fay *et al.* 2016), individuals that recruited early had both higher breeding performance and higher adult survival than those that recruited at advanced ages. In territorial raptors, higher breeding performance could be explained by good territory quality (Ferrer *et al.* 2008) and higher survival by differences in survival after entering in the breeding pool of the population (Ferrer *et al.* 2004).

In a new area without conspecific breeders, the opportunity to find a mate during the first years of life will determine to a large degree the success of the colonization. In fact, other studies on Spanish Imperial Eagles show that reintroduced individuals stay significantly more time (+50%) during their returns to the release area in comparison to returns of non-manipulated birds to their natal population (Muriel *et al.* 2016). The absence of territorial adults in the area allows young to remain in the natal area over a longer period than young from high density populations which are frequently attacked by the territorial adults already in the area (Ferrer 1993; Ferrer, Morandini & Newton 2015). In addition, the availability of high quality habitat (Ferrer & Bisson 2003; Ferrer *et al.* 2006) and of nests sites (Lõhmus 2001; Martin *et al.* 2005; Schmidt-Rothmund, Dennis & Saurola 2014) could both allow reduction in the age of first breeding and increase productivity. Factors (i.e, high quality habitat, opportunity to find a mate and nest site availability) that could facilitate breeding at a younger age could also decrease mortality rates and consequently increase the growth rate and persistence probability of colonizing populations.

In some bird species, the possibility to decrease the age of first breeding is limited by migratory behavior, as many individuals do not return to their breeding areas in the first few years of life (Newton 1979). Any birds which changed their behaviour from migratory to sedentary, as happens occasionally, for example, in the colonization of islands (Ferrer *et al.* 2011), could gain the advantage of earlier breeding in the initial stages of population establishment, thereby raising the chances of population survival. Reintroductions could be represented as the colonization of an island (especially for isolated populations) and in consequence, in migratory species, we might expect a decrease in the age of first breeding and a tendency to change the migratory behavior to a sedentary one. Future studies should be designed to assess the migratory behavior of reintroduced populations of migratory species. Knowledge of this tendency would permit modifications to the simulations of future reintroduction projects.

Summarizing, populations of long-lived birds resulting from reintroductions or colonizations of new areas increase at maximum rate only when the age of first breeding is reduced. Additionally, increases in productivity seem to be important only when age of first breeding is also reduced.

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Table 1: Summary of input parameters used in the Vortex for Spanish Imperial eagle and Osprey. Values were obtained from previous studies and reintroduction programs data.

	Spanish Imperial eagle	**Osprey**
Mean first year juvenile survival	0.16 (Ferrer 2001)	0.20 (Monti *et al.* 2014)
Mean non breeding annual survival	0.75(Ferrer *et al.* 2004)	0.64- 0.69 (Klaassen *et al.* 2014; Monti *et al.* 2014) [a]
Mean breeding adults annual survival	0.94(Ferrer 2001)	0.85 (Spitzer 1980); 0.93 (Monti *et al.* 2014)
Maximum life expectancy	22 years (Ferrer 2001)	20 years (Poole 1989)
Mean productivity[b]	0.75 (Ferrer & Donazar 1996; Ferrer *et al.* 2004)	0.67(Cartron 2000)
Usual age of first breeding in established population	5(Ferrer & Calderón 1990)	5(Poole 1989) [c]

[a] *Klaassen et al. 2014 evaluate survival in adult Ospreys without distinguishing between non-breeders and breeders. Even then, values of survival are very close to the survival rate of non-breeding Ospreys reported in Monti et al. 2014.*

[b] *Productivity is the average number of fledglings produced per occupied nest or per nesting pair per year.*

[c] *From the Chesapeake Bay population in 1963-1964 before the population began declining in 1970's.No declining or recovering populations were included in the calculation of this value.*

Table 2: Productivity values and age of first breeding in Ospreys from the Southern Spain reintroduced population and stable populations elsewhere.

	Reintroduced population	Stable population
Productivity	1.11	0.67 (Cartron 2000)
Age of first breeding	2	5 (Poole 1989)

Table 3: Productivity values and age of first breeding in Spanish Imperial eagle from the southern Spain reintroduced population and stable populations.

	Reintroduced population	Stable populations
Productivity	1.17	0.75 (Ferrer & Donazar 1996; Ferrer *et al.* 2004)
Age of first breeding	2	5 (Ferrer 2001)

Table 4: Simulation results for 1000 replicates of each combination of age of first breeding (Age 2–6 years) and additions of 20%, 40%, 60% and 80% to the base productivity (from Tables 2 and 3).

Scenario	Age of first reproduction	Extinction probability	Mean time to extinction (years)	r (SD)	Species
Base	2	0.0020	40.0	0.0007 (0.1556)	*Pandion haliaetus*
Base	3	0.2360	36.5	-0.0349 (0.1692)	*Pandion haliaetus*
Base	4	0.7410	33.6	-0.0530 (0.1947)	*Pandion haliaetus*
Base	5	0.9400	29.3	-0.0639 (0.2174)	*Pandion haliaetus*
Base	6	0.9860	26.4	-0.0716 (0.2315)	*Pandion haliaetus*
Base + 20% productivity	5	0.9070	30.6	-0.0610 (0.2131)	*Pandion haliaetus*
Base + 40% productivity	5	0.8620	31.5	-0.0581 (0.2082)	*Pandion haliaetus*
Base + 60% productivity	5	0.7800	32.1	-0.0546 (0.2054)	*Pandion haliaetus*
Base + 80% productivity	5	0.7210	32.7	-0.0517 (0.2012)	*Pandion haliaetus*
Reintroduced	2	0.000	0	0.0476	*Pandion*

population				(0.1364)	*haliaetus*
Base	2	0.0050	43.6	0.0037 (0.1474)	*Aquila adalberti*
Base	3	0.1280	40.9	-0.0242 (0.1562)	*Aquila adalberti*
Base	4	0.5110	38.7	-0.0405 (0.1739)	*Aquila adalberti*
Base	5	0.8280	35.8	-0.0504 (0.1950)	*Aquila adalberti*
Base	6	0.9320	32.7	-0.0574 (0.2114)	*Aquila adalberti*
Base + 20% productivity	5	0.7210	36.7	-0.0467 (0.1884)	*Aquila adalberti*
Base + 40% productivity	5	0.5820	37.7	-0.0426 (0.1819)	*Aquila adalberti*
Base + 60% productivity	5	0.4370	38.2	-0.0378 (0.1767)	*Aquila adalberti*
Base + 80% productivity	5	0.3520	38.7	-0.0338 (0.1720)	*Aquila adalberti*
Reintroduced population	2	0.0100	89.0	0.0147 (0.1046)	*Aquila adalberti*

Table 5: Results of the generalized linear mixed model of factors influencing r, including productivity, age of first breeding and species (*Aquila adalberti* and *Pandion haliaetus*) as factors.

MS Type: I	Tests assume that entangled fixed effects are 0						
	Effect (F/R)	df Effect	MS Effect	df Error	MS Error	F	p
Productivity	*Fixed	1	0.001095	4.176483	0.001918	0.57078	0.490324
{1}Species	Fixed	1	0.000149	4.807110	0.000332	0.44840	0.533907
{2}Age of first breeding	Random	4	0.003773	4.383257	0.000150	25.19373	0.002930
1*2	Random	4	0.000161	9.000000	0.000059	2.71575	0.098196

Figure 1: Extinction probability at different ages of first breeding (2, 3, 4, 5 and 6).

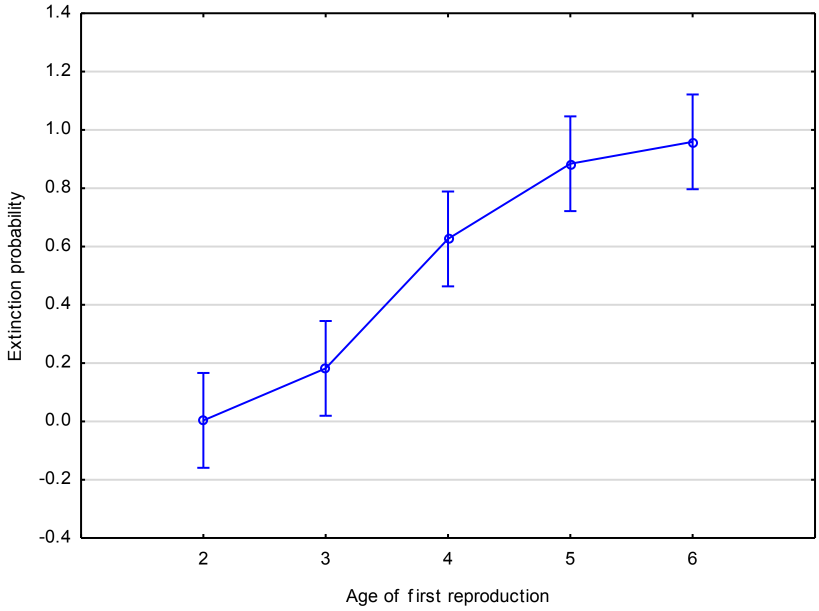
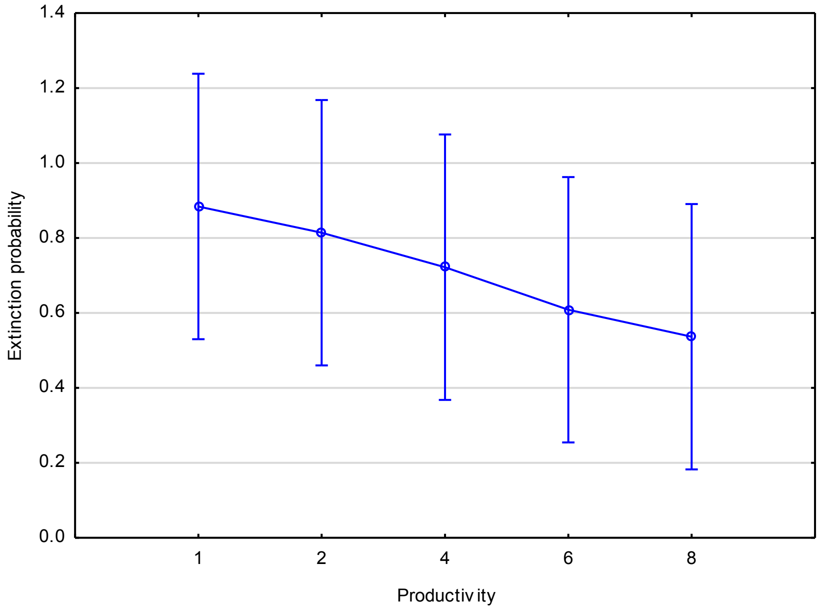


Figure 2: Extinction probability at different productivity values (base, +20%, +40%, +60% and +80%).



Sex specific dispersal and sex ratio adjustment as a strategy to optimize colonization processes

Morandini V., Muriel R., Newton I, and Ferrer M. (2017)

Biological Conservation: submitted

Sex specific dispersal and sex ratio adjustment as a strategy to optimize colonization processes

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Abstract:

With recent increases in the numbers of reintroduction projects, to know the main factors that allow colonization of new areas and prevent the extinction of small and reintroduced populations has become a crucial issue.

Dispersal is one of the most important phenomena in population biology with consequences in the proportion of individuals that keep breeding in the natal population and the number of individuals that visit other populations to breed. We studied changes in offspring sex ratio and differences in dispersal pattern between sexes in a reintroduced population of Osprey. Results showed that at the beginning of the colonization process breeding pairs produce more males, dispersing shorter distances and being more philopatric than females. However, with higher densities the offspring production is skewed to females that tend to breed in other populations. Here we conclude that changes in offspring sex ratio during colonization processes could affect the dispersal pattern of populations and in consequence the colonization rate. Differences in dispersal between sexes affects the colonization speed and in consequence the probability of success of future reintroduction projects.

Introduction:

Dispersal is one of the most important phenomena in population biology (Gadgil 1971) and may affect many aspects of demography in birds, influencing population dynamics and potential range expansion (Newton 1998). The possibility to breed near the place of birth could benefit an animal in several ways, including pre-existing knowledge of the local environment, interaction with known individuals and awareness that the area concerned can support a population (Waser & Jones 1983). Yet, in almost all species studied, most juveniles and sub-adults leave their natal area, indicating that, despite the advantages of phylopatry, factors promoting dispersal usually prevail (Ferrer 1993a; b; Newton 2008, Penteriani, Ferrer & Delgado 2011; López-López *et al.* 2013; Muriel *et al.* 2015, 2016).

In dimorphic species, differences in phylopatric behaviour between sexes are often associated with differences in body size, leading to differences in dispersal distances (Newton 2008), and hence in the capacity to connect with other populations (Muriel et al., 2016). In consequence, the dispersal pattern shown by populations of dimorphic species could be influenced by prevailing offspring sex ratios (Dale, 2001). For this reason, determining trends in sex ratios of locally distributed populations becomes important in understanding their conservation.

Various hypotheses have been proposed to explain different offspring sex ratios (Miguel Ferrer, Newton, & Pandolfi, 2009; Gerlach & Le Maitre, 2001; Lehikoinen et al., 2008; Lenz, Jacob, & Wedekind, 2007; Shyu & Caswell, 2016; Trivers & Willard, 1973; Wedekind, 2002). Some studies show how differences in nestling sex ratios are related to population density (Miguel Ferrer et al., 2009; Santoro, Green, Speakman, & Figuerola, 2015). Other studies have explored the effects of short and long term deviations in sex ratio for population dynamics (Miguel Ferrer, Newton, & Muriel, 2013; Miguel Ferrer et al., 2009; Gerlach & Le Maitre, 2001; Lambertucci, Carrete, Speziale, Hiraldo, & Donázar, 2013). However, most such studies involved small and isolated populations where changes in dispersal patterns are not related to possibilities of connecting with neighbouring populations.

Nevertheless, dispersal and metapopulation connectivity are key components of population dynamics and potential factors preventing the extinction of small populations (Muriel et al., 2015; Newton, 1998; Vincenzo Penteriani & Delgado, 2009; Whitfield et al., 2009). Studies taking into account consequences of changes in sex ratios in connected populations would therefore place considerations of population dynamics in a more realistic context.

Reintroduced populations, with all individuals monitored since the beginning of the colonization, provide rare opportunities to examine in particular populations the dispersal patterns among individuals, changes in natal sex ratios and ages of breeders during different stages of the colonization process. The prediction is that changes in offspring sex ratio could influence the growth, persistence and connectivity of reintroduced populations. In the present study, we analysed trends in natal sex ratios and natal dispersal patterns in a reintroduced population of Ospreys (*Pandion haliaetus*) in southern Spain. For this marked population, information is available for all released individuals and chicks hatched within the project since its inception.

Methods:

Study species

The Osprey breeds in all continents except Antarctica, being resident in some areas and migratory in others (Poole, 1989). It is a specialist fish-eating raptor; with a breeding dispersion ranging from solitary to loosely colonial (Poole 1989). Over the years, it has suffered heavily from various human impacts, becoming extinct over large areas due to human persecution in the late 19th and early 20th centuries (Poole, 1989; Saurola, 1997). In mainland Spain, after a continuing decline in the number of breeding pairs at least from the 1960s, the last pair bred in the province of Alicante in 1981 (Urios et al. 1991).

To re-establish the species, a reintroduction program was undertaken in Andalusia province, during the ten years 2002-12. Over this period, 180 young Ospreys were released by means of hacking (Dzialak, Lacki, Carter, Huie, & Cox, 2006) at two locations 125 km apart, a reservoir in the province of Cádiz and a coastal marshland in the province of Huelva. The first breeding pair became established in 2005 in the province of Cádiz (Muriel, Ferrer, Casado, &

Schmidt, 2006) and the first successful pair reared a brood in 2009 in the same territory (Muriel, Ferrer, Casado, & Pérez Calabuig, 2010).

The Iberian Peninsula is an important passage area for migratory Ospreys traveling between Europe and wintering grounds in Africa, and a small number of northern European birds winter in southern Spain (Saurola, 1997; Schmidt-Rothmund, Dennis, & Saurola, 2014). Because of this, reintroduced populations in southern Spain are in contact with migratory individuals from other populations.

Data collection

All released individuals were ringed with metal and PVC rings. They were obtained as chicks from populations further north in Europe, including Scotland (27), Germany (144) and Finland (20). We surveyed the study area at the beginning of each breeding season (January–February, during the courtship and nest site selection period; Poole 1989) to find any pairs that had settled and established territories. Nests were visited to ring the young when they reached 40 days old, providing information about the secondary sex ratio. In addition, the identity of every breeder was determined from the ring number. Non-ringed breeders were captured at the beginning of the breeding cycle using a dho-gaza mist net and an owl to attract the individual to the net; all individuals captured were ringed to allow individual identification thereafter. Some unringed individuals were identified over the years by their unique pattern of spots on the head feathers.

Sex ratio

For our sex ratio analysis, we considered population density, age of breeders and sex ratio of all broods from 2009 (the year of first successful breeding) to 2016. The sex ratio among young was expressed as the number of males per total number of nestlings in all broods at ringing, including only those broods composed of non-translocated (locally produced) nestlings. In all, sex was determined for 86 wild-hatched nestlings in 39 different broods, using molecular analysis of feather samples (Ellegren, 1996).

As the usual age of first breeding is considered as 3-4 years in Europe and the Mediterranean region (Dennis, 2015), we considered as “young” any pair with at least one member younger than 5 years old.

Philopatric behavior

In order to study the dispersal pattern of the population we analyzed all ringed breeding adults and compared the distance between the breeding site and the natal nest. All territorial adults since 2005 were used in this analysis, including those released by hacking, considering the release site (hacking tower) as the natal location.

Statistical analysis:

We conducted two analyses, one examining differences of nestling sex ratio in the population since the first breeding pair in 2009, and the other the dispersal distances among breeders.

First, we used a nonparametric method (Fisher exact p, one tailed) to compare observed sex ratios against expected ratios under an overall ratio of 1:1. Then, in order to detect factors involved in sex ratio deviations, we used a generalized linear mixed model (GLMMs; with age of breeders (older or younger than 5 years old) and population (Cadiz or Huelva) as fixed factors, and population size as a covariate. The response variable (nestling sex) was binary (male or female). Therefore, we fitted GLMMs with a binomial error structure and logit link using the lmer function in R (Bates and Maechler 2010). When analyzing factors affecting sex ratio, the unit we considered was the brood. Our model evaluated the number of male chicks as a proportion of total chicks including a unique brood identifier as a random effect (Katzner, Jackson, Ivy, Bragin, & Dewoody, 2014; Krackow & Tkadlec, 2001). Annual population level was expressed as number of pairs in the population.

Another generalized linear mixed model GLMM was used to check for differences in philopatry among the 23 ringed breeders. In this case, we used the logarithms of the dispersal distances to achieve normality of the function. Analyses were conducted using the STATISTICA 10.0 package (Statsoft Inc., Tulsa, USA). Logarithm of distance between the natal site or release site (for reintroduced individuals) and the breeding site and was taken as the response variable, while sex and reintroduction (separating between reintroduced n = 19, and wild individuals n = 4) were included as fixed factors in the analysis.

Results

By 2016 the breeding population in southern Spain reached 23 pairs. Throughout the study period (2009–2016), fledgling sex ratio was not significantly different from 1:1 (40 males, 46 females, $\chi2 = 0.707$, $p = 0.998$). However during the first half of the colonization (2009-2012), the fledgling sex ratio was biased toward males (24 males and 10 females, Fisher exact test, $p= 0.068$, marginally significant despite the small sample size at the beginning of the colonization process). And during the later years, (2013-2016) when the population was larger, the fledgling sex ratio was significantly different from 1:1, being biased toward females (16 males, 36 females, Fisher exact p one tailed, $p =0.035$).

Offspring sex ratio was significantly related to population density, but not to parental age (N= 72; population density: $p= 0.013$; parental age: $p= 0.206$; see Table1). No differences between the Cádiz and Huelva populations were found (Table 1). From 2009, when the first two pairs bred successfully in southern Spain, until 2016, when the population reached 23 territorial pairs, the sex ratio deviation changed from 0.8 to 0.26 in 2016 (Figure 1). The total males and females produced over the study period were 40 and 46 respectively, but 78% of the total females and 40% of the total males were produced in the last 3 years (2014 to 2016).

The 23 ringed adults (10 females and 13 males) whose natal dispersal distances were known included 19 individuals released during the reintroduction project, 2 individuals coming from other populations (Morocco and Balearic islands) and 2 adults hatched in the reintroduced populations. Interestingly, all the males but only 3 females bred in their natal population, whereas 7 females but no males bred in a different population. The differences between the sexes in tendency to breed in their own natal population were statistically significant (Table 2). No significant differences in dispersal distances were found that were related with the reintroduction site, donor country or year.

Discussion:

As previous studies suggest, the probability of a bird starting to breed in its own natal population depends largely on the chance of its finding a mate on an appropriate territory (Dale, 2001; Lenz et al., 2007). For that reason, in breeding populations the optimum chick sex-ratio necessary to generate a sex-balanced proportion in adults will be that which maximizes the number of breeding pairs and gives the highest population growth rate (Dale, 2001; Lambertucci et al., 2013).

In a metapopulation context, the dispersal likelihood of individuals between populations at different densities and degrees of isolation is of central importance in understanding extinction and colonization dynamics (Hanski, 1998). In this sense, sex-biased interchange among populations could affect the optimum nestling sex ratio necessary to attain the maximum mating probability in the breeding population. Our results showed a differential natal dispersal between males and females, as already shown in other studies of birds (Greenwood & Harvey, 1982; Monti et al., 2014; Newton, 1979). In Ospreys and other raptors, males are the philopatric sex while females are more liable disperse further and breed in a different population. Under this scenario, the proportion of males in a new population is expected to be the limiting factor for mating prospects and local population growth, as females should arrive from neighboring populations. Our results suggest that males, being the most philopatric sex, would work as attractors for dispersive females coming from other populations and looking for breeding opportunities. From an evolutionary viewpoint, the benefits of a strategy to produce more males at the beginning of the colonization process should be related with the individual parental benefit associated with this strategy. At low densities, high quality territories and low competition for resources is expected, thus favouring the philopatric sex (Miguel Ferrer & Donazar, 1996; Miguel Ferrer, Newton, & Casado, 2008; Kokko, Harris, & Wanless, 2004; Krüger et al., 2012). Later in the colonization process, when competition for territories is high, the dispersive sex should be favoured because the chance of breeding may be greater elsewhere, away from the natal area. Moreover, in a developing population, the age of first breeding should at first be low but then increase with increasing breeding density, as competition for territories and other researches intensifies (Miguel Ferrer et al., 2013; Miguel; Ferrer, Otalora, & García-Ruiz, 2004). Any individuals able to breed at an early age, whether by settling in a newly-establishing population or dispersing away from a well-established high density one, could start breeding at a young age, and thereby gain a higher residual reproductive value (Pianka & Parker, 1975).

According to theory, we found changes in offspring sex ratios related to population density (Figure 1), with a tendency of breeders to produce more males at the beginning of the colonization process and more females when density increased. A similar study in the Spanish Imperial Eagle also in south of Spain, suggested differences in sex ratios that were related to changes in population density, producing more of the smaller, cheaper sex (males) when population density was low and increasing the proportion of larger female offspring when density increased (Miguel Ferrer et al., 2009). In this case, variations in nestling sex ratio were associated with changes in the proportions of immature breeders, which tended to produce more males. Nevertheless, as the proportion of breeders in immature plumage increases when population density decreases (Ferrer *et al.* 2003), it is not possible to discard an underlying effect of changes in density. However, our studied population being in the early stages of establishment, tended to have a high proportion of young pairs and an absence of really old birds. For this reason, findings concerning the relationship of sex ratio to parental age should be treated with caution. Nor is it possible in either study to eliminate the possibility that sex ratios changed through time for some totally different reason, unrelated to either population density or age-composition of breeders. Only further studies along the same lines as ours will help to separate these confounding factors.

On the other hand, previous studies have explored the relationship between nutritional conditions and dispersal distances (Miguel Ferrer, 1993b; Muriel et al., 2016). Under the "wandering hypothesis", individuals in better nutritional conditions will disperse longer distances than individuals in poor conditions, independently of availability of territories or the presence of adults in the area (Muriel et al., 2016, 2015). In this context, we expect that reintroduced populations will show higher dispersal distances than established populations regardless of changes in offspring sex ratio. Breeding pairs occupying high quality territories in low density situations will provide better nutritional conditions to their offspring and with low variance among occupied territories than in a population with both high quality territories and poor territories occupied (Miguel Ferrer & Donazar, 1996; Miguel Ferrer, Newton, & Casado, 2006; Miguel Ferrer et al., 2008). However, the wandering hypothesis include only juvenile dispersal distances and the associated opportunity to prospect a bigger area in better nutritional conditions. Knowing that, sexual differences in natal dispersal distances are also expected under the assumption of the wandering hypothesis.

In reintroduction and reinforcement programs of species with sex-biased dispersal, the sex ratio of released individuals may play a key role in the speed of population establishment. In spite of the difficulty of assigning a cause to changes in offspring sex ratio, consequences of a biased sex ratio and an associated differential dispersal behavior in a growing population are clear. In consequence, when re-establishing a population in a metapopulation scenario the advantageous strategy would be to favor the release of the most philopatric gender (males) initially in order to attract conspecifics of the wandering sex. Depending on the possibilities of immigration from other populations, a large number of males, at least during the first years of releases would be likely to increase the growth of the new population. However, depending on the growth of the reintroduced population, different strategies could be carried out, depending on the distribution of other populations and the chances of immigration. We anticipate our results to be a starting point for simulation models to predict the viability of small connected populations, taking account of sex differences in dispersal.

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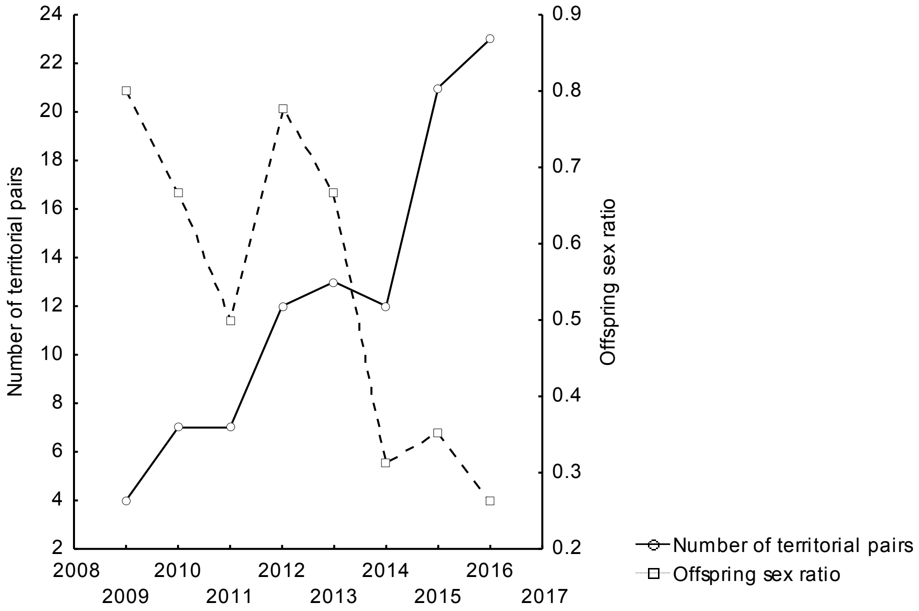
Table 1: Result of binomial GLMM considering the sex of an individual as the response variable. Age of parents was analysed as fixed factor ("young" and "old") and annual population density as a percentage of maximum-recorded density in 2016 (23 pairs). Identity of population (Cádiz or Huelva) was included for the analysis.

	Estimate	**Std. Error**	**z value**	**P value**
Intercept)	5.0062	2.7015	1.853	0.0639
Age	-0.9914	0.7839	-1.265	0.2060
Population identity	-0.5905	0.7115	-0.830	0.4066
Population density	-3.5825	1.4448	-2.480	0.0132

Table2: Result of GLMM considering natal dispersal as response variable. Factor included in the analysis were sex (male or female) and origin (wild or reintroduction). Distribution : NORMAL ; Link function: LOG.

	Degr. of - Freedom	**Wald - Stat.**	**P value**
Intercept	1	5350,465	0,000000
(1) Sex	1	19,558	0,000010
(2) reintroduction	1	0,190	0,662798
1 x 2	1	1,268	0,260197

Figure 1: Annual number of breeding pairs and offspring sex ratio (expressed as number of males/total number of nestlings per year) of the reintroduced Osprey populations in south of Spain from 2009 to 2016.



Chapter 4: How to design reintroductions

Reintroduction has been recognized as an important tool in conservation and particularly in restoration ecology. A high proportion of reintroduction programs concern charismatic species and among them numerous raptor species (Monti et al., 2014; Muriel, Ferrer, Casado, Madero, & Calabiug, 2011; Muriel, Ferrer, Casado, & Pérez Calabuig, 2010; Whitfield et al., 2009). It is likely that the results of these programs will be considered as models of what might be done to restore locally extinct fauna.

The monitoring and comparison of the dynamics of reintroduced population with the dynamics of the natural established populations is a key approach to assess the success of reintroduction and to validate the strategy that could be used in other projects (Parker, Ewen, Seddon, & Armstrong, 2013; Sutherland et al., 2010; Wakamiya & Roy, 2009). Knowledge of these rates allows us to conduct population viability analyses that can provide decisive insights into management (Bustamante, 1998). Quantitative demographic analyses of reintroduced species are scarce (Sarrazin, 1998) and biased towards successful projects (Seddon, Armstrong, & Maloney, 2007).

We conclude this thesis with an applied assessment on the optimal design of future reintroduction projects. First, we analyzed the effectiveness of supplementary feeding in territorial raptors as a tool to increase productivity, allowing the extraction of additional eggs or nestlings for reintroduction programs. Finally, we estimated the number of young per year and number of years of released necessary to more readily achieve a successful reintroduced population.

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Reintroducing endangered raptors: a case study of supplementary feeding and removal of nestlings from wild populations

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Reintroducing endangered raptors: a case study of supplementary feeding and removal of nestlings from wild populations

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Abstract:

Supplementary feeding is a common practice to raise reproductive output in raptors and other species, either for experimental or for conservation purposes. Despite the widespread use of this technique over the last 50 years, its application in conservation has only recently been critically discussed, revealing important differences in evaluation of the technique. Here we critically analyse the effect of supplementary feeding in territorial raptors, taking advantage of two long-term data sets for the Spanish imperial eagle (*Aquila adalberti*) and bearded vulture (*Gypaetus barbatus*).

Using a GLMM, no differences in the intensity of response between species was found (P=0.890). However, in both species a significant effect of supplementary feeding on relative productivity was found (P=0.013). This productivity did not seem to be affected by territories alone (P=0.192), but by the interaction between territory and supplementary feeding (P=0.030). This implied a different response among territories to supplementary feeding. Poor quality territories with low productivity levels responded more strongly to supplementary feeding than did territories with higher levels of natural productivity (r=-0.435, n=45, P=0.002).

A reintroduction based on supplementary feeding and extractions would costs 8 times less than the same program based on captive breeding, and take 10 years less.

Keywords: *reintroductions, productivity, Aquila adalberti, Gypaetus barbatus*

INTRODUCTION

Supplementary feeding is a common practice to raise reproductive output in raptors and other species, either for experimental or for conservation purposes (e.g. California condor, Wilbur, Carrier & Borneman 1974; sparrowhawk, Newton & Marquiss 1981; various vulture species, Terrasse 1985; common kestrel, Wiehn & Korpimaki 1997; Spanish imperial eagle, Gonzalez et al.2006; Ferrer & Penteriani 2007; bearded vulture, Margalida 2010). Despite the widespread use of this technique over the last 50 years, particularly in endangered species, its application in conservation has only recently been discussed (Cortés-Avizanda et al. 2016), revealing important differences in evaluation among authors. Some claim major beneficial effects at the population level, and others little or no effect (Carrete et al. 2006, Gonzalez et al. 2006, Margalida 2010, Margalida et al. 2016, Oro et al. 2008).

Additional potential problems with this technique have been suggested, for example, that predictable human-provided food sources could increase the survival of individuals that would otherwise disappear as a result of natural selective processes, favouring some kind of artificial selection (Blanco 2006; Oro et al. 2013). They consider that such human-based food supplies could lead to an uncertain future for populations, functional guilds, and, ultimately, communities (Cortés-Avizanda et al. 2016). They see supplementary food as representing a major modification of the natural distribution of resources, the consequences of which may reach the ecosystem level, potentially influencing vegetation and abiotic components such as soil nutrients and water.

Differences in the evaluation of the effectiveness of supplementary feeding among authors could be due partly to differences between feeding programs. One type aims to feed large numbers of birds in one place, as occurs incidentally at rubbish dumps and by design at, for example, “vulture restaurants”. At such communal feeding stations, food provision usually takes place year round, and over many successive years, all the time providing enough food for many birds at once. In conservation, such programmes are aimed mainly to increase overall population size; but they often also have educational or touristic value.

In a second type, supplementary feeding is targeted at particular territorial pairs within a population. Typically, food is placed every day or two close to the nests of selected pairs for part or all of the breeding cycle from before laying to independenceof young, depending on the objective. Limited quantities of food are provided each day, the main objectives being to increase clutch size and prevent nestling deaths. For this reason, cainistic species (which often lay two eggs but raise only one young) are frequently targeted, so as to increase overall productivity (Ferrer & Penterian 2007; Morandini & Ferrer 2015). This technique works particularly well in populations where territories vary in quality. The feeding can then be concentrated in the poor-quality territories, in which the parents readily respond by producing extra young, bringing their brood sizes up to those typical of good territories. Consequently, providing food to poor-quality territories, the total productivity of the population can be raised. These "extra young" could then enable a depleted population to expand more rapidly, or could be used in reintroduction programs for other areas, all without reducing the reproduction of the existing population below its natural level (Ferrer et al. 2014, 2016). According these authors, supplementary feeding of pairs in poor territories, whose natural reproductive rate would be low, could provide a source of young for reintroduction programmes cheaper than captive breeding.

Here we attempt to analyse the real effect of supplementary feeding in territorial raptors, taking advantage of two long-term data sets involving the Spanish imperial eagle (*Aquila adalberti*) and bearded vulture (*Gypaetus barbatus*). In both species, supplementary feeding was used over some years to increase productivity, allowing the extraction of eggs or nestlings for reintroduction programs. In both species, reproduction was density-dependent in relation to heterogeneity (Ferrer & Donazar 1996, Ferrer et al. 2014, Morandini et al. 2017). Some (high quality) territories showed consistently high productivity and others consistently low productivity. At low population levels, mainly high quality territories were occupied, but as numbers grew more poor territories were occupied, lowering the overall production per pair in a density dependent manner. Our aims here are to determine the real effect of supplementary feeding on the number of extra-young produced and to analyse the cost of both alternative approaches, extractions and captive breeding. On the basis of these findings, we make recommendations for the use of targeted supplementary feeding in the future.

MATERIAL AND METHODS

Study species

The Spanish imperial eagle is one of the rarest eagles in the world (Vulnerable in the IUCN Red List), with around 500 breeding pairs in 2016 (National Working Group, unpublished data 2016), located entirely in the Iberian Peninsula. The species is a large (2500-3500 g), long-lived raptor with a maximum recorded lifespan of 22 years, with delayed maturity (adult plumage at 4–5 years old, Ferrer 2001). It is a monogamous, sedentary and territorial species, with a low annual productivity averaging 0.75 chicks/pair (range 0-4; Ferrer &Calderón 1990). Reproduction usually lasts 8 months from February, when laying starts, until October when the latest juveniles leave the natal area (Miguel Ferrer, 2001).This species is considered to be a facultative cainist. The monitored nests were the northern limit of Andalusia (≈38°22'N 3°50'W),in the Sierra Morena, occupying a large part of the southern Iberian Peninsula and a wide altitudinal range (0-2000 m.a.s.l.), with a dry-humid Mediterranean climate (annual rainfall: 300-2000 mm, average annual temperature: 9-19ºC). The landscape consisted of a mosaic of Mediterranean forests, scrublands and grasslands in hilly and mountainous areas, crops in lowlands and coastal wetlands. A reintroduction program is running in Cádiz province (south of Spain) since 2003.

The bearded vulture is another large (4,500-7,000 g) long-lived territorial raptor, with a maximum recorded lifespan of 32 years (Lopez-Lopez et al. 2013; Ferrer et al. 2014 and references therein), and delayed maturity (adult plumage at 5–7 years old), that breeds in sparsely distributed territories in mountainous regions (Donázar, Hiraldo & Bustamante 1993). Average productivity in Spain is 0.65 young per pair (range 0-1). It is considered an obligate cainist, laying two eggs but raising at most one young. The species feeds mainly on large fresh bones of ungulates which it swallows whole or in pieces. Its numbers and breeding range declined throughout Europe during much of the twentieth century (Hiraldo, Delibes & Calderón 1979; Mingozzi & Estève 1997), and three reintroduction programs are currently running in Europe, one in Switzerland and two in Spain (Ferrer et al. 2014). The only surviving bearded vulture population in the Spanish Pyrenees is composed of 150 reproductive units (mostly pairs, but some polyandrous trios), 78 of them in the region of Aragon (Spanish bearded vulture working group unpublished data).

Data collection and supplementary feeding

During the study period, for the Spanish imperial eagle, the data were derived from a total of 91 different territories in the Sierra Morena from 2012 to 2015 (n=325). We considered a territory as occupied when a pair showed breeding behavior (nest construction, defense or incubation). All nests were monitored from the beginning of the breeding season (January–February, during the courtship and nest site selection stages; Ferrer, 2001) until the last chick left the natal territory. Productivity was calculated as the number of fledglings per territorial pair. Supplementary food in the form of domestic rabbits (around 400 g.) was provided to individual pairs. Technical workers deposited 1–2 rabbits each day on ledges unreachable by terrestrial carnivores, at a medium distance of 340 m from the nest. The eagles readily accepted this supplementary food. Feeding started in February and finished in June, when the young were large, and was provided to 35 different territories, some in more than one year (n=86). The young were removed at 35-45 days old.

The whole bearded vulture population in the Aragonese Spanish Pyrenees area (approx. 7600 km^2) was monitored for 25 years from 1988 to 2012 inclusive. Each year, all known territories as well as other potential breeding areas were carefully searched for birds, nests or other signs of occupancy during the breeding season (November to August). Occupied territories were located on the basis of territorial or courtship activity and breeding parameters were then recorded on later visits (see Margalida et al. 2003). At the population level, productivity was measured as the mean number of fledglings raised per territorial pair, including breeding failures and taking into account that no more than one nestling could be reared per breeding attempt. Supplementary feeding was conducted over 4 years (2007–2010) with the aim of improving the physical condition of particularbreeders in the pre-laying period and stimulating the layingof viable eggs. Feeding started on 31 October and finished on 31 March, about 30 days after egg laying. Technical workers deposited 15–18 kg of bones (acquired from a slaughter house) each day on ledges unreachable by terrestrial carnivores, at a medium distance of1118 m from the nest. During the 4 years, around 5,108 kg of bones were supplied, divided among 11 different territories. In order to avoid competition with other more generalist scavengers, such us griffon vultures *Gyps fulvus* or corvids, a specific diet was provided for individual reproductive units based on sheep and goat bones. Supplementary feeding was provided to 11 different territories (n=22). The young were removed at different ages (from 10-45 day-old), and hand-reared for later release. In some cases also eggs were removed before hatching.

Cost analyses

In order to analyse the relative financial costs of alternative approaches to obtaining young for reintroduction, we compared the budget of two typical captive breeding programs, one of bearded vulture, conducted by the Gypaetus Foundation in Spain (http://www.gypaetus.org/), and other of Spanish imperial eagles, operated by Migres Foundation (www.fundacionmigres.org/es/), with the cost of two supplementary feeding and extractions programs, one with bearded vultures conducted by Fundación para la Conservación del Quebrantahuesos in the Pyrenees (http://www.quebrantahuesos.org/), and the other affecting Spanish imperial eagles in Andalucía conducted by the Andalusia Environmental administration(https://www.juntadeandalucia.es/medioambiente/portal_web/web/temas_ambientales/biodiversidad/0_conservacion_biodiversidad/planes_conservacion_recuperacion/Programas%20de%20actuacion/programa_actuacion_aguila_imperial_%20anexo_II.pdf).

We also estimated the annual cost of a standard reintroduction program, using data from the following programs developed in Spain: Osprey reintroductions in Huelva and Cádiz (Muriel *et al.* 2010), Spanish imperial eagle reintroduction in Cádiz (Madero & Ferrer 2002; Muriel *et al.* 2011) and Bearded vulture reintroduction (http://www.gypaetus.org/) in Cazorla (Simón *et al.* 2005). Obviously the costs could change through time, but it is the relative costs of the different procedures that are important here.

Statistical analyses

For the calculation of productivity values for territories, we controlled for a potential year effect by subtracting mean annual productivities from the original data on breeding success (relative productivity, Ferrer & Bisson 2003; Penteriani, Balbontin & Ferrer 2003; Horváth *et al.* 2014). Hatching date was given a numerical value by considering the earliest hatching date of each year as day 1. We tested for trends in response to supplementary feeding with linear analysis using the F-ratio statistic to find whether the slope of the data was significantly different from zero. Variances of the linear models were tested for homogeneity using Cochran's C statistic. Generalized linear models

(GLMM) with normal distribution function were used to examine differences in relative productivity among territories as well as to compare productivity in the same territories with and without supplementary feeding. To avoid potential pseudo-replication due to the high potential for strong site-fidelity and pair-fidelity in this long-lived species, a generalized linear mixed model (GLMM) was conducted with territories as a random effect. In this case, relative productivity was considered as the dependent variable over the years. To remove the effect of territory quality, we compared productivity parameters in the same territory with and without supplementary feeding with a nonparametric Wilcoxon Matched Pairs Test. To analyze potential deleterious effects on productivity of supplemented pairs in the following years without supplementation, paired comparisons using Wilcoxon Matched Pairs Test were conducted. Statistical significance was set at $P< 0.05$, and analyses were conducted using the Statistica 8.0 package (Statsoft Inc., Tulsa, OK, USA).

RESULTS

Supplementary feeding and extractions

Both populations increased during recent decades. In 2001 only 10 Spanish imperial eagle pairs were found in Sierra Morena, increasing to 91 pairs in 2015, a total increase of 910%. The Bearded vulture population in Aragon increased from 15 occupied territories in 1988 up to 67 in 2012, which represents an increase of 446%. Density-dependent productivity by habitat heterogeneity was established in both populations (Ferrer et al. 2014, 2016; Morandini et al. 2017).

Results of GLMM analysis with relative productivity as the dependent variable and species and supplementary feeding as fixed factors and territory as random factor are presented in Table 1. No differences between species were found ($P=0.890$), including in their response to supplementary feeding ($P=0.367$). A significant effect of supplementary feeding on relative productivity was found ($P=0.013$). Relative productivity did not seem to be affected by territories alone ($P=0.192$), but by the interaction between territory and supplementary feeding ($P=0.030$). This implied a different response among territories to supplementary feeding.

To control for potential interaction effects, paired comparisons of the same territories with and without supplementary feeding were conducted. Relative productivity emerged as significantly higher when supplementary food was provided

(Wilcoxon Matched Pairs Test; Z=2.906, n=45, P=0.003). To measure differences in the intensity of response to supplementary feeding by territory we subtracted relative productivity without supplementary feeding from the values obtained in the same territory under supplementation. No difference in the intensity of response between species was found (ANOVA; F= 0.642, P=0.427). Differential response among territories was significantly related to the mean productivity of those territories without supplementation. Poor quality territories with low productivity levels responded more strongly to supplementary feeding than those with higher levels of natural productivity (r=-0.435, n=45, P=0.002; Fig 1).

A very significant relationship between relative productivity without supplementation and hatching date was found (r = -0.2474, n=222,P= 0.0002), with later pairs in the season producing few nestlings. Selecting only those nests with hatching dates earlier than the median value for the total population (34 days) and repeating the GLMM for relative productivity with supplementary feeding as a fixed factor and territory as a random factor, any effect of supplementary feeding disappeared, showing that earlier nests do not respond to supplementary feeding in a significant way (relative productivity without supplementary feeding =0.533, and with supplementary feeding =0.582, F=0.090, P=0.764). These were in any case the best territories, as judged by their productivity over a period of more than 15 years.

To estimate the potential over production of young with supplementary feeding in both species, we compared mean productivity in poor quality territories in years with and without supplementation (Table 2). To over-produce 10 extra young per year in Spanish imperial eagles we needed to supplement 20 poor quality territories per year (10/(1.3430-0.8373)), and 37 territories in the case of the bearded vulture (10/(0.4135-0.1436)). With 10 released young per year over 10 years we could achieve a viable new reintroduced population of both species (Morandini & Ferrer 2017).

Paired comparisons by territories of the natural relative productivity without supplementation against the relative productivity the year after a supplementation of food was conducted, no effect in subsequent productivity (Wilcoxon Matched Pairs Test; Z=0.495, n=49, P=0.619) was found.

Cost analyses

The cost of supplementary feeding and extraction programs, including 2 technicians during 5 months per year, was 28,833 €. Reintroduction annual cost, including transmitters and bands for the released birds, information cost, technicians, food and other costs was between 59,000 € per year to 100,000 € /year depending on the program, with a mean cost of 78,000 € per year.

Considering only the annual cost of maintenance of the captive program, the Spanish imperial eagle mean annual budget in the period 2005-2011 was 275,000€ in salaries and 86,000 € the facility running cost, giving a total annual cost of 361,000 €. The bearded vulture program budget, using mean values from 1996 until 2014, was 300,000 € in salaries and 120,000 € in operation costs, giving a total annual cost of 420,000 €. Consequently, annual mean cost for these two captive programs was 390,500 €, about five times more than the supplementary feeding programmes.

Both captive breeding programmes, as is usual, started with young individuals as breeding stock. Owing to the deferred sexual maturity of these species, both programmes needed a longperiod of years before they could produce young for releases. In the case of the bearded vulture this initialperiod was 10 years, and in the Spanish imperial eagle it was 7 years. Obviously, these pre-production periods must be included in the total cost of the breeding in captivity programs. Consequently, a reintroduction program based on captive bearded vultures as the source of young needs 10 years of pre-production plus the necessary years of releases in the reintroduction. Assuming a standard reintroduction period of 10 years of releases, we need to include 20 years of operating costs for the facility (7,81 millions) plus 10 years of the reintroduction cost (780,000 €); giving a total of 8,590,000 €.

Alternatively, a reintroduction based on supplementary feeding and extractions would cost 10 years of supplementations (288,830 €) plus 10 years of releases (780,000 €), that is a total cost of 1,068,830 €. Consequently, a supplementary feeding and extraction based programs cost 8 times less than the same program using a breeding in captivity approach, and takes 10 years less.

DISCUSSION

According our results, supplementary feeding is an effective technique able to increase significantly the productivity of certain territories when correctly applied. Selecting poor quality territories, supplementary feeding increased by 160% the mean annual productivity inthe Spanish imperial eagles and by 288% in the bearded vultures. Interestingly, using relative productivity, no differences between species in response to supplementary feeding was found, suggesting that our findings would be applied to yet other species of similar life history.

According to theory of habitat heterogeneity, when density increases, a large proportion of new pairs are forced to select poor quality habitat for breeding. In these conditions, the population operates as a source-sink system with poor quality territories, mostly unproductive, being maintained by the high quality territories with adults producing more young than are needed to replace themselves (Ferrer & Donazar 1996). Differences in quality among territories have been explained by differences in food availability, degree of human disturbance, mortality factors and other differences (Newton & Marquiss 1976; Newton 1991; Ferrer & Donazar1996; Ferrer & Bisson 2003). Food availability seems to be one of the most common factors limiting territory quality and also one of the easiest to manipulate. Our results demonstrated that in a high-density population, food supplementation in sink territories produced a significant increase in productivity. In both species, the intensity of response to supplementary feeding was stronger in those territories with lower productivity without intervention, suggesting that poor quality territories were limited by food availability. Consequently, the selection of specific territories for food supplementation is a critical factor in achieving an increase in the total production of young. This is turn requires prior knowledge of the population, so that poor territories can be recognised. The highly significant relationship between productivity and hatching date provides us with an easy and accurate way of distinguishing territories of different quality. Selecting territories where laying is later in the season on which to provide supplementary food could give significant increases in the final number of young produced, on the basis on minimal prior information.

This resulting surplus of young produced can then be removed without any obvious effect on the donor population. Alternatively, we can leave these extra young in their natal population, increasing the stock of floaters, but the demographic value of these extra young is higher in a well-designed reintroduction programme in a new but suitable area (Morandini et al. 2017). Even if supplementary feeding is not able to produce the minimum necessary number of annual extra young to release in order to guarantee a successful reintroduction program (Morandini & Ferrer 2017), it always allows us to reduce to a minimum the impact of repeat extractions in the donor population (Ferrer et al. 2014).

Consequently, in our opinion, supplementary feeding could be most usefully applied in two different situations; (i) in an episodic main prey collapse, as occurred in Doñana

National Park in 1991, when a new viral disease decreased by 7-fold the normal density of the wild rabbit, the main prey of the Spanish imperial eagle (Ferrer, Newton & Muriel 2013), and (ii) in poor quality territories in a high density population to produce extra young for reintroduction programs. Suggestions to extend this technique to most or all the pairs in a population due to the beneficial effect on productivity (Gonzalez et al. 2006) may not be the best strategy, because some of the territories may already be producing at maximum rate. For maximum efficiency, feeding needs to be targeted at the poorer territories in which the reproductive rate has the potential to be raised by provision of extra food. The extra young produced can be most effectively be used in reintroduction programmes in which their chances of recruiting to a breeding population are high.

Some authors have suggested that food provisioning would constitute a major modification of the natural distribution of resources at the ecosystem level, leading to 'an uncertain future for populations, functional guilds, and, ultimately, communities' (Cortés-Avizanda et al. 2016). Obviously, if they consider natural as not human-influenced, there is already in Europe nothing like a natural distribution of resources. Perhaps in vulture restaurants some cautions must be taken about potential effects of prolonged and predictable provisioning of food, but this is not the case of the supplementary feeding of targeted breeding pairs.

According some authors (Blanco 2006) an unintended consequence of supplementary feeding would be a decrease of productivity or survivals of adults involved due to the exhaustion after raise extra young. However, no effects of supplementation of food in subsequent productivity of the same territories the following year without supplementation were found indicating that the production of extra young seems no to exhausted the parents feeding extra young. Probably supplementary feeding and extraction of young should have less deleterious effect due to the shorter time of parental care devoted to the extra young. Usually, young are extracted when they are around 40 days old, when dependence period in eagles for example takes around 130 days (Ferrer 2001).

Our cost analysis demonstrated that, for a reintroduction programme, production of young from supplementary feeding and extraction is around 8 times cheaper than production of young in a captive breeding programme. When captive breeding is used as a source of young for reintroduction, account must be taken, in such a long-lived species, of the lengthy period in captivity before individuals taken early in their lives start to breed. In the case of bearded vultures, according to the

Gypaetus Foundation (electronic bulletins 2008-2012), the program started in 1996, and the first releases were made ten years later in 2006. Obviously, this ten year budget is part of the total cost of the programme. Even in the case that the adults for breeding were donated free of charge by zoos (thus eliminating the pre-breeding costs for the reintroduction programme), still breeding in captivity based reintroduction would be about five times more expensive than the supplementary feeding based programmes.

Another consideration is the actual capacity of production in captivity of young per year, which greatly affects the duration and hence the cost of any reintroduction program (Morandini & Ferrer 2017). Again, using the information provided by the Gypaetus foundation, during the ten years of releases, 37 individuals have been set free (3.7 per year). According to simulations, with this number of young per year, releases need to continue for more than 23 years to achieve a viable population (see Ferrer et al. 2014, Morandini & Ferrer 2017). Consequently, the real total cost of this approach based in captive breeding would be 14,680,500 € (33 years of operating cost: 12,886,500 € plus 23 years of released: 1.794000 €), against 1,068,830 € using our suggested approach (extracting wild young from food supplemented nests). In other words, in an standard reintroduction program releasing 10 young during 10 years, each one of the released young bred in captivity costs around 146,805 € and each young coming from a food-supplemented wild population that we released costs 10,680€.

We fully accept that captive breeding programmes can be the only option when the remaining wild populations are so small that extractions would not be possible or if no wild populations remain. Additionally, we sometimes have captive animals that could not themselves be released but could be useful for producing young for release. Nevertheless, when we are planning a reintroduction program, differences in the total cost of the two alternative strategies (breeding in captivity versus the harvesting of wild nestlings) are so great as to settle any argument over methodology, other things being equal.

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Table 1: Results of GLMM analysis with relative productivity as the dependent variable and species and supplementary feeding as fixed factors and territory as random factor. No differences between species were found, including in their response to supplementary feeding. A significant effect of supplementary feeding on relative productivity was found. Relative productivity did not seem to be affected by territories alone, but by the interaction between territory and supplementary feeding. This implied a different response among territories to supplementary feeding.

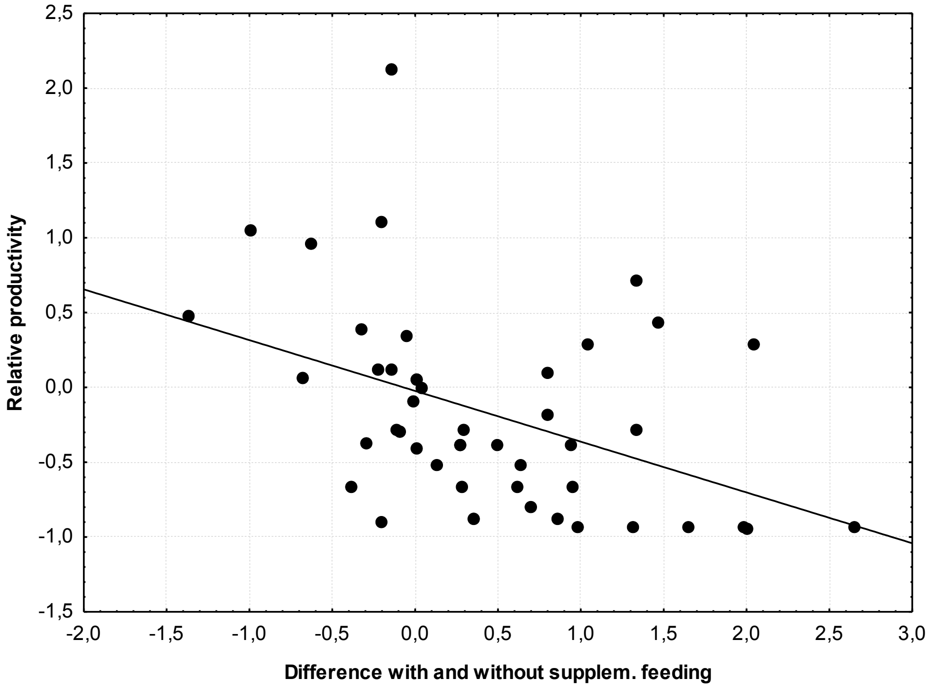
	Factors	**df-Factor**	**MS - Factor**	**df - Error**	**MS - Error**	**F**	**P**
(1)Specie	Fixed	1	0.022296	164.6890	1.168583	0.019080	0.8907
(2)Supplementary feeding	Fixed	1	6.435504	158.0235	1.040051	6.187684	0.0139
(3)Territory	Random	168	1.129538	20.6699	0.812563	1.390092	0.1929
1*2	Fixed	1	0.524861	46.1736	0.633368	0.828683	0.3673
2*3	Random	38	0.664224	298.0000	0.436578	1.521433	0.030

							2

Table 2: Paired comparisons of the same territories with and without supplementary feeding by species. Significantly higher relative productivity was found when supplementary food was provided (Wilcoxon Matched Pairs Test; Z=2.906, n=45, P=0.003)

Species	**Mean Product. without suppl. feeding**	**Mean Product. with suppl. feeding**	**Increment**
Aquila adalberti	0.8373	1.3430	160%
Gypaetusbarbatus	0.1436	0.4135	288%

Fig 1: Linear regression between relative productivity of territories and response of these same territories when supplementary feeding is conducted. Poor quality territories with low productivity levels respond more strongly to supplementary feeding than those with higher levels of natural productivity (r=-0.435, n=45, P=0.002).



How to plan reintroductions of long-lived birds

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How to plan reintroductions of long-lived birds

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Abstract:

Reintroductions have been increasingly used for species restoration and it seems that this conservation tool is going to be more used in the future. Nevertheless, there is not a clear consensus about the better procedure for that, consequently a better knowledge of how to optimize this kind of management is needed. Here we examined the dynamics of released long-lived bird populations (lesser kestrel, Falco naumanni, Bonelli's eagle Aquila fasciata, and bearded vulture Gypaetus barbatus) in object-oriented simulated reintroduction pro- grams. To do that, number of young per year and number of years of released necessary to achieve a successful reintroduced population were calculated. Wedefine a successful reintroduction as one in which when the probability of extinction during two times the maximum live-span period for the species (20, 50, and 64 years respectively) was less than 0.001 (P<0.001) and they showed a positive trend in population size (r>0.00). Results showed that a similar total number of young (mean 98.33±5.26) must be released in all the species in all the scenarios in order to get a successful reintroduction. Consequently, as more young per year are released the new population is going to be larger at the end of the simulations, the lesser the negative effects in the donor population and the lowest the total budget needed will be.

Keywords: *population viability analysis, PVA, Falco naumanni, Aquila fasciata, Gypaetus barbatus*

RESEARCH ARTICLE

How to plan reintroductions of long-lived birds

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Abstract

Reintroductions have been increasingly used for species restoration and it seems that this conservation tool is going to be more used in the future. Nevertheless, there is not a clear consensus about the better procedure for that, consequently a better knowledge of how to optimize this kind of management is needed. Here we examined the dynamics of released long-lived bird populations (lesser kestrel, *Falco naumanni*, Bonelli's eagle *Aquila fasciata*, and bearded vulture *Gypaetus barbatus*) in object-oriented simulated reintroduction programs. To do that, number of young per year and number of years of released necessary to achieve a successful reintroduced population were calculated. We define a successful reintroduction as one in which when the probability of extinction during two times the maximum live-span period for the species (20, 50, and 64 years respectively) was less than 0.001 (P<0.001) and they showed a positive trend in population size (r>0.00). Results showed that a similar total number of young (mean 98.33±5.26) must be released in all the species in all the scenarios in order to get a successful reintroduction. Consequently, as more young per year are released the new population is going to be larger at the end of the simulations, the lesser the negative effects in the donor population and the lowest the total budget needed will be.

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Introduction

The global loss of biodiversity is a well-documented phenomenon, with increasing numbers of species at risk of extinction due to direct or indirect anthropogenic causes, e.g. [1, 2]. Management to reduce risk of species extinction includes a wide variety of actions, one of the more intensive of which is reintroduction. Reintroductions are intentional translocations of species into parts of their historically known range from which they have been extirpated [3]. Wildlife reintroductions are becoming increasingly common, being now considered to be an important tool for conservation of endangered or threatened species [4, 5].

In an attempt to improve success in reintroductions projects, the International Union for the Conservation of Nature (IUCN) Guidelines for Re-introductions were published in 2013 providing specific policy guidelines for each phase of a reintroduction project [3]. Also, other authors suggest a series of standards for documenting and monitoring the methods and outcomes associated with reintroduction projects for birds [2, 6].

The final objective of any reintroduction is the persistence of the new population without intervention, but it is not very clear what criteria would be used to define what constitutes a successful reintroduction [6–12]. Some definitions of success that have been proposed include: (i) breeding by the first wild-born generation [13]; (ii) a three-year breeding population with recruitment exceeding adult death rate [13]; (iii) an unsupported wild population of at least 500 individuals [14]; or (iv) the establishment of a self-sustaining population [8, 15]. However, a major problem with defining a reintroduction as a success or a failure is that, by any criteria, this definition is limited in time [7]. Even taking this into account still we need some objective criteria to decide when to stop releasing animals. This is important in order to plan any reintroduction adequately as well as to get the necessary political and public support for a long term conservation action [16, 17].

One of the first challenges for a reintroduction is to secure the source of animals to be released. There are two main sustainable sources of animals for a reintroduction program: extraction from wild populations or breeding in captivity. After an intensive human persecution during the second half of the 20th century, many endangered species, such as raptors, persist at high local density in small and relatively isolated populations [18]. This is a common pattern for most of large endangered species, which have suffered in the past from habitat destruction and human persecution. Those remaining high-density small populations of raptors often show low fecundity, resulting from density-dependent reproduction [19–21]. Because fecundity is low, public opinion is not very prone to extractions, making sensible management difficult, especially if extractions can put the donor population at risk [22]. Consequently, it is necessary to analyze the potential effect that different strategies of repeated extractions would have on donor population.

Another important consideration for reintroductions is the monetary expense. However, this factor is often overlooked when planning reintroductions [22]. Especially when animals are sourced from captive propagation programs, reintroductions may be an expensive option for managers of endangered species [22]. On the other hand, young released per year determines the length of the reintroduction project, affecting in a very significant way the total cost of these programs [22].

In this paper, we present different simulated scenarios of extractions and releases of animals, identify the impact of each scenario on monetary cost of reintroduction programs and discuss a criterion to define success in reintroductions. We present the results for simulated reintroduction programs of long-lived birds, selecting three different species that vary in body size, fecundity and population dynamics: the small lesser kestrel, *Falco naumanni*, the medium-size Bonelli´s eagle *Aquila fasciata*, and the large bearded vulture *Gypaetus barbatus*.

We examine the potential success of reintroductions under our different simulated scenarios, combining number of young per year and the length of the reintroduction necessary for each species with the effect of the repeat extraction of young in the donor population, in an attempt to find an optimal combination of monetary cost and probability of success. We try to determine the minimum number of young that we need to release each year and the minimum number of years of releases for each species as well as the final population size of the new population in each one of the scenarios

Material and methods

The species

The lesser kestrel (*Falco naumanni)* is a small (120–145 g), long-lived (maximum live-span 10 years) colonial falcon, being females large than males [23] and references therein. The species feeds mainly on invertebrates, and has experienced a marked decline in some areas of its breeding range during the last 30 years, being the target species for several reintroduction programs [24]. The lesser kestrel data on demographic parameters was taken from literature [23] coming from a color-ringing and monitoring of breeding performances in 12 colonies in the Seville province (Spain) during 6-year period (1988–1993).

The Bonelli's eagle (*Aquila fasciata*) is a Mediterranean and long-lived bird of prey of medium size (1,600–2,200 g) with a maximum life span of 25 years [25]. The species has experienced a severe decrease in Spain during the past decades, mainly as a result of power line accidents and human persecution [26]. Currently the species appears to be recovering slowly but its conservation status is under discussion [27]. Bonelli's was extirpated from the Balearic Island (Spain) during the 20th century and a reintroduction program to recover this population started in 2011. Estimates for Bonelli‘s eagle were taken from literature [25] and were based on data of 7 subpopulations in Spain summarizing 142 pairs that were surveyed during 1994–2005 period.

The bearded vulture (*Gypaetus barbatus*) is a large (4,500–7,000 g) long-lived territorial raptor, with a maximum life span of 32 years [22] and references therein, that breeds mainly in mountainous areas [28]. The species feeds mainly on bones and meat of ungulates which it swallows whole or in pieces. During the 20th century its numbers and distribution area declined due to human persecution and at present, three reintroduction programs are running in Europe, one in Switzerland and two in Spain [22]. Estimates of demographic parameters for bearded vultures were taken from literature [22, 28]. Data was from the only Spanish population of the species situated in Pyrenees. The population increases from 40 pairs in 1970 to 150 by 2011.

Simulations

We conducted simulations to analyze the viability of reintroduction programs for this three species under different scenarios. We used the Vortex simulation software (Vortex, version 10.0.76, [29, 30]). Vortex is an individual-based model for population viability analyses (PVA). It models population dynamics as discrete, sequential events that occur according to probabilities defined by the user, and model constant or random variables that follow specified distributions. The events used for modeling describe the typical life cycle of sexually reproducing, diploid organisms. This method is particularly appropriate for species showing low fecundity, long life span, small population size, estimable age-specific fecundity and survival rates, and monogamous breeding, as in the species and populations we modeled here [31]. In fact, Vortex has already been used to analyze the viability of populations of Bonelli´s eagles [25] or bearded vultures [22]. In the bearded vulture study, reintroduction scenarios and effect in donor populations were analyzed. Using estimates of fecundity and mortality rates for the three species previously published (Table 1) we conducted several simulations for different scenarios, performing 1000 replicates for each one.

First, we simulated reintroduction programs of the three species considered. To do that, we calculated the number of released juveniles per year and during how many years that we need to achieve a successful new population. We considered a new population to be successful when the probability of extinction during two times the life-span period for the species (lesser kestrel: 20 years, Bonelli‘s eagle: 50 years and bearded vulture: 64 years) was less than 0.001 ($p<0.001$) and they showed a positive trend in population size ($r>0.00$). We simulated reintroduction programs from 5 to 20 years of duration calculating the minimum number of juveniles we have to release per year with a sex ratio of 1:1. We consider the minimum number of young in each scenario the values below which the probability of extinction of the simulated population was $>\underline{0.001}$. In these simulations, no density-dependence or ceiling population limit was considered due to small size of the simulated population at the end of the simulations.

Table 1. Summary of parameter values used in Vortex for the simulations of trends in the donor population and in the hypothetical reintroduced population.

Parameter	Lesser kestrel	Bonelli's eagle	Bearded vulture
Age of first breeding	2	4	7
Maximum live-span of reproduction	10	25	34
Maximum number of broods per year	1	1	1
Maximum progeny per brood	4	2	1
Sex ratio at birth	50%	50%	50%
Density dependent fecundity rate	1.99 at low density 1.50 at high density	1.02 at low density 0.78 at high density	0.60 at low density 0.35 at high density
Preadult mortality	64%	73%	50%
Adult annual mortality	20%	8.53%	6%

Based on data from [23], [25] and references therein and [22] and references therein.

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Second, we simulated for each one of the species and scenarios, the effect on the wild donor populations of repeated extraction of the minimum number of young needed for a successful reintroduction according previous simulations. In order to standardize the potential effect of repeat extractions on wild donor populations among species, we simulated for each one of the three species a donor population of the necessary size to produce 100 young per year. According to the mean fecundity for each species (see Table 1), we need 26 pairs (100 individuals of all ages) of lesser kestrels to produce 100 young per year, 40 pairs of Bonelli's eagles (140 individuals in total) and 83 pairs of bearded vultures (335 individuals). We set donor populations at their maximum limit when the simulation started and we introduced density dependence in fecundity in the simulations as shown in Table 1. Simulations started with a stable age distribution and equilibrate sex ratio (1:1).

Cost analyses

We estimated the annual cost of a standard reintroduction program based on extraction of young from wild populations, using data from the following reintroduction programs developed in Spain: (i) osprey reintroductions in Huelva and Cádiz [32]; (ii) the Spanish imperial eagle reintroduction in Cádiz [33] and (iii) the bearded vulture reintroduction in Cazorla (http://www.gypaetus.org/) and in Picos de Europa (Asturias, Spain, http://www.quebrantahuesos.org/). The estimate cost includes the personal necessary to take care of the extracted young until de age of release, the feed and monitoring during the dependence period until the young leaves the area, plus the cost of emitters, hacking towers and educational programs. Obviously, the costs could change through time, but it is the relative costs of the different strategies that are important here.

Statistical analyses

We tested for trends with linear analysis and we used the F-ratio statistic to test the slope. Variances of the linear models were tested for homogeneity using Cochran's C statistic. GLM with appropriate distribution and link function were used to assess differences among species or scenarios. Friedman ANOVA tests were used to examine differences in mean number of breeding pairs in reintroduced or donor populations according different strategies of extraction and releases. Statistical significance was set at $p<0.05$ and analyses were conducted using the STATISTICA 8 package (Statsoft Inc., Tulsa, OK, USA).

Table 2. Different combinations of young released per year and number of years of released to achieve successful reintroductions.

Species	Years of releases	Young per year	Total number of young	Stochastic *r*	Sd (*r*)	Probability of extinction	Number of pairs
Lesser kestrel	5	20	100	0.056	0.164	<0.001	19.81
	10	10	100	0.090	0.159	<0.001	16.94
	15	6	90	0.110	0.167	<0.001	13.36
	20	4	80	0.127	0.184	<0.001	9.33
Bonelli´s eagle	5	19	95	0.051	0.153	<0.001	17.91
	10	10	100	0.063	0.164	<0.001	16.83
	15	6	90	0.066	0.161	<0.001	14.19
	20	5	100	0.067	0.158	<0.001	11.43
Bearded vulture	5	21	105	0.022	0.129	<0.001	14.92
	10	10	100	0.032	0.139	<0.001	13.79
	15	6	90	0.038	0.142	<0.001	13.37
	20	5	100	0.042	0.142	<0.001	11.79

Simulation time was double the live-span period for the species (lesser kestrel: 20 years, Bonelli's eagle: 50 years and bearded vulture: 64 years).

Total number of young was years of releases*young per year.

Number of pairs was the mean value of the 1000 replicates performed for each scenario at the end of the simulation.

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Results

Different combinations of number of released young each year and number of years of releases to obtain a successful reintroduction (Probability of extinction < 0.001 and $r > 0$) are show in Table 2. For all the species, the minimum number of young per year necessary for a successful reintroduction varies from 18 young per year during 5 years to 5 young per year during 20 years. Interesting, in all the cases and with all the species, a similar total number of young (mean 98.33±5.26) must be released in order to get a successful reintroduction. No significant effect of the species in the number of young to release was found, being only significant the number of years of releases (GLM normal distribution and log link function, "years": Wald statistic = 1402.05, $p<0.001$; "species": Wald statistic = 0.94, $p = 0.625$). A negative significant exponential relationship between young per year and years of releases was found (r = -0.934, n = 48, $p<0.001$). Consequently, number of years necessary to obtain a successful reintroduction increases exponentially as we decrease the number of young released per year (Fig 1).

For all the species, final mean population levels increased with the number of young released per year (ANOVA F = 9.22, $p = 0.011$), thereby shortening the duration of the reintroduction (Figs 2–4). No differences among species in final number of pairs were found (ANOVA F = 1.13, $p = 0.383$).

Mean number of pairs in the new populations during all the years of simulation showed a significant relationship with number of young released per year, increasing as number of juvenile individuals released per year increased (Friedman ANOVA; lesser kestrel: chi square = 54, n = 20, df = 3, $p<0.001$; Bonelli´s eagle: chi square = 138, n = 50, df = 3, $p<0.001$; bearded vulture: chi square = 174, n = 64, df = 3, $p<0.001$).

Simulating the removal of nestlings from the donor population resulted in significant variation depending on the duration of extraction (Figs 5–7). The longer the extraction period, the lower the size of the modeled donor population during all the years of simulation was (Friedman ANOVA; lesser kestrel: chi square = 10.45, n = 20, df = 3, $p = 0.035$; Bonelli´s eagle: chi square = 38.56, n = 50, df = 3, $p<0.001$; bearded vulture: chi square = 51.56, n = 64, df = 3, $p<0.001$). However, at the end of all these simulations the number of breeding pairs in the donor populations was the same being always the maximum possible for each one of the

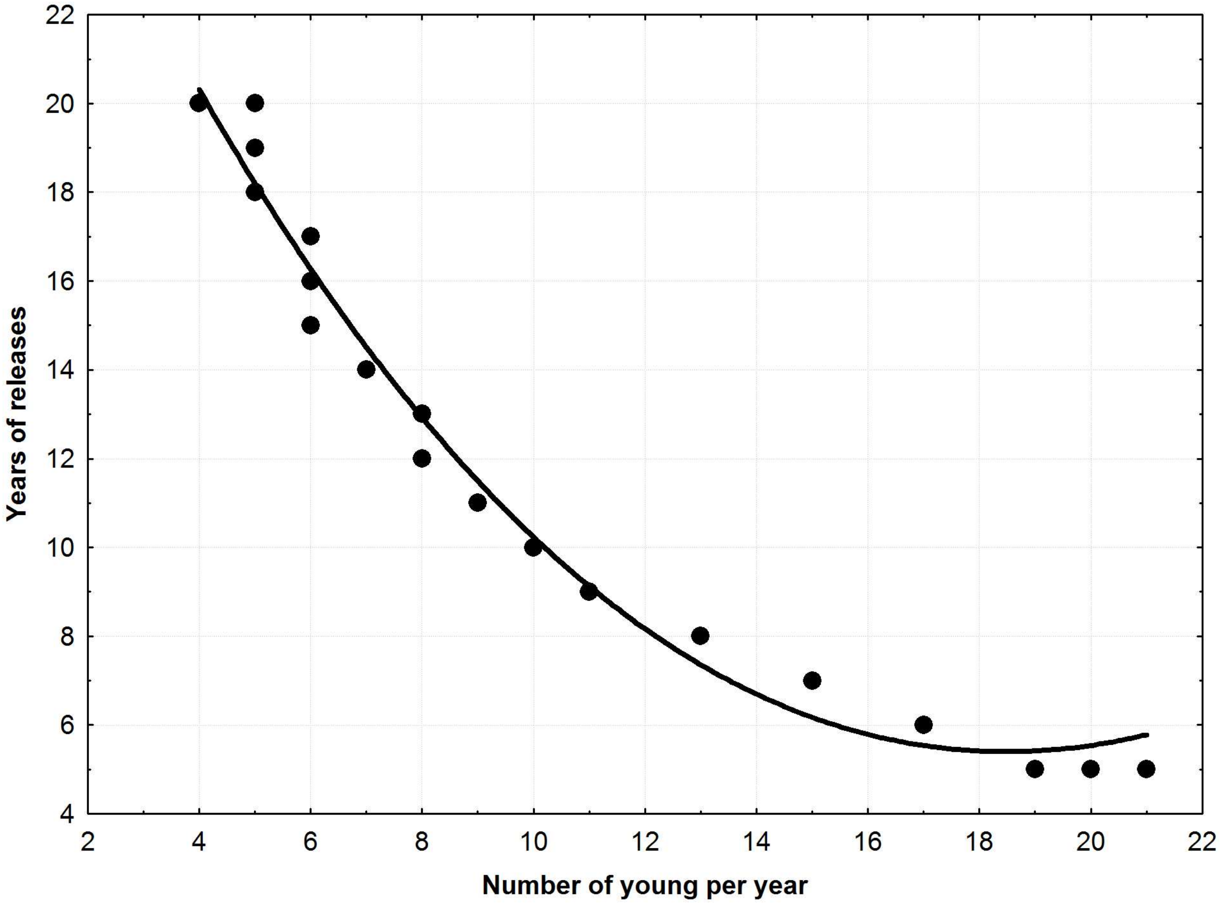

Fig 1. Negative exponential relationship (r = -0.934, n = 48, p<0.001) between the number of young released per year and number of years necessary to obtain a probability of extinction below 0.001 for all the species.

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species (lesser kestrel = 26, Bonelli´s eagle = 40 pairs and bearded vulture = 83 pairs). The temporary decreases in the number of breeding pairs in donor populations lasted longer as years of extraction increaseds (Figs 5–7). Time required to recover the initial donor population size (standardized according total simulation time) was only affected by the number of young extracted per year (GLM normal distribution and log link function, Wald statistic = 190.7, p<0.001), being shorter as the number of young per year increases. Recovery time of the initial donor population size was not significantly affected by species (GLM normal distribution and log link function, Wald statistic = 0.4, p = 0.803). Anyways, for all the species and in all the scenarios, the probability of extinction of the donor populations was always below 0.001.

The cost of reintroduction programs based on extraction form wild populations analyzed in Spain (Ospreys, Spanish imperial eagles, and Bearded Vultures), including cost of hacking and any associated costs of the program, give an annual estimated budget of 100 000€. Considering that the main component of the total budget per year is personal salaries and that number of persons needed is nearly the same when releasing 5 or 20 young per year, number of years of releases is the main factor affecting monetary cost of these programs. When captive breeding is used as a source of young for reintroduction programs, account must be taken, in such a long-lived species, of the lengthy period in captivity before individuals taken early in their lives start to breed. Additionally, we have to consider all-year running cost of the

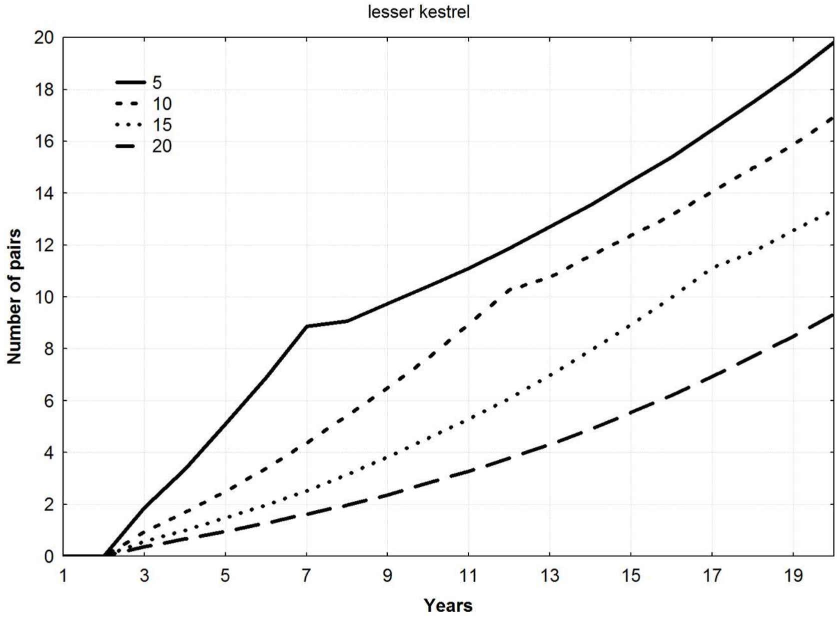

Fig 2. Trajectories of new populations according to different combinations of young released per year and duration of the releases for the specie *Falco naumanni* (5 years–20 young, 10 years–10 young, 15 years–6 young, and 20 years–5 young).

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necessary facility and personal involved plus the cost of the release of young at the field (the only one we have to consider using extraction of young from wild population). In other words, reintroductions using captive breeding would be around 17 times more expensive than the alternative of harvesting wild young [22].

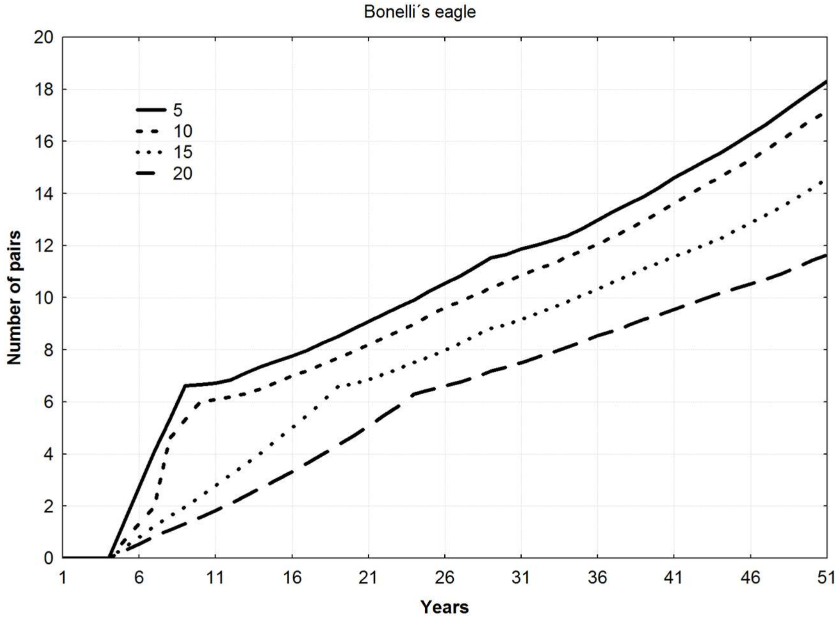

Fig 3. Trajectories of new populations according to different combinations of young released per year and duration of the releases for the specie *Aquila fasciata* (5 years–20 young, 10 years–10 young, 15 years–6 young, and 20 years–5 young).

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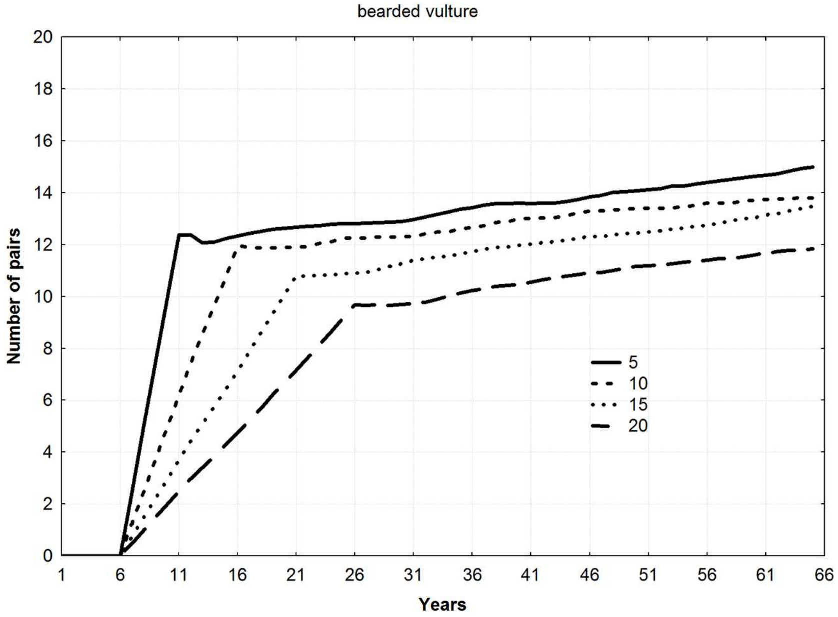

Fig 4. Trajectories of new populations according to different combinations of young released per year and duration of the releases for the specie *Gypaetus barbatus* (5 years–20 young, 10 years–10 young, 15 years–6 young, and 20 years–5 young).

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Discussion

In this study we use a definition of success in reintroductions that is mainly functional. In small populations of endangered species, population viability analyses are the usual way to make predictions and guide decisions about conservation actions. Reintroduced populations

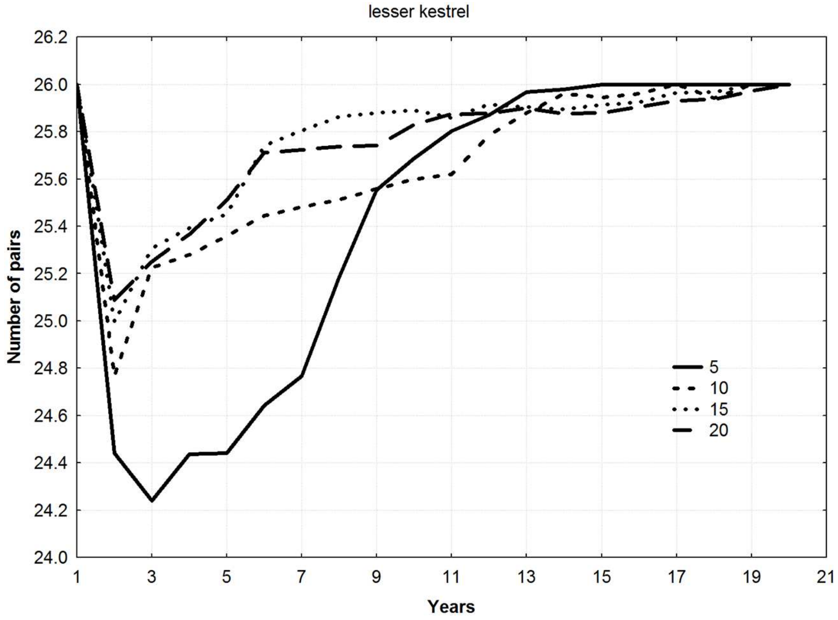

Fig 5. Effect of different combinations of young removed per year and number of years of extraction on the number of breeding pairs in the donor population the specie *Falco naumanni* (5 years-20 young, 10 years-10 young, 15 years-6 young and 20 years-5 young).

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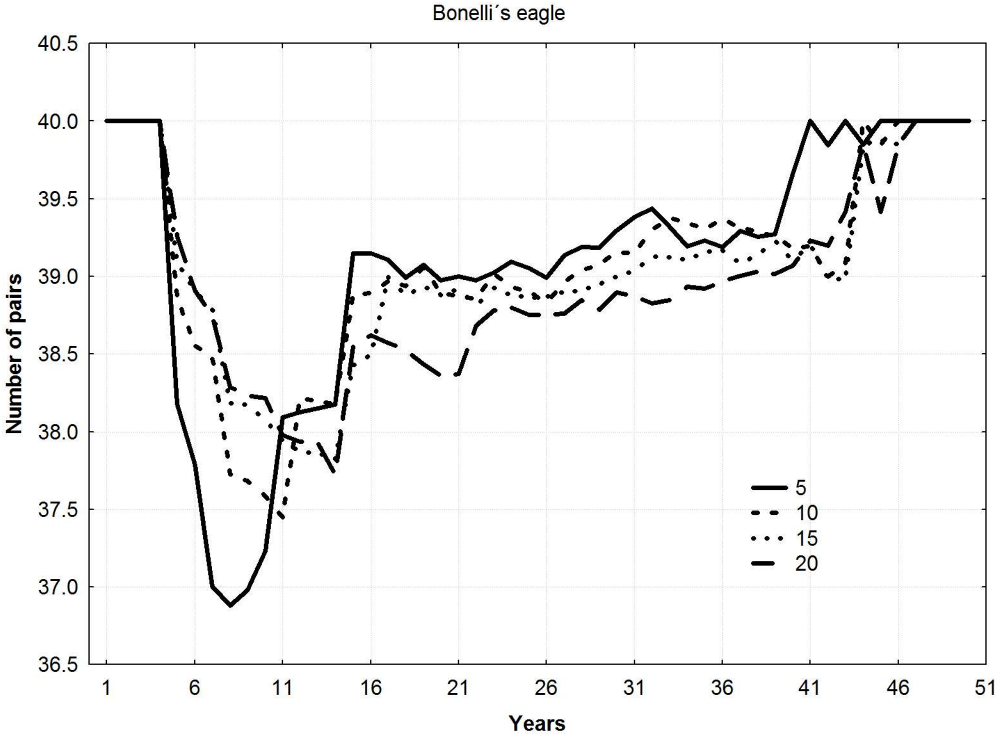

Fig 6. Effect of different combinations of young removed per year and number of years of extraction on the number of breeding pairs in the donor population the specie *Aquila fasciata* (5 years-20 young, 10 years-10 young, 15 years-6 young and 20 years-5 young).

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should be no different, as by definition, reintroduced populations are small and endangered at the beginning. The main point for us is not to secure forever this new population but to decide when new releases are not necessary with objective criteria. Using simulations and objective criteria, like probability of extinction below 1% and positive trend during twice the live span of the species, we can make predictions about the length of the program and the number of young to release. Predicted trajectories of the simulations can be used to check annually if the evolution of the new population is over, on, or under expectations. Adjusting the simulated period to twice the life span of the species allows us to compare species with different life histories in comparable units of time. Interestingly, no differences among species in number of young to released, final population size or negative effects on donor population were found, being only significant the number of years of releases or extractions.

Other definitions of success like breeding by the first wild-born generation are dependent of the demography of each particular species and don't give us any idea about viability of the new established population [13]. The same problems arise with "an unsupported wild population of at least 500 individuals" [14] again depending on the demography of the species (500 individuals would means few breeders or a lot of them), or with "a three-year breeding population with recruitment exceeding adult death rate" [13], giving us no information about viability or predicted persistence of the new population [14]. The establishment of a self-sustaining population [15] is similar to our definition of success but here we propose that the time we have to consider for these calculations must be based on the live-span of the specie, allowing us to compare species with a different live history in comparable units of time.

Results showed that a similar total number of young (mean 98.33±5.26) must be released of all the species and in all the cases in order to get a successful reintroduction. As we decrease

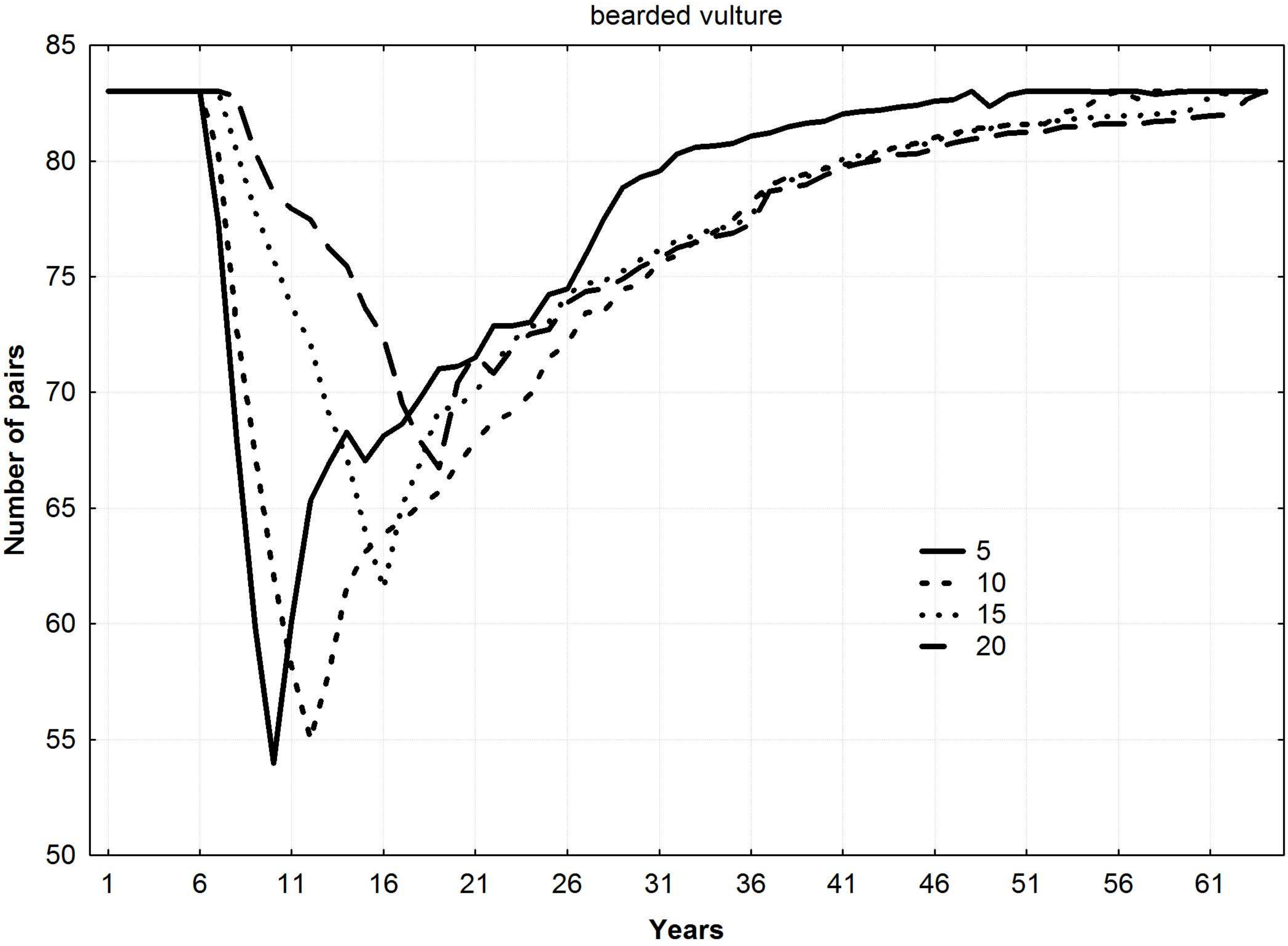

Fig 7. Effect of different combinations of young removed per year and number of years of extraction on the number of breeding pairs in the donor population the specie *Gypaetus barbatus* (5 years-20 young, 10 years-10 young, 15 years-6 young and 20 years-5 young).

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number young released per year we need to increases exponentially number of years of releases. In the other hand, the number of young per year also affects in a significant way the final reintroduced population size, the effect of extractions in donor population, and the total cost of the project.

As more young per year are released the larger the new population is going to be at the end of the simulations. These differences are due to a different number of breeding pairs in the new population at the early stage of the reintroduction. When we release a large number of young with the same age, as soon as the survivals reach sexual maturity, the number of pairs is going to increase accordantly, increasing the number of new young born in the new population. In the other hand, even releasing the same total number of young, we have to wait longer an increase in young production of the new population if we release few young per year.

Differences in number of young extracted from the donor population per year have significant effects on the size of the donor population. The size of the modeled donor population became lower as the extraction period lengthened and the number of young extracted per year decreased. The duration of temporary decreases in the number of breeding pairs in donor populations was significantly related to the length of the extraction period, even if in all the cases donor population size was at population ceiling at the end of the simulation. Temporal decreases in the number of breeding pairs would generate a negative public perception of this management action.

Result showed that time necessary to achieve a successful reintroduction increases exponentially as we decreases number of young released per year. As total annual budget of a reintroduction program is, to a certain degree, independent of the number of released young, the most important component of the total cost of these programs is their length number of years. In our case, we can make a reintroduction releasing 20 young per year during 5 years (approximate cost 100,000€ per year, total cost 500,000€) or alternatively with 5 young per year during 20 years (total budget 2,000,000€).

It is important to point out that whatever the number of released young will be, there are additional analyses that must be done to assure a successful reintroduction. Following IUCN guidelines we must be sure that causes that provoke extinction in the past are not operating now. In raptors the main historical factor driving local extinctions was human persecution. Nowadays, human attitude have change substantially allowing the recovery of these former populations, but new threats must also be determined and corrected if necessary (power lines, wind farms, poisoning, etc). Also, habitat availability analysis, including density and diversity of preys must be conducted before any releases.

Summarizing, a good general suggestion is to increase as much as possible the number of released young per year, reducing the length of the program, increasing the final size of the new population, avoiding significant effects on donor population and, of course, using the money in an optimal way. Optimal design of reintroduction program for long-live birds is to use a donor population of the appropriate size (this is always cheaper than any breeding in captivity program [22] and to releases 20 young per year during 5 years, independently of the species. Reducing significantly the total cost and limiting in time the conservation program would increases the public support to these reintroduction actions. Of course, theoretically we can conduct a reintroduction within one year if we release the necessary number of nestlings (around 100 according our results). Nevertheless, we did not conducted these simulations because a unique releases would be very dangerous according environmental (or others) stochastic fluctuations. Episodic effect or any unnoticed mortality factor only detected after the first released would be a high risk.

Many endangered species recovery programs could benefit from these suggestions. Reintroduction programmes of various animals have increased greatly during the last decades, and are likely to become more common in the future [33]. The use of population simulations with objective criteria could reduce the costs, increasing at the same time the probability of success. Additionally, having predicted trajectories for the new and donor populations facilitates critical future monitoring of these reintroduction programs to detect and correct any bias in mortality or fecundity that could put species survivorship at risk.

Author Contributions

Conceptualization: VM MF.

Data curation: VM MF.

Formal analysis: VM MF.

Methodology: VM MF.

Project administration: MF.

Software: VM MF.

Supervision: MF.

Validation: VM MF.

Visualization: VM MF.

Writing – original draft: VM MF.

Writing – review & editing: VM MF.

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Discussion

During the previous two centuries, many predator species have experienced substantial population declines, geographic range contractions, and fragmentation of their habitat distribution (Ripple et al., 2014). However the direct war against wildlife seems to be waning in Europe (Martínez-Abraín, Crespo, Jiménez, Gómez, & Oro, 2009), in consequence, wildlife is expanding their range in Europe especially species previously persecuted, such large raptors. In addition, as a response to a change in human attitude towards wildlife, the number of animal translocations with the objective of restore species in their original habitat has increased.

In this context, colonization is taking place mostly in human dominated landscapes, but nowadays the impact of human activities has changed compared with the previous century. The decrease in the direct human persecution and the mitigation of the impact of human activities toward wildlife (e.g. power lines correction measures) is allowing a sharing of landscapes between humans and wildlife, including raptors. The appropriate conservation measures and the continuous study of mitigation measures will increase the colonization possibilities of previously human persecuted species. In our study with the Spanish Imperial eagle population, we found that territories closer to human activity are significantly more productive than nests with longer neighbor distances. These results suggest that past refuges areas were not necessarily high quality habitat for the species and probably were selected to avoid the direct human persecution in the past. As other studies suggest, these past habitats were occupied mainly because of the inaccessibility for humans (González, Bustamante, & Hiraldo, 1992).

According that, the availability of suitable habitat is increasing in European landscapes as the war against predators is decreasing (Martínez-Abraín et al., 2009). Even thought past refuges served well for the protection of target species in the era of human persecution, now with changing human attitudes, the best habitats for the species may be empty and far away from existing population nuclei. In this context, some previously persecuted species, like raptors, suffer from limitations of dispersal and in consequence the colonization of new suitable habitats far away of existing populations. The tendency to breed close to other existing populations, called philopatric behavior, constitute a barrier for the colonization of territories without breeding adults in the area and inconsequence productivity is limited by the habitat present in the areas previously occupied. According with our results, translocations constitute a useful tool to re-establish species in areas where factors that promoted the previous extinction of the species have now disappear but that now are far away of existing populations and have no breeding adults in the area. In a natural colonization, breeding pairs prefer to settle near existing ones and productivity is limited by the habitat quality present in those areas. In contrast, translocations are not limited to areas surrounding existing populations and the selection of good habitats for the species is the main criteria in the choice of a release site (Armstrong & Seddon, 2008). Our study with Spanish Imperial eagles found that reintroduced populations were at least more than twice productive than those of natural colonization in the peripheral limits of the existing population.

Our results show that, territory quality seems to be a major driver of productivity (Osborne & Seddon, 2012) and the assessment of high- quality habitat is a key step before starting a reintroduction project.

➢ Juvenile dispersal behavior: territory quality, local experience, social attraction and nutritional conditions

According to the ’interference’ hypothesis, as density increases, the frequency of floater intrusion increases, resulting in a decrease in productivity across the population. In contrast, under the ’habitat heterogeneity’ hypothesis, as density increases a higher proportion of individuals is forced to occupy lower quality habitats. Support of this hypothesis requires that floaters detect differences in quality among territories and prefer the better ones.

Our results show that floater intrusions and productivity were highly positively correlated, supporting the ’habitat heterogeneity’ hypothesis, where floaters must are able to distinguish differences in quality among territories.

In an established population of Spanish Imperial eagles we found that visits by floaters to occupied territories are concentrated at the beginning of the breeding cycle when, if they found a vacancy, they would be able to breed that year. Floaters spent around 30% of their time in returns to their natal population (Miguel Ferrer, 1993b), but intrusions into territories were concentrated only in certain months. The mean time that the floaters spent in the natal population during these returns was significantly shorter than the period they spent in temporary settlement areas outside the natal population area (Miguel Ferrer, 1993a). Returns to the natal population could be interpreted in two ways. First, the natal population could be used as another area of temporary settlement, in which the average stay is shorter due to expulsion by territory owners, but the frequency of returns is higher due to a high motivation to settle there (perhaps because of the chance of obtaining a meal in this area of high prey density). An alternative possibility is that the returns could be used by the floaters to explore the possibility of pair formation with a territorial bird that had lost its mate. These two possibilities are not mutually exclusive.

Analyzing dispersal distances of juveniles in a reintroduced population, without breeding adults in the area, we found that individuals disperse despite the availability of high quality territories in the release area. It seems that all juvenile eagles disperse, even in the absence of a parent-offspring conflict (Trivers & Willard, 1973), suggesting the existence of an important selective advantage in the dispersal process.

Our results showed significant differences in Dmax, with close to double mean distances in young released without adult in the area than young born or released with breeding adults in the area (from 132 km to 232km). It seems that social attraction has a critical role in determining maximum dispersal distances. The existence of the social attraction even in released individuals has consequences for the success of reintroduction projects and should be taken into account in population viability analyses when planning reintroductions. Selection of reintroduction sites relatively close to former existing population may enhance immigration of released young whereas breeding nuclei may hinder the establishment but enhance the growth of the incipient population. In addition, the use of captive adult birds from recovery centers during the first years of releases might decrease Dmax, increase return rates and earlier settlement, which in turn would accelerate the establishment phase.

Another factor to take into account during the planning of a reintroduction program is related to the nutritional condition of the released individuals and its effects on dispersal distances.

In most studies of bird dispersal, a leptokurtic distribution of distances has been found (Miguel Ferrer, 1993b; Newton, 2008), with most of the individuals relatively close to the natal nest and few of them dispersing large distances, forming the tail of the distribution. Two main hypotheses to explain this form of distribution of dispersal distances have been proposed. Some authors have proposed that this distribution could arise due to competition among dispersing individuals (i.e. competitive displacement hypothesis), with individuals at lower competitive advantage dispersing longer distances. Those individuals that form the tail of the distribution, are supposed to be later nestlings in the season with a poor nutritional condition and taking longer to disperse (Waser, 1985). An alternative explanation is the ‘wandering’ hypothesis (Miguel Ferrer, 1993a). In this hypothesis, again a skewed distribution of dispersal distances is expected but with juveniles that are hatched early in the season, with a better nutritional status, dispersing longer distances, and young that hatched later remaining close to the natal population.

Our results support the idea of general improvement in nutritional condition of these kinds of dispersants due to the *ad libitum* feeding program. Analyses of Dmax and hatching dates demonstrated that leptokurtic distributions disappeared when ad libitum feeding programs generally improve nutritional conditions, as all birds moved long distances.

The effect of nutritional conditions on dispersal distances may entail important consequences on metapopulation dynamics and population management. This nutritional-dependent emigration process should be expected in those reintroductions where other breeding populations occur within the dispersal range, and may affect the establishment and growth of an incipient restored population (Muriel, Morandini, Ferrer, & Balbontin, 2015). For instance, pre-existing populations can decreases the growth rate of an incipient reintroduced population by increasing immigration (Dale, 2001). Due to a general improvement of the nutritional status of released young that have been fed *ad libitum* as is usual in reintroduction programs, a higher proportion of dispersant would contact the existing population. However, this effect may differ according to the translocation status, relative population densities and breeding prospects.

➢ Demography of reintroduced populations

Regulation of growth in populations is mediated by density dependent parameters that act more severely to constrain growth as densities rise (Bretagnolle, Mougeot, & Thibault, 2008; Miguel Ferrer & Donazar, 1996; Miguel Ferrer, Newton, & Casado, 2006; Miguel Ferrer & Penteriani, 2008; Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999; Santoro, Green, Speakman, & Figuerola, 2015). Both age of first breeding and fecundity have consequences for the intrinsic growth rate of the population (“r”); populations with faster growth will show greater ability to colonize new areas than populations with typically low fecundity and delayed maturity (Miguel; Ferrer, Otalora, & García-Ruiz, 2004). The ability to modify these parameters according to the density of populations could play a key role in determining the success of colonization processes, including reintroductions.

Our results show that reintroductions or colonization of new areas by long-lived birds with deferred sexual maturity increase at maximum rate only when age of first breeding is reduced. Additionally, the increase in productivity seems to be important only when age of breeding had also been decreased. In long-lived territorial raptors, entry to the breeding pool is assumed to bring about a reduction in the probability of mortality. Mortality associated with the first year of life and the immature period show a significant decrease following entry to the breeding population. In fact, previously published studies (Miguel; Ferrer et al., 2004; Miguel Ferrer, 2001; Monti et al., 2014; Penteriani, Otalora, Sergio, & Ferrer, 2005) showed that the immature annual survival increases by 20% and 30% the year after first entry into the breeding population. Decreasing the minimum age of first breeding affects population growth rate in two ways: individuals can contribute with offspring to the population at an earlier age and can live longer once they gain a territory (Miguel; Ferrer et al., 2004).

Our results show that under simulation models the only way for colonizing populations to persist is to decrease the age of first breeding. Populations without possibility to decrease this parameter will fail in the colonization process.

In addition, the probability of a bird starting to breed depends largely on the chance of its finding a mate on an appropriate territory (Dale, 2001; Lenz, Jacob, & Wedekind, 2007). Our results showed a differential natal dispersal between males and females, as already shown in other studies of birds (Newton 1979, 2008; Greenwood & Harvey 1982; Monti *et al.* 2014). In Ospreys and other raptors, males are the most philopatric sex while females are more liable disperse further and breed in a different population. Under this scenario, the proportion of males in a new population is expected to be the limiting factor for mating prospects and local population growth, as females should arrive from neighboring populations. Our results suggest that males, being the most philopatric sex, would work as attractors for dispersive females coming from other populations and looking for breeding opportunities. In fact, we found that, at the beginning of the colonization process, the offspring sex ratio of reintroduced populations is biased toward females and change to females when densities increase. From an evolutionary viewpoint, the benefits of a strategy to produce more males at the beginning of the colonization process should be related with the individual parental benefit associated with this strategy.

In reintroduction projects, parameters that could facilitate breeding at a younger age, such as vacant high quality habitat and opportunity to find a mate, will determine the persistence of colonizing populations and should be considered when planning and estimating the success of reintroductions.

- **Applying the demography of reintroduced populations to improve the success of future reintroduction projects.**

Colonizations processes by called emblematic species are more and more frequent in Europe and density dependent parameters play a key role in regulating population growth in a new area. Evaluation of the effectiveness of different reintroduction management models is a previous step to assess decisions in future reintroduction projects.

Even, success of reintroduction projects as been previously debated some management aspects like source of nestlings and how to plan the number of released young or the duration of the program were still unclear.

According to our results, supplementary feeding is an effective technique able to increase significantly the productivity of certain territories when correctly applied. Food availability seems to be one of the most common factors limiting territory quality and production of young, and also one of the easiest to manipulate. Our results demonstrated that in a high-density population, food supplementation in sink territories produced a significant increase in productivity and the intensity of response to supplementary feeding was stronger in those territories with lower productivity without intervention. Consequently, the selection of specific territories for food supplementation is a critical factor in achieving an increase in the total production of young. The young produced can then be removed without any obvious effect on the donor population. Alternatively, we can leave these extra young in their natal population, increasing the stock of floaters, but the demographic value of these extra young is higher in a well-designed reintroduction programme in a new but suitable area (as results of Chapter 1 suggested).

In addition, giving a source of young the next step is to plan the number and duration of releases in a reintroduction project.

According to our results, a similar total number of young (mean 98.33±5.26) must be released in all species varying a size from kestrel to eagle and in all the cases in order to get a successful reintroduction. As we reduce the number young released per year we need to increase exponentially number of years of releases. The number of young released per year also affects in a significant way the final reintroduced population size, the effect of extractions in the donor population, and the total cost of the project. As more young per year are released the larger the new population is at the end of the simulations.

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Conclusions:

(1) Previously persecuted species, after a change in human attitude, are expanding their range into human dominated landscapes, which with the appropriate conservation measures provide suitable habitats for species. In consequence, the habitat selection analyses conducted during the second half of the XX century should be revised. At least, for some species, changes in human attitude resulted in a huge increase of the potential suitable habitat.

(2) Reintroductions are a useful tool to re-populate areas that have remained far away from established populations and that have available habitat for the species. In addition, reintroduced population show higher productivity and growth rate than naturally expanded populations which tend to expand around the peripheral limits of the already existing populations.

(3) During a colonization process, species are able to change demographic parameters that allow them to increase the growth rate of the population. Without the possibility to change these key parameters (offspring sex ratio, age of first breeding and productivity) the colonization will fail. Density dependent age of first breeding seems to be the most sensitive parameter explaining the ability to colonize in long-lived birds.

(4) Supplementary feeding is a useful technique to increase natural productivity minimizing the impact of repeated extractions of nestlings on the donor population. Depending of the circumstances a reintroductions program based on supplementary feeding and extractions would be between five and seven times cheaper than a reintroduction based in breeding captivity program.

(5) The total number of young that must be released in order to get a successful reintroduction is similar in a different species. As a general suggestion to release more young during less years is the best approach, reducing the total cost of the reintroduction and increasing the final size of the reintroduced population.