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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 analyzed 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

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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.

Key words: floater; interference; density dependence; Doñana National Park; habitat heterogeneity; 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, Ferrer & Donazar 1996, Newton 1998, 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

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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 (Kopimaki 1988, Kadmon 1993, Ferrer & Donazar 1996, Newton 1998, Ferrer & Bisson 2003, Sergio & Newton 2003, Penteriani *et al.* 2004, Casado *et al.* 2008, Taferna *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 maintained, 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 prospection/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.

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Here, we report an 11-yr study of floater interference and territory productivity in the Spanish Imperial Eagle *Aquila adalberti* population at Doñana National Park in Spain during the period 1986-1996. 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 settling areas away from breeding territory. Each settling area was used intensively for a variable but short period, and each individual used the same areas (between three and eight) in rotation during at least the first three years of life, returning occasionally to the natal population (Ferrer 1993). During this period, more than 41.3% of floaters were radio-tagged 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, as well as productivity of those territories. The aim of this study was to analyze the relationship between frequency of floater intrusions and breeding output, thereby testing predictions of these two hypotheses of density-dependent productivity. During the whole 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).

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METHODS

Study area

The study was conducted in Doñana National Park (37° N, 6° 30' W), southwestern Spain. The data used in this study were collected during 1986-1996 inclusive. Three habitat types are present in the area: (1) Mediterranean scrubland, formed by the shrubs *Halimium* spp., *Cistus libanotis*, *Erica* spp., with scattered Cork Oaks *Quercus suber* and small Stone Pine *Pinus pinea* woods; (2) marsh, comprised principally of *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 of 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 (Ferrer & Calderón 1990). During most of the study period (1986-1993), 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, Ferrer & Penteriani 2008, Ferrer *et al.* 2013a). Eagle territories were exclusive and vigorously defended throughout the year (Ferrer 1993). Nests were located in Cork Oaks and Stone Pines not far 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.*

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2003). Evidence for density dependence in this species, and specifically in this population, has previously been published (Ferrer & Donazar 1996, Ferrer *et al.* 2004, Penteriani *et al.* 2008).

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 to the nest at each visit.

Brood size is defined as 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 radio-transmitters (type HSPB 1400 3XA, Wildlife Materials Inc., Carbondale, Illinois, USA) during the years 1986-96 inclusive. During this 11-year period, a total of 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

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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 one year and 12 for at least two 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 radio-tagged 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 radio-tagged 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 center of the circle. Only records of young birds older than 200 days of age were considered as 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

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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 (GLMM) 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 Satterthwaite 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 to the number of visits made to other territories. Then we compared this distribution against a distribution generated assuming 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

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by floaters to their natal territories and checked if 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 analyze differences among territories in the number of intruders and frequency of intrusions. We finally 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 radio-tagged floaters per year. Statistical significance was assumed at $P < 0.05$ and analyses were conducted using the STATISTICA 8.0 package (Statsoft Inc., Tulsa, USA).

RESULTS

A total of 825 intrusions by 50 individual floaters into territories of their natal population were recorded during the 11-year period. Analyzing floater intrusions into their own natal territory against 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 with 8.63 intrusions per year and the lowest in Territory 6 with 1.62 intrusions per year. During the study period the mean number of radio-tagged floaters of all ages in

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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 mean number of intrusions per nest as the response variable in the following analyses.

Fig. 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 the three 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 tried 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. Floater 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, $P < 0.001$). However, males visited more territories per day (0.64 territories per day) than females (0.26 territories per day; GLM Poisson distribution and log link, Wald statistic 63.78, $P < 0.001$).

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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 more frequently their own nest, 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, to 6.5 in territories with one fledgling, 13.3 in territories with two fledglings and 14.0 in territories with three fledglings. Removing territories in years with zero productivity from the analyses 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 than 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.

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DISCUSSION

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

Results showed a clear trend for the intrusions to be concentrated in some months of the year, coinciding with the beginning of the breeding cycle (Calderon *et al.* 1987). In the Spanish Imperial Eagle, the breeding cycle lasts some eight 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 took place from end of January to end of April, peaking in early March, and laying occurred between mid-February and 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, and that they must be using 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 which enabled them to be in the right place at the right time. Alternatively, floaters may be avoiding territories when they have nestlings, because aggression by owners could be more

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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-live birds (Newton 1979, 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, 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

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owners. This finding fitted the fact that male Spanish Imperial Eagles are more active than females in nest building and territory defense (Ferrer 2001), as in some other raptors (Newton 1979). The relatively longer stay of the females could be a consequence of their reduced aggressive interactions with territories 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 don't 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 to 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 more visited 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. This basic assumption, however, is seldom tested (Kokko *et al.* 2004, Ferrer *et al.* 2013b, Stamps 2006). 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 most clear (Kokko *et al.* 2004). This critical assumption of correct assessment of the

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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 5 times more different floaters, than low quality territories. This strongly implied that individual eagles, too young to have bred, knew which where 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 (Newton 1979, Högstedt 1980, Newton 1991, Ferrer & Donázar 1996, Penteriani *et al.* 2002). In some sedentary long-live 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, Ferrer *et al.* 2011). For this mechanism to work, young birds that are 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).

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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 neighboring territorial eagles 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.* 2009). 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 & Donázar 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

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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 showing, 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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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 individual or the interaction of territory and individual.

| | Effect | df | <i>F</i> | <i>P</i> |
|----------------------|-----------|-----|----------|----------|
| 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 |

Fig.1. Distribution of territories inside Doñana National Park population.

Fig.2. Non-homogeneous monthly distribution of recorded intrusions during the study period ($\chi^2_{11} = 1336.21$, $P < 0.001$), 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).

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

Fig. 1

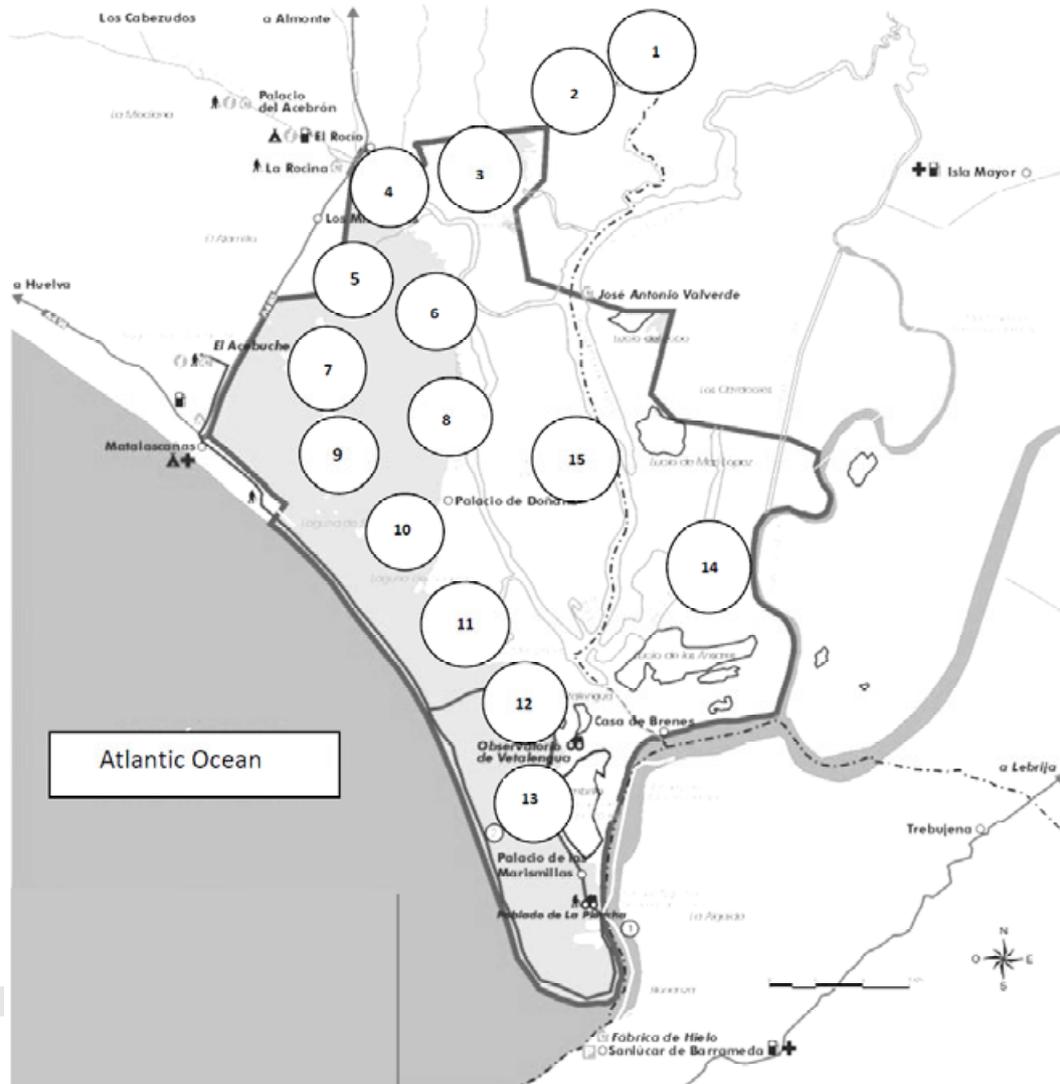


Fig. 2

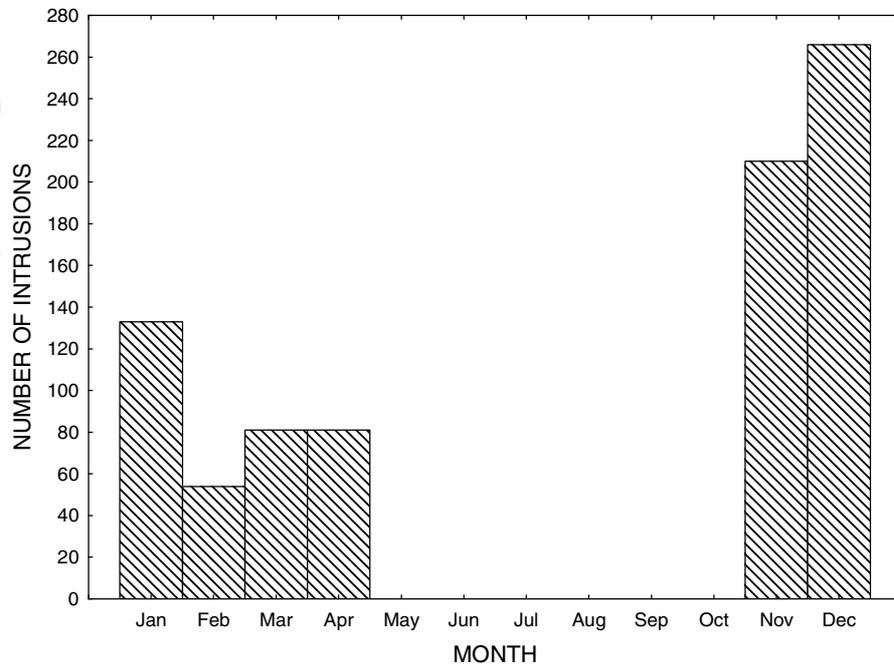
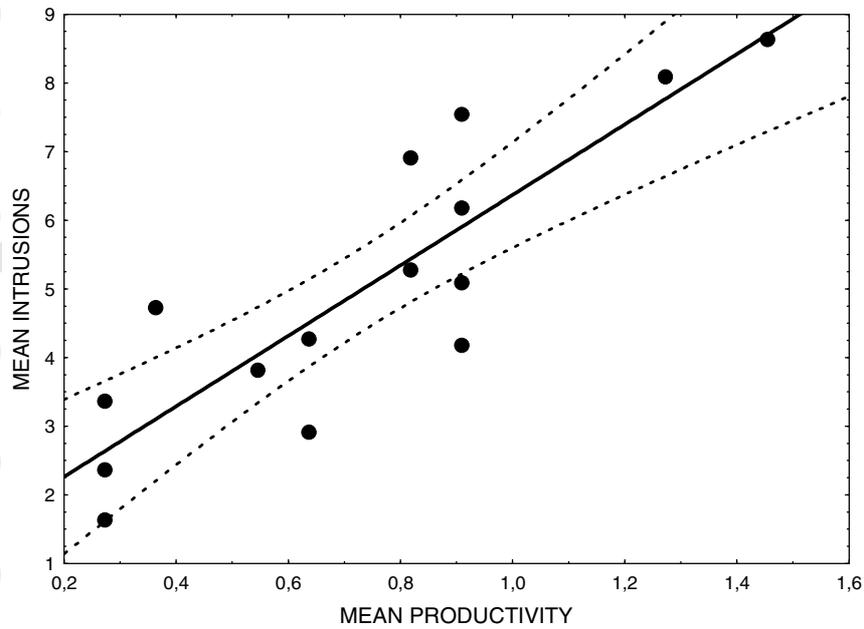


Fig.3



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