

Density dependence in a recovering osprey population: demographic and behavioural processes

V. Bretagnolle^{1,*}, F. Mougeot^{2,3,4} and J.-C. Thibault⁵

¹CEBC-CNRS, 79360, Beauvoir sur Niort, France; ²School of Biological Sciences, University of Aberdeen, AB24 2TZ, Scotland, UK; ³Instituto de Investigación en Recursos Cinegéticos (UCLM-CSIC-JCCM), Ciudad Real, Spain; ⁴Estacion Experimental de Zonas Aridas, CSIC C/General Segura 1, 04001 Almeria, Spain; ⁵Muséum National d'Histoire Naturelle, Département Systématique et Evolution, Case postale 51, 55 rue Buffon, F-75005 Paris, France

Summary

1. Understanding how density-dependent and independent processes influence demographic parameters, and hence regulate population size, is fundamental within population ecology. We investigated density dependence in growth rate and fecundity in a recovering population of a semicolonial raptor, the osprey *Pandion haliaetus* [Linnaeus, 1758], using 31 years of count and demographic data in Corsica.

2. The study population increased from three pairs in 1974 to an average of 22 pairs in the late 1990s, with two distinct phases during the recovery (increase followed by stability) and contrasted trends in breeding parameters in each phase.

3. We show density dependence in population growth rate in the second phase, indicating that the stabilized population was regulated. We also show density dependence in productivity (fledging success between years and hatching success within years).

4. Using long-term data on behavioural interactions at nest sites, and on diet and fish provisioning rate, we evaluated two possible mechanisms of density dependence in productivity, food depletion and behavioural interference.

5. As density increased, both provisioning rate and the size of prey increased, contrary to predictions of a food-depletion mechanism. In the time series, a reduction in fledging success coincided with an increase in the number of non-breeders. Hatching success decreased with increasing local density and frequency of interactions with conspecifics, suggesting that behavioural interference was influencing hatching success.

6. Our study shows that, taking into account the role of non-breeders, in particular in species or populations where there are many floaters and where competition for nest sites is intense, can improve our understanding of density-dependent processes and help conservation actions.

Key-words: density dependence, interference competition, osprey, *Pandion haliaetus*, population growth rate, population regulation, resource depletion

Introduction

Population regulation and its effects on demographic parameters are considered as a paradigm in ecological theory (Ray & Hastings 1996; Hixon, Pacala & Sandin 2002; Sibly *et al.* 2005). Population regulation results from mechanisms that cause demographic density dependence: a negative feedback between population growth rate and population density (Murdoch 1994; Turchin 1995; Newton 1998). Density dependence is notoriously difficult to detect (Sinclair 1989; Murdoch 1994) because of problems associated with time-series analyses (Lebreton & Clobert 1991; Lande, Engen &

Saether 2003) and because of difficulties in conducting experiments (Shenk, White & Burnham 1998). Moreover, spatial population structure (its variance in density) may obscure density dependence (Ray & Hastings 1996), and additional effects are expected in small populations, such as an Allee effect, in which density dependence can be positive. Ideally, in order to measure density dependence in the wild, we need populations that have changed over time (in a constant environment) from low size to a size in which regulation occurs, that is, demographic density dependence halts population increase (Hixon *et al.* 2002; Sutherland & Norris 2003). This situation exists in recovering populations (Sinclair 1996; Nicoll, Jones & Norris 2003; Sutherland & Norris 2003) that have suffered strong human-induced reduction through direct

*Correspondence author. E-mail: breta@cebc.cnrs.fr

(e.g. killing) or indirect (e.g. poisoning) persecution, and in which persecution has stopped.

Once density dependence has been detected for a given population, both its mechanisms and demographic target remain to be established. These are two main approaches (Sibly & Hone 2002; Krebs 2003): the density-demographic approach (density paradigm) and the mechanistic paradigm. The later searches for the extrinsic (food, predation) and intrinsic (social behaviour) factors responsible for the density-dependent relationships. Competition for (limiting) resources is a possible source of density dependence, especially in predators. Regulation by competition occurs through two main processes: direct behavioural interference (Lopez-Sepulcre & Kokko 2005; Carrete, Donazar & Margalida 2006) and resource depletion (Charnov *et al.* 1976; Sutherland 1996). Although interference refers to food intake rate (Sutherland 1996), it can also apply to copulation, territory establishment or mate choice (Alatalo *et al.* 1996; Mougeot, Thibault & Bretagnolle 2002) and demography (Newton 1998; Gill *et al.* 2001).

Here we report on the role of behavioural processes in density-dependent regulation using a 31-year study (1974–2004) of a recovering population of a raptor, the osprey *Pandion haliaetus* [Linnaeus, 1758], in Corsica in the Mediterranean Sea. Because our study population is small, sedentary and from an isolated island, we could define it unambiguously as a closed population and determine its size accurately. During the first 15 years the population increased, then it stabilized for another 15 years. Analysing population trends and contrasting these two periods, we investigated: (1) the relationship between population growth rate and density; (2) which breeding parameters varied with density; and (3) the roles of food depletion and behavioural interference as drivers of density dependence in fecundity. In raptors, territoriality is the main form of density dependence (Newton 1998). However, in our study species the territory is limited to the nest site. We hypothesized that as osprey density increased, so would competition for food outside breeding territories, leading to a reduced food-provisioning rate (less frequent or smaller fish deliveries) and reduced breeding success. We also expected food depletion to affect all pairs within the population more-or-less equally, irrespective of local density. There is growing evidence that non-breeders (floaters) can play important roles in population regulation (Penteriani, Otalora & Ferrer 2005; Carrete *et al.* 2006). We expected interactions with other ospreys to increase with density at the nest level: behavioural interference should affect pairs breeding at higher density in a given year more than solitary ones. We thus conducted analyses both at population (year) and pair levels, contrasting global and local measures of density.

Materials and methods

STUDY SPECIES AND AREA

The osprey is a widespread fish-eating raptor, with breeding dispersion ranging from solitary nesting to loosely colonial (Poole 1989).

Breeding individuals defend their nest site, but not feeding territories (Poole 1989). Corsica (42°N, 9°E), an island situated in the western Mediterranean, holds a resident osprey population. There, ospreys breed on the sea coasts and therefore occupy a linear habitat. In the beginning of the 20th century, the population occupied most rocky coasts except the east coast, and was estimated at approximately 40–100 pairs (Thibault, Bretagnolle & Dominici 2001). However, the population declined dramatically, mainly because of human persecution, with only three breeding pairs remaining in the early 1970s (Thibault *et al.* 2001). Since then, the population has gradually recovered (Thibault & Bretagnolle 2001).

POPULATION MONITORING

The whole osprey population was monitored from 1974 to 2004. In Corsica, ospreys nest on pinnacles between March and August (Thibault *et al.* 2001). Occupied nests were searched for during coastal surveys, and each occupied territory was monitored each year. As the number of pairs was small, it was possible to check every territory and to survey unoccupied cliffs. We are therefore confident that all the occupied territories were found. From 1974 until 1990, all territorial pairs (breeding or non-breeding) remained exactly within the same original area of coastline (Thibault, Bretagnolle & Dominici 1995). After 1991, a few pairs (1–4, see Appendix S1 in Supplementary material) colonized new breeding sites, which historically had been occupied (Thibault *et al.* 2001), located 10–50 km from the original area (see maps in Thibault *et al.* 1995). We excluded those pairs from the present analysis, therefore the area under study is strictly constant and is referred to here as to the 'original area'.

Measures of global and local density

All occupied territories were mapped onto a geographic information system (ARCVIEW ver. 3.2). As the geographical area (coastline) under consideration remained strictly identical over the 31 years of the study, the number of pairs provided a first direct measure of density. In raptors, two measures of local aggregation are used: nearest-neighbour distance, and number of neighbours within a given radius (Arroyo, Mougeot & Bretagnolle 2001; Mougeot *et al.* 2002). For each nest and year, we calculated (i) the distance (in m) to the nearest occupied nest; and (ii) the number of occupied nests within a 5-km radius around the nest (NN5k). The latter was used both as a global measure (the average for a given year of all values, hereafter 'average population density') and locally at the pair level (hereafter 'local density').

Population parameters

During monitoring visits, observers checked nest occupancy and the nest contents from land and from a distance, using a telescope (×20–45). Nests were checked at least once a month from March to May, then once a week between June and August. During each visit, the presence and number of birds, eggs and young were recorded (for additional details see Thibault *et al.* 1995). Because we could watch the nest content from above, we are confident that our counts of eggs and young were accurate. However, only a limited number of clutch sizes were checked before 1990. A nest was considered occupied if a pair attended it in spring, and it was considered active if at least one egg was laid. Laying date was estimated as the week of laying (from week 1 = first week of March), and was determined either

when nests were checked during the course of laying, or by back-calculation from hatching dates either obtained from field observations or derived from chick measurements (Thibault *et al.* 2001). We calculated total productivity (total number of young fledged), breeding success (young fledged/eggs laid), hatching success (young hatched/eggs laid) and fledging success (young fledged/young hatched). We calculated coefficients of variation of breeding parameters for each year as the standard deviation divided by the mean and multiplied by 100. From 1992, most young were ringed at the nest when 4–7 weeks old. We weighed each young (with a Pesola spring balance, to the nearest 10 g), recorded their rank within the brood (hatching order), and measured their wing length (with a ruler, to the nearest mm).

BEHAVIOURAL OBSERVATIONS

We studied the behaviour of ospreys in 1977, 1979, 1981, 1991, 1993 and 1995–97 using a focal animal sampling methodology. Study pairs were selected for ease of observation and access to viewpoint. Observations were made with a $\times 20$ –60 telescope at a distance of ≈ 100 –400 m from study nests, and from a hide when the observer was <250 m from the nest (Bretagnolle & Thibault 1993; Mougeot *et al.* 2002). As in most raptors, food provisioning to the female and nestlings is mainly by males. During focal observations, we recorded all fish deliveries, territorial intrusions and interactions (i.e. the entry of a non-mate osprey into the breeding territory, which resulted in conspicuous defence or protection displays by pair members; Bretagnolle & Thibault 1993). A total of 267 focal observations (2206 h) were conducted on 34 pair/years between 1977 and 1997. Behavioural observations lasted 3–5 h on a given day, and each pair/year was observed 66 h on average. We used a rotational schedule to cover all daytime periods on consecutive watches. For the analyses, we summarized the data by averaging frequency of prey deliveries or territorial intrusions for a given pair in a given year and period (pre-laying/incubation vs. chick rearing). Interactions are more frequent in the pre-laying/incubation period, while feeding rate is higher during the chick-rearing period (Mougeot *et al.* 2002). Nests were observed during chick-rearing in all years and during incubation only in 1991–97. We tested whether hatching success and fledging success were related to the frequency of interactions during the incubation and chick-rearing periods, respectively.

DIET ANALYSES

In 1983–92 and 1996–98, food remains were collected systematically at the nest when the young were 4–7 weeks old and ringed. Samples were collected for 57 pair/years on 22 different nest sites. Fish remains were identified from reference collections. Although ospreys' diet in Corsica includes 12 species of fish (belonging to six families), mullets (four species, family Mugilidae) and bream (two species, family Sparidae) accounted for 86% of fish caught (Francour & Thibault 1996). Mulletts are the only fish known to be resident, scoaling and spending a significant proportion of time close to the surface (Francour & Thibault 1996). Mulletts alone accounted for 75% of prey remains. A total of 590 fish remains were identified and assigned to one of two genera (*Diplodus* and *Mugil*, in particular *Mugil cephalus*). The size of opercula of mulletts was also measured as an index of fish size (following Desse, Desse-Berset & Rocheteau 1987). A total of 227 opercula were measured from 56 pair/years (range 1–11 territories per year).

STATISTICAL ANALYSES

We used generalized linear models (GLM) and generalized linear mixed models (GLMM) (Genmod and Glimmix procedures, respectively; SAS 2001) to analyse the data. Dependent variables were fitted to models using the following error distributions. Normal error distribution: average distance to nearest neighbour; yearly average laying date; clutch size; hatching; fledging or breeding success; body mass of fledging. Poisson error distribution: counts of eggs laid; young hatched and fledged. For analyses of breeding success at the pair level, we fitted response variables to a binomial error distribution, using hatch brood size/clutch size for hatching success; number of young fledged/hatch brood size for fledging success; and number of young fledged/clutch size for breeding success.

We used GLMM to analyse breeding success data at the nest level, or data from focal observations (prey delivery and interaction rates). All these models included the variable 'nest' as a random effect, to account for variations at the level of territories, and to account for the fact that the same birds probably bred repeatedly at the same nest sites (Poole 1989).

Population growth rate (r) between years t and $t + 1$ was calculated as $r = \log_e(N_{t+1}/N_t)$. N_t here is the total number of pairs at year t , including breeders and territorial non-breeding pairs (Taylor 1994). Density dependence was examined by fitting regression between r and either population size (total population size of original area) or average population density at year t (Caughley 1980). The use of linear regression techniques to test statistically for density dependence in population growth rate, has been criticized because of autocorrelation (Lande *et al.* 2003) and measurement errors (Griffiths 1998; Krebs 2003). In our study, we can be confident that our counts are exact counts, thus we minimized measurement error problems. We also used Monte Carlo simulation (Dennis & Taper 1994) to account for autocorrelated variables. All statistical analyses were performed using SAS ver. 8.01 software (SAS 2001); all tests are two-tailed.

Results

TRENDS IN POPULATION SIZE

The Corsican osprey population increased from three to 31 pairs (for raw data see Appendix S1). Since the 1990s there have been up to 27 occupied nests (24 breeding pairs) within the same original area of coastline (Fig. 1a).

Two main phases are apparent from the time series: a period of increase, and then a period of relative stability with fluctuations in population size around 23 occupied nests (Fig. 1a). The population increase phase could be subdivided into a phase of rapid increase in population size with a decrease in distance to nearest neighbour, and a phase of clustering with a slower increase in population size and density, during which the distance to nearest neighbour did not change (Fig. 1a–c). The average number of neighbours around occupied nests increased regularly, up to an average of about three to four neighbouring pairs within 5 km (Fig. 1b). In contrast, the average distance to nearest neighbour decreased rapidly only during the early phase of the recovery and remained stable afterwards, with an average spacing between nests of 1.8 km (Fig. 1c). The exact cut-off point between the period of increase and that of stability was determined using piecewise regression on $\ln(N_t)$ with year, with

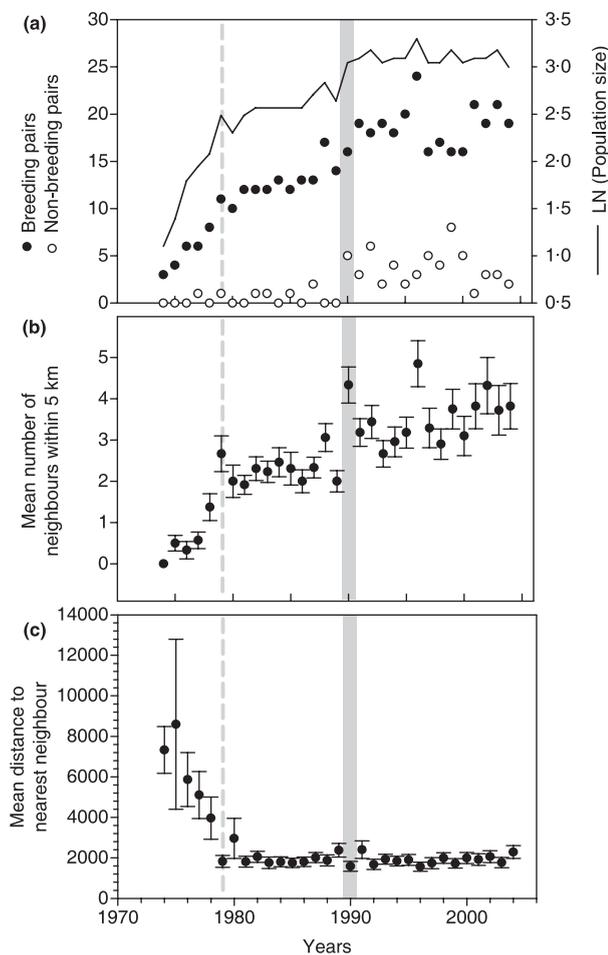


Fig. 1. Changes over time in population size and density. (a) Number of breeding pairs (black circles) and of non-breeding pairs (white circles), and total population size (log-transformed). (b) Mean (\pm SE) number of territorial pairs within a 5-km radius around occupied nests. (c) Mean (\pm SE) distance (m) to nearest territorial pair. Vertical grey bar, 1990 cut-off point (see text); vertical dashed grey bar highlights two periods during the increase phase (rapid increase followed by clustering).

years tested for cut-off point ranging from 1987 to 1995. Akaike's Information Criterion (AIC) values were lowest when the cut-off point was 1989 or 1990, and we chose to split the two periods at 1990 for homogeneity of sample sizes.

From 1990, the number of nests occupied by non-breeding pairs started to increase, while total population size remained stable (Fig. 1a). In 1974–89 the population comprised, on average, 3.7% of non-breeding pairs (range 0–14.3%), whereas after 1990 it comprised, on average, 16.4% of non-breeding pairs (4.5–33.3%; Fig. 1a).

TRENDS IN BREEDING PERFORMANCE

Breeding performance in osprey is the result of breeding effort (number of eggs laid) and breeding success (hatching and fledging success), and varies with laying date (Poole 1989; Thibault *et al.* 2001). Time-series of each of these parameters

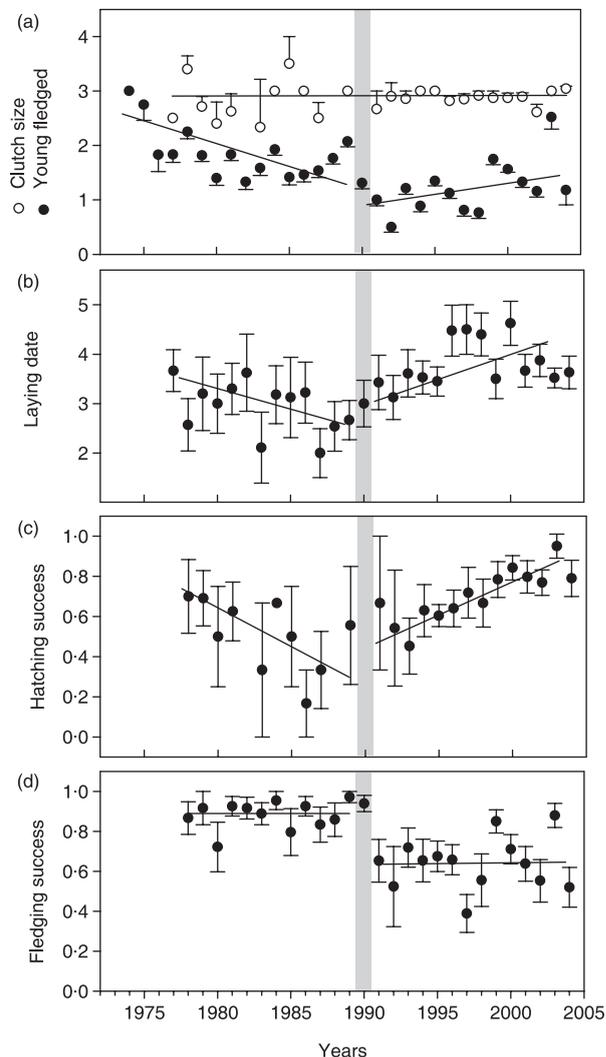


Fig. 2. Changes over time in breeding performance. (a) Mean (\pm SE) number of eggs laid (white circles) and young fledged (black circles) per pair. (b) Mean (\pm SE) laying date (1 = first week of March). (c) Mean (\pm SE) hatching success (chick hatched/eggs laid). (d) Mean (\pm SE) fledging success (young fledged/chick hatched).

are shown in Fig. 2. As population size and density increased, the average productivity per breeding pair declined from 1974 to 2004 (GLM: $F_{1,30} = 10.88$, $P < 0.001$; Fig. 2a), while clutch size remained fairly stable over the same period ($F_{1,24} = 0.46$, $P = 0.501$; Fig. 2a). We further tested each breeding parameter for differences between the two periods highlighted above (1974–89 vs. 1990–2004; effect of period and year) and for differences in linear trends before and after the 1990 cut-off point (period \times year interaction). Mean laying date overall increased during the study period, with pairs laying approximately 2 weeks later in the late 1990s than in the late 1970s (Fig. 2b). Variation in average laying date differed between periods, and trends differed between the two periods (period, $F_{1,24} = 4.18$, $P = 0.052$; year, $F_{1,24} = 4.47$, $P < 0.05$; interaction, $F_{1,24} = 5.03$, $P < 0.05$). Between 1974 and 1989, laying tended to be earlier every year, whereas over the period 1990–2004, average laying date was delayed every year (Fig. 2b). A similar

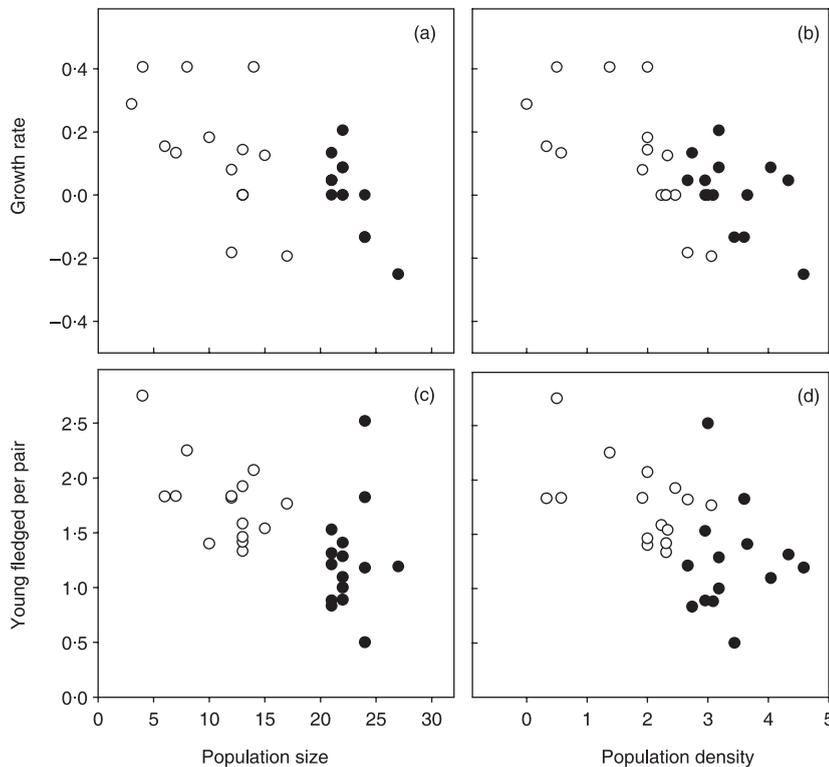


Fig. 3. Density dependence in population growth rate and productivity. (a,b) Relationship between population growth rate [$r = \log_e(N_{t+1}/N_t)$] and population size (number of territorial pairs) and density (mean number of neighbours within 5 km of active nests) in year t . (c,d) Relationship between mean number of young fledged per pair in year t and population size and density in year t . Years before 1990, white; years after 1990, black dots.

pattern was found for hatching success (period, $F_{1,21} = 19.69$, $P < 0.001$; year, $F_{1,21} = 17.63$, $P < 0.001$; interaction, $F_{1,21} = 20.90$, $P < 0.001$). Hatching success decreased throughout 1974–89, but recovered after 1990, and increased regularly during 1990–2004 (Fig. 2c). In contrast, fledging success was significantly higher in 1990–2004 than in 1974–89, with no obvious linear trends in each period (period, $F_{1,24} = 37.29$, $P < 0.001$; year, $F_{1,24} = 0.39$, $P = 0.540$; interaction, $F_{1,24} = 0.00$, $P = 0.956$; Fig. 2d). Overall variation in productivity (number of young fledged per pair) was explained by period ($F_{1,27} = 11.39$, $P < 0.01$), year ($F_{1,27} = 10.25$, $P < 0.01$) and period \times year interaction ($F_{1,27} = 10.39$, $P < 0.01$). Between 1974 and 1989, productivity declined regularly, but the trend changed after 1990, with a slight recovery in productivity between 1990 and 2004 (Fig. 2a).

DENSITY DEPENDENCE ON POPULATION GROWTH RATE

The regression of $\ln(N_t)$ over time showed a typical logistic population growth indicative of density-dependent regulation (Fig. 1a). Population growth rate was significantly and negatively related to density in year t , either measured by population size (number of occupied nests, $F_{1,29} = 15.79$, $P < 0.001$; Fig. 3a) or average population density (average number of neighbours within 5 km radius, $F_{1,29} = 20.98$, $P < 0.001$; Fig. 3b). The density-dependence relationship appeared to be linear in both cases (Fig. 3a,b). Using Monte Carlo simulations did not change the results, with exact P values (two-sided) of 0.001 for both measures of density. Based on the shape of the relationship, the carrying capacity

for the original area is estimated at about 21 territorial pairs, and $r_{\max} = 0.31$ for territorial pairs (Fig. 3a,b).

We compared the slope and intercept of density-dependence relationship between the two periods (before and after 1990). There was a slight effect of period on the density-dependence relationship when using population size ($F_{1,29} = 8.9$, $P < 0.001$; comparison of slopes, $F_{1,29} = 3.35$, $P = 0.082$; comparison of intercept, $F_{1,29} = 4.55$, $P < 0.05$), but no effect of period when using average population density ($F_{1,29} = 6.9$, $P < 0.01$; comparison of slopes, $F_{1,29} = 0.23$, $P = 0.637$; comparison of intercept, $F_{1,29} = 0.42$, $P = 0.521$).

DENSITY DEPENDENCE ON REPRODUCTIVE PARAMETERS

Most breeding performance parameters were density dependent (Table 1), except clutch size. Laying date was positively related to population size and density. Conversely, productivity and fledging success showed negative relationships with both population size and average population density. Hatching success was positively related to population size and average density, although the relationships were not statistically significant (Table 1).

Coefficients of variation of productivity tended to increase with density (total population size, mean nn5k), but not significantly so (Table 1). Coefficients of variation in hatching success were not significantly related to density (Table 1); in contrast, variance in fledging success was positively related to density (Table 1).

We also tested for an effect of density on the body mass of young at fledging, using a mixed model with territory

Table 1. Density dependence in average breeding parameters of osprey in Corsica, 1974–2004, and their variance (coefficients of variation)

Breeding parameters	Population size				Population density			
	<i>F</i>	d.f.	<i>P</i>	Slope ± SE	<i>F</i>	d.f.	<i>P</i>	Slope ± SE
Year averages								
Productivity	22.42	1,30	<0.001	-0.056 ± 0.012	17.64	1,30	<0.001	-0.289 ± 0.069
Laying date	9.14	1,27	<0.01	0.061 ± 0.020	5.24	1,27	<0.05	0.281 ± 0.123
Clutch size	0.04	1,24	0.852	-0.002 ± 0.012	0.01	1,24	0.910	-0.008 ± 0.069
Hatching success	3.21	1,24	0.083	0.011 ± 0.006	4.13	1,24	0.061	0.072 ± 0.035
Fledging success	14.86	1,27	<0.001	-0.018 ± 0.004	9.09	1,27	<0.01	-0.086 ± 0.029
Coefficients of variation								
Productivity	3.65	1,26	0.070	1.698 ± 0.889	2.83	1,26	0.108	8.752 ± 5.201
Hatching success	0.52	1,22	0.485	-1.166 ± 1.620	0.99	1,22	0.339	-9.531 ± 9.571
Fledging success	6.17	1,26	<0.05	1.998 ± 0.805	4.62	1,26	<0.05	10.224 ± 4.758

Density each year was measured either as total population size within the original area (see Methods) or as population density (average number of occupied nests within a 5-km radius around each active nests; see Appendix S1 in Supplementary material).

included as a random factor. Variation in (log-transformed) body mass of young at fledging was significantly explained by the age at which the young were weighed (mixed model, $F_{1,175} = 20.21$, $P < 0.001$); their wing length ($F_{1,175} = 89.55$, $P < 0.001$); and their rank within the brood ($F_{2,175} = 12.55$, $P < 0.001$), but was not significantly explained by population size ($F_{1,175} = 0.12$, $P = 0.743$) or density ($F_{1,175} = 0.10$, $P = 0.768$) after controlling for these variables.

Comparisons between years thus indicated significant density dependence in productivity, laying date and fledging success, but no significant density dependence in clutch size, hatching success or condition of young at fledging (body mass corrected for wing length as an index of size).

We further analysed whether breeding performance at the nest level varied with local density within year, using the number of neighbours within 5 km as a measure of local density for each breeding pair. To do so, we used mixed models that included nest as a random effect, and we controlled for differences between years by including year as a fixed effect. Relative within-year productivity (young fledged per pair) was significantly negatively affected by local density ($F_{1,51} = 5.80$, $P < 0.05$), but relative laying date ($F_{1,69} = 0.18$, $P = 0.672$), clutch size ($F_{1,28} = 2.28$, $P = 0.145$) and fledging success ($F_{1,241} = 1.37$, $P = 0.243$) were not. However, relative hatching success was significantly negatively related to local density ($F_{1,145} = 4.24$, $P < 0.05$), with pairs breeding at higher density achieving a relatively lower hatching success than others breeding at higher density in a given year (Fig. 4a). Comparisons within years thus indicated density-dependent depression in productivity and hatching success.

INTERFERENCE COMPETITION AND FOOD DEPLETION

The rate at which male ospreys provisioned fish to their female and young increased during the study period (1977–97, GLMM with territory as a random effect; year effect, $F_{1,25} = 6.52$, $P < 0.05$; Fig. 5a). Provisioning rates averaged 0.198 ± 0.127 fish deliveries h^{-1} in 1977–81 ($n = 204$ focal

observations on 11 pairs) compared with $0.258 \pm 0.229 \text{ h}^{-1}$ in 1991–97 (68 focal observations on 23 pairs).

Between 1984 and 1998, the percentage of mullets in the remains decreased ($F_{1,11} = 11.67$, $P < 0.01$; Fig. 5c), but their average size increased significantly (mixed model with territory as a random effect; year effect: $F_{1,207} = 37.99$, $P < 0.001$; Fig. 5b). Average fish size was negatively related to mean laying date ($F_{1,11} = 24.16$, $P < 0.001$), indicating that ospreys fed on larger fish in years when they bred later, conversely to diet composition ($F_{1,11} = 2.84$, $P = 0.129$). The average percentage of mullets in the diet tended to be negatively related to population size ($F_{1,11} = 4.47$, $P = 0.061$) but the average size of fish was not ($F_{1,11} = 2.17$, $P = 0.177$).

Interaction rate with other ospreys (between breeders and non-breeders or neighbouring breeding birds) increased six-fold between 1977 and 1997 (GLMM with territory as a random effect; year effect, $F_{1,13} = 8.07$, $P < 0.01$; Fig. 5d), from 0.101 ± 0.144 interactions h^{-1} in 1977–81 to $0.623 \pm 0.692 \text{ h}^{-1}$ in 1991–97. Mean yearly interaction rate was positively correlated with (log-transformed) population size ($F_{1,6} = 12.86$, $P < 0.05$) and density (mean NN5k, $F_{1,6} = 10.22$, $P < 0.05$). Within years, pairs breeding at higher density also tended to experience more frequent territorial intrusions (mixed model with territory and year as random effects; NN5k, $F_{1,6} = 5.15$, $P = 0.061$). The hatching success of individual pairs was negatively related to the frequency of territorial interactions at the breeding sites during incubation (GLMM with territory and year as random effects, $F_{1,5} = 13.77$; $P < 0.05$; Fig. 4b), but fledging success was not significantly related to interaction rate during chick rearing ($F_{1,3} = 2.01$; $P = 0.256$).

Discussion

EXISTENCE AND TYPE OF DENSITY DEPENDENCE

Over the past 30 years, the osprey population of Corsica has recovered from near-extinction (three pairs left in 1974), with

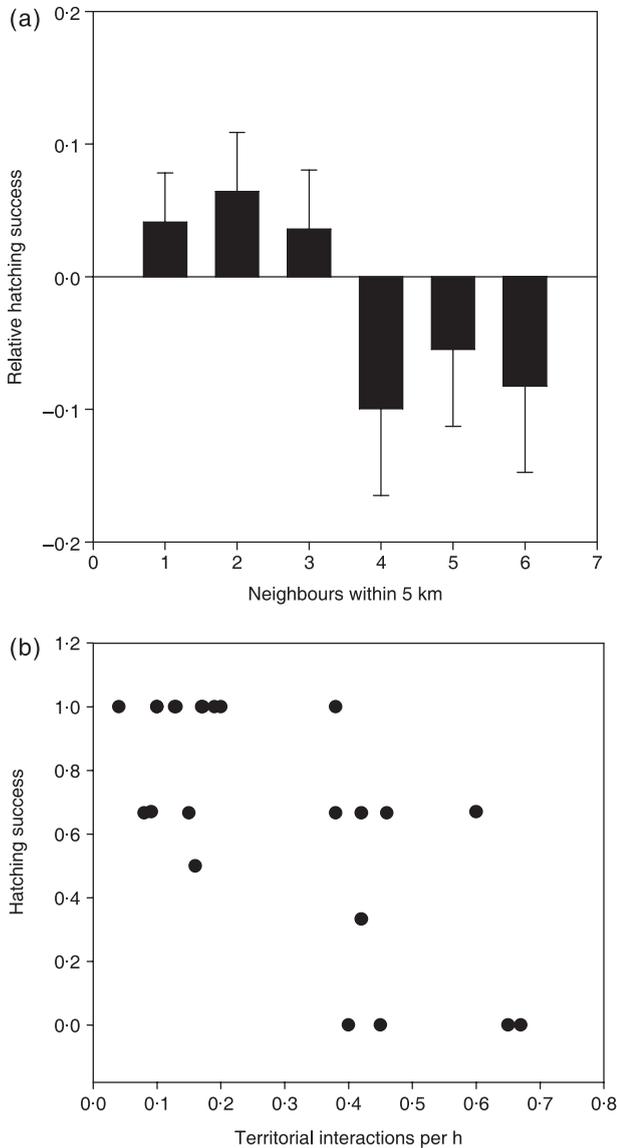


Fig. 4. Variation in hatching success (mean \pm SE) according to (a) local breeding density (number of breeding neighbours within a 5-km radius; relative hatching success is hatching success corrected for average hatching success in a given year); (b) frequency of interaction with conspecifics during incubation period and hatching success of breeding pairs ($N = 22$ breeding pairs, years 1991–97).

numbers increasing tenfold. This recovery has, however, been heterogeneous in both space and time. Spatially, during the first 17 years, all pairs have remained exactly in the original area of coastline (Thibault & Bretagnolle 2001). Since then, no more than four pairs have bred outside this original area, despite a further 50% increase in population size. Temporally, the recovery has been two-phased: during the first 15 years, the population grew at $\approx 15\%$ per year; since then, it has stabilized. The population increase followed a clear logistic pattern, which is best interpreted as a sign of direct density-dependent population regulation. Population growth rate was negatively related to population size in the stable phase.

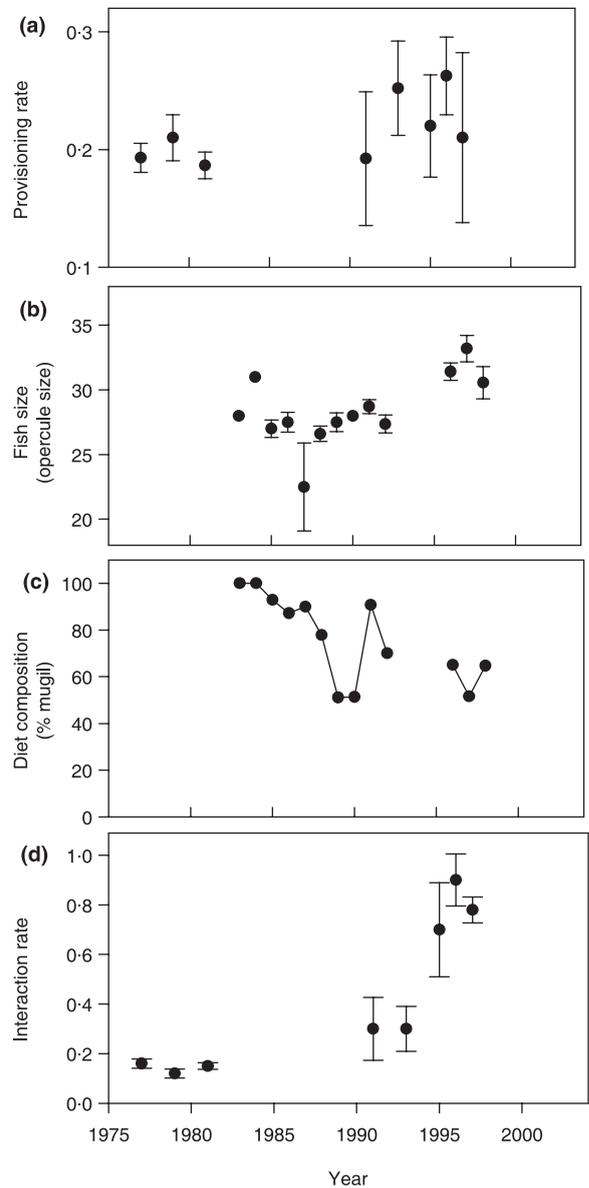


Fig. 5. Changes over time in fish provisioning rate, fish size and interaction rate with conspecifics. (a) Mean (\pm SE) number of fish deliveries h^{-1} per active nest. (b) Mean (\pm SE) size (mm) of opercula of fishes (mullet) collected in active nests. (c) Mean proportion of mullet in the diet. (d) Mean (\pm SE) interaction rate with conspecifics (territorial interactions h^{-1} per nest).

Monte Carlo simulations (Dennis & Tapper 1994) indicated that the relationship between population growth rate and density was not an artefact of autocorrelated data. Therefore the population was regulated after 1990. The density-dependent relationships showed different slopes and intercepts before and after 1990, suggesting that different mechanisms may have been operating, and/or that the carrying capacity changed during the recovery.

Long-term population monitoring is available for several other osprey populations (Schmidt, Dennis & Saurola 2001). These populations increased by 1–17% $year^{-1}$ (Thibault & Bretagnolle 2001), with the smallest growth rates being found

in the largest breeding populations (northern Europe). The rate of initial population increase found in Corsica (15%) is similar to that found in other populations (e.g. 17% in Oregon, Witt 1996; 13% in Scotland, Dennis 1995; 16% in central France, Thiollay & Wahl 1998). However, in none of these did reproductive rate decrease with increasing density (Witt 1996; Thiollay & Wahl 1998; Steen & Hansen 2001; Dennis & McPhie 2003). For instance, while the Scottish population increased from a single pair in 1954 to 145 pairs in 2000, no consequences for breeding success have yet been detected (Dennis & McPhie 2003). Unlike the Corsican ospreys, those populations are still increasing and may not have yet reached carrying capacity. They are all continental (occupying lakes or river systems), which differs from the linear coastal marine habitat of Corsican ospreys, with small foraging areas (deep sea ≈ 1 km offshore) and limited suitable breeding habitat. This may have influenced the intensity of intraspecific competition on both foraging and breeding sites.

Competition between individuals, either for food or for breeding sites, often determines the distribution and density of animal populations (Milinski & Parker 1991; Kacelnik, Bernstein & Krebs 1992). In birds, two types of density-dependent process have been identified: regulation by intraspecific competition for food (Lack 1966; Martin 1987) and regulation through social intolerance and territorial behaviour (Smith, Arcese & Hochachka 1991; Mougeot *et al.* 2003). Many raptor populations show remarkably stable population sizes (Lack 1966; Newton 1991). Stabilizing population regulation by food supply might thus be particularly intense in raptors through a process that involves the dispersion of breeders as a consequence of territorial behaviour (Newton 1979, 1998), although nest-site availability may also affect carrying capacity (Newton 1991). Evidence from Corsica suggested that nest-site limitation probably played a major regulatory role after the recovery. Providing new, artificial nests, outside the core area allowed new pairs to settle rapidly and breed (see below). After 1990, the non-breeding part of the population increased significantly. Crowding within the core area and the lack of nesting sites outside the core area, together with a strong conspecific attraction in this raptor, could explain this increase in non-breeding osprey numbers.

DENSITY DEPENDENCE IN BREEDING PERFORMANCE

We found that several breeding parameters were negatively related to average density (or total population size). A negative relationship between increasing density and breeding success has been found repeatedly in raptor species (Houston & Schmutz 1995; Carrete *et al.* 2006; Ferrer, Newton & Casado 2006), and have been explained in terms of either reduced prey availability (Houston & Schmutz 1995) or increased use of territories of lower quality (Ferrer *et al.* 2006) together with a negative impact of non-breeders (floaters) on the performance of breeding birds (Carrete *et al.* 2006).

A negative relationship between fecundity and density may result from density dependence or from habitat heterogeneity

(at low density the best habitats are occupied; Ferrer & Donazar 1996) or from a buffer effect (lower-quality individuals occupy lower-quality sites thus reducing average demographic rates; Sutherland & Norris 2003; Ferrer *et al.* 2006). Sequential habitat occupancy and decline in breeding performance may therefore be an alternative explanation, as the increase in the number of pairs may have spread birds to poorer habitats. In that case, however, the birds in good habitats (presumably those breeding on territories that were recolonized first) would show a constant breeding performance, as has been found in some colonial seabirds (Harris *et al.* 1997) and raptors (Mearns & Newton 1988; Ferrer & Donazar 1996). In Corsican ospreys, we had little evidence that variance in productivity increased with density (Table 1), although we observed a positive trend. We found that variance in hatching success was not related to density, whereas variance in fledging success increased with density. Thus habitat heterogeneity might explain density dependence in fledging success, but not in productivity and hatching success. We also found that not all fecundity parameters decreased with increasing density: for instance, laying date and hatching success showed opposing trends before and after 1990. Osprey breeding success, and in particular hatching success, increases with age and experience (Thibault *et al.* 2001). Thus an increasing proportion of young, inexperienced pairs could account for a lower hatching success during the initial increase in population size, but probably not after the population size stabilized, when most breeders were old and experienced.

Adult survival can also be negatively related to population density (Altwegg *et al.* 2003; Nicoll *et al.* 2003) or local density (Serrano *et al.* 2005). This could remain a potentially important factor for population regulation, especially for a long-lived bird like the osprey, but this could not be evaluated in our study.

TROPHIC VS. SOCIAL PROCESSES INVOLVED IN DENSITY DEPENDENT FECUNDITY

We evaluated both the food depletion and behavioural interference hypotheses for density dependence in fecundity. Our data supported the latter for the observed reduction of fecundity, and hatching success in particular, with increasing density. In Corsica, ospreys feed their chicks with sea fishes, mainly mullets (Francour & Thibault 1996). We found that the rate at which male ospreys provisioned fish to their female and young, as well as the average size of fish collected at nest sites at the end of the breeding season, increased with population density. This might be explained by an increase in fish abundance, or increased use of public information about good foraging areas with increasing osprey numbers. We had no evidence that the condition of young at fledging was negatively related to density, as would also be expected under a food depletion mechanism. The only significant change during the time series was a reduction in the percentage of mullet, which is not necessarily a sign of food depletion. We lack detailed data on fish abundance, but food availability might have increased during the study period as a

consequence of the legal protection of the original breeding area, which was declared as a Nature Reserve in 1975, with strict fishing restrictions. The change in density dependence relationships before and after 1990 also suggested that the carrying capacity of the original area might have increased by three or four pairs during the study period.

During the population recovery, the frequency of territorial intrusions and behavioural interference with conspecifics dramatically increased (five- to sevenfold), presumably as a consequence of decreasing average distance between active nests and an increase in non-breeding individual numbers. Close proximity of neighbour nests (sometimes as close as 200 m) also results in increased risk of extra-pair copulation (Birkhead & Møller 1992) and can elicit increased mate guarding, which can be costly in male raptors, as shown in ospreys (Mougeot *et al.* 2002). Interference is supposed to decrease rapidly with the distance to the nearest neighbour nest (Newton 1979), and probably for this reason has not been very much studied. However, in closed populations (such as those on islands) or in colonial species, interference might be much more significant. Previous work on Corsican ospreys has shown that interaction rate with conspecifics during the pre-laying period increases with local density, and is associated with increased male attendance, reduced food provisioning, and reduced copulation rate and success (Mougeot *et al.* 2002). Here we showed that hatching success was negatively related to local density within years, and to the frequency of territorial intrusions and interactions with conspecifics during pre-laying and incubation. Interactions with conspecifics may have negatively affected hatching success, directly (disturbance during incubation), or indirectly via a reduction of the number of successful copulations during the pre-laying period, reducing egg fertilization and hatching success (Mougeot *et al.* 2002).

THE ROLE OF BEHAVIOUR IN DENSITY DEPENDENCE: CONSEQUENCES FOR CONSERVATION MANAGEMENT

By incorporating behaviour into the traditional demographic approach of density dependence, we found that regulation probably occurred mainly through competition for nesting sites. As the population grew, the number of non-breeding floaters increased, especially after 1990 when the carrying capacity was reached. At that point, immature birds could not establish new breeding sites. Because the osprey is gregarious, floaters have been attracted to, and frequently visited, breeding pairs. This led to behavioural interference, which contributed to reducing fecundity. Intrusions by non-breeders (or floaters) have seldom been identified as a behavioural mechanism that depress fecundity (but see Smith *et al.* 1991; Carrete *et al.* 2006). Floaters were nonetheless shown to affect population growth rate in several territorial and non-territorial species (Lopez-Sepulcre & Kokko 2005). Understanding the role of interference behaviour in population regulation provided new insights into population management. Once the key role of non-breeders had been identified, we suggested that attracting non-breeders to other areas would reduce

interference in the original area. This was achieved from 1991 (first trial) to 1998, with the establishment of nine artificial nests and decoys outside the original area (V.B. and J.-C.T., unpublished data). Between 1991 and 1995, five territories were established outside the original area, and since 1995, average pair productivity, as well as hatching success, have stabilized, possibly as a consequence of reduced numbers of non-breeding birds by emigration to these new areas.

By combining a unique data set of long-term population counts with detailed data on breeding performance, diet and behaviour, we have highlighted how behavioural interference can influence density dependence in productivity. Such a mechanism might not be uncommon in natural populations, especially in species in which competition for nest sites is intense and negatively affects breeding success, or in species such as raptors, in which floaters often account for a large proportion of the population at high density (Kenward *et al.* 2000; Lopez-Sepulcre & Kokko 2005).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Count data for the osprey population in Corsica, 1974–2004, and population parameters used in this study.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.1418.x>

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