Long-term breeding demography and density dependence in an increasing population of Golden Eagles *Aquila chrysaetos*

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Few studies have quantified the dynamics of recovering populations of large raptors using long-term, spatially explicit studies. Using data collected over 37 years in the western Italian Alps, we assessed the trends in distribution, abundance, fecundity and breeding population structure of Golden Eagles *Aquila chrysaetos*. Using the spatial distribution of territory centroids in 2007, we found that the spatial distribution of eagle territories was over-dispersed up to 3 km. Although population size and total productivity increased from 1972 to 2008, the proportion of pairs that laid eggs showed a strong decline, falling to no more than 50% after 2003. On average, 15% of successful nests produced two fledglings, and productivity also declined over time. No significant relationship between population growth rate and total population size was detected, but the percentage of pairs that bred and breeding success showed evidence of density dependence, as they declined significantly with increasing density. Our results suggest that density dependence, operating across heterogeneous habitats, is currently regulating this population, while the carrying capacity may still be increasing. This may explain the apparent paradox of reduced breeding effort despite increasing total productivity.

Keywords: buffer effect, habitat heterogeneity, Italian Alps, long-term study, population dynamics, population regulation.

Population regulation through density-dependent processes and its effects on demographic parameters are central issues in ecological theory (Sibly *et al.* 2005). To measure density dependence in the wild, one needs populations that have increased in a relatively constant environment to a size at which demographic density dependence halts population increase (Sutherland & Norris 2002). Conservation actions taken during recent decades have allowed the recovery of several raptor species through legal protection from persecution, population reinforcement, the banning of pesticides and poisoning, or the establishment of protected areas (e.g. Donazar 1990, Sinclair 1996, Sutherland &

Norris 2002, Nicoll *et al.* 2003). However, although some studies (Carrete *et al.* 2005, Bretagnolle *et al.* 2008, Evans *et al.* 2009, Krüger *et al.* 2010) have addressed the question of the demography of increasing large raptor populations, offering an opportunity to examine factors involved in the regulation of populations, fewer (but see Bretagnolle *et al.* 2008) have actually examined the dynamics of populations close to carrying capacity.

The Golden Eagle *Aquila chrysaetos* is a large raptor distributed at low densities in the Palaearctic, Nearctic and Africa (Ferguson-Lees & Christie 2001). In Europe, most populations declined over the last two centuries (Watson 1997, Bechard & McGrady 2002) mainly through human persecution (Whitfield *et al.* 2004) or changes in land use (Whitfield *et al.* 2001, Bechard & McGrady 2002).

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Since the late 1970s, however, many Golden Eagle populations have recovered, although the conservation status of the species remains poor in many countries. For example, populations have increased in Italy (Fasce & Fasce 1984, 2003), France (Goar 2004), the United Kingdom (Watson 1997, Eaton *et al.* 2007), Sweden (Tjernberg 1990) and Switzerland (Haller 1988, Jenny 1992) and are apparently stable in Spain (Arroyo 2003), but are declining in several Eastern European countries (Watson *et al.* 1992, Haller 1996). In North America, the Golden Eagle population has increased (Kochert *et al.* 2002, Wheeler 2003).

Few long-term studies of population size are available for Golden Eagle (Mathieu & Choisy 1982, Watson *et al.* 1992, Haller 1996), but studies of other large raptors, such as Osprey *Pandion haliaetus* (Bretagnolle *et al.* 2008), Bearded Vulture *Gypaetus barbatus* (Margalida *et al.* 2008, Oro *et al.* 2008) [Correction made after online publication 19 May 2011 - 'Oro *et al.* 2006' changed to 'Oro *et al.* 2008'] and Spanish Imperial Eagle *Aquila adalberti* (Ortega *et al.* 2009), suggest that these species are particularly sensitive to density-dependent regulatory processes, which include regulation through intraspecific competition for food (Lack 1966, Martin 1987, Krüger & Lindström 2001, Krüger *et al.* 2010) and territorial behaviour (Smith *et al.* 1991, Sinclair 1996, Sibly *et al.* 2005, Bretagnolle *et al.* 2008). Density-dependent processes are expected to be strong in raptors because many populations show remarkably stable population sizes (Newton 1991), and it has been suggested that population regulation through food limitation should be more intense in territorial raptors than in semi-colonial or colonial species because the latter do not defend feeding territories (Newton 1979, Newton 1998). Furthermore, nest-site availability may also affect carrying capacity (Newton 1991). Using data on a population of Golden Eagles breeding in the western Italian Alps, where an annual large-scale census started in 1972, we assessed density dependence in breeding parameters and examined the underlying causes of population regulation in this study population. We first analysed this population's increase in distribution and time and assessed trends in fecundity and breeding population structure. A negative relationship between fecundity and density in a territorial species may result either from interference competition or from habitat heterogeneity (Both 1998). We assessed the two density-dependent hypotheses using the method proposed by Ferrer *et al.* (2006).

METHODS

Study species

In continental Europe, Golden Eagles are encountered at middle to high altitudes (400–2000 m asl) and usually inhabit open landscapes. Each territorial pair may have between one and 10 or more nest-sites used alternatively during consecutive breeding attempts (Watson 1997), generally located on cliffs, more rarely on trees or on the ground. In Italy, copulation starts in January, egg-laying occurs from March to early April, and fledglings leave the nest in July (latest on 12 September, P. Fasce, L. Fasce, pers. obs). [Correction added after online publication 19 May 2011 - 'A. Villers, F. Bergese, V. Bretagnolle' removed from pers. obs. citation]. Fledglings stay on their natal territory for about 2–3 months before dispersing (Soutullo *et al.* 2006). Plumage variation allows adult (> 6 years old), sub-adult (4–5 years old), immature (3 years) and juvenile birds to be distinguished (Watson 1997). Eagles prey on mid- to large-sized birds and mammals such Alpine Marmots *Marmota marmota*, Mountain Hares *Lepus timidus*, ungulates and grouse, but may also feed on carrion of large wild or domestic mammals in winter (Watson *et al.* 1993, Watson 1997).

Study area

The study area was a mountainous region of approximately 8600 km^2, ranging from the Mediterranean Sea to the northern Italian Alps (Fig. 1). The climate varies from Mediterranean to continental. The vegetation is characteristic of the Alpine altitudinal succession, from woods to alpine grasslands. Several national and regional parks and nature reserves were included in the area.

Surveys and monitoring

Fieldwork was carried out almost entirely by the same observers over the full course of the study. Suitable nesting habitat was identified on maps according to landscape structure (cliffs surrounded by open habitats) and searched. Searches for nests were conducted in February and March when Eagles are building nests and when they spend much of their day near the eyries. Outside this period, potential nesting cliffs were searched for signs of past nests or nests that were recently
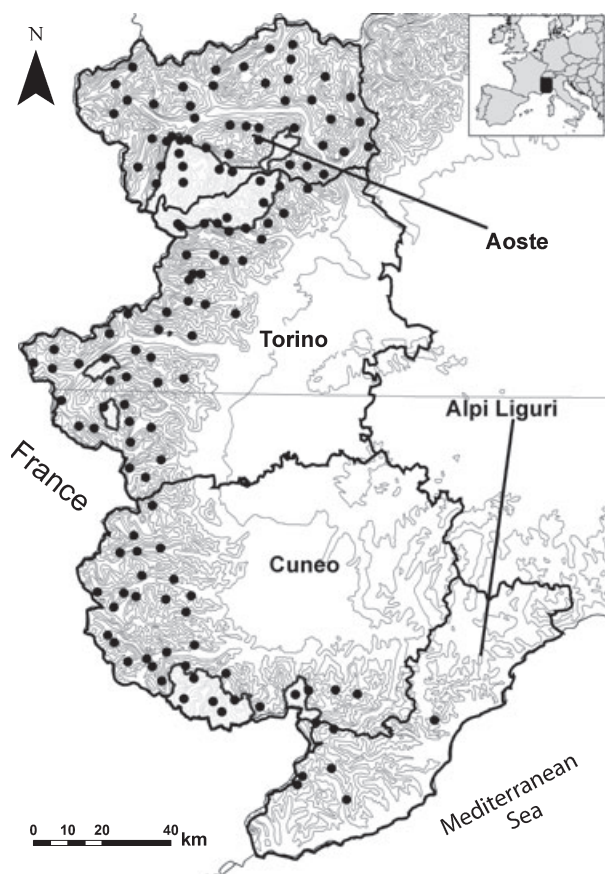
Figure 1. Centroids of known Golden Eagle territories in 2007 in the western Italian Alps.

renovated, indicating the presence of a breeding pair.

Nest contents were not always easily visible, and for about 8% of the nests we were only able to confirm breeding when chicks became visible. Egg-laying was checked in March–April, production of chicks was checked in May–July, and fledgling counts were made in August and September. Nests were usually visited at least three times per year and observations were made from 100 to 400 m away in conditions of reasonable light. In some instances, changeover of breeding parents during incubation and brooding or other behaviours helped to determine the breeding stage.

Breeding parameters and population size: definition and calculation

We adopted the terminology of Steenhof *et al.* (1997), except for the definition of breeding suc-

cess (see below). As Eagles were not individually marked, characterizing territories was to some extent arbitrary. We defined a territory as a geographical area in which one nest or more are found but where only one territorial pair nests each year (this is the equivalent of nest area in Pedrini & Sergio 2001). A territorial pair was defined as pair holding and defending at least one nest, or showing nest-building behaviour, and population size was taken to be the total number of territorial pairs. A breeding pair was defined as a territorial pair that laid at least one egg; otherwise, a pair was considered a non-breeding pair. Breeding failure may occur during egg-laying or incubation (when eggs do not hatch), or during chick-rearing (when chicks do not fledge). Successful pairs were those with at least one young fledged (> 51 days old). Breeding success, usually defined as the number of young fledged per egg laid, could not be estimated in most cases because the number of eggs (which in the Golden Eagle is usually two, but sometimes one or three) was unknown. We therefore measured apparent breeding success as the number of pairs that fledged at least one young out of the number of pairs that laid eggs. We also used a measure of average productivity, defined as the number of young fledged per surveyed pair. Total productivity was defined as the total number of fledglings produced in a given year.

Statistical analyses

Given the large size of the study area, some territorial pairs were inevitably missed. This was certainly the case before 1985, when only a fraction of territories were known. It is therefore difficult to assess trends in the population before this date. It is likely that at that time the Golden Eagle was already widespread throughout the Alps, with a tentative estimate of 70–90 breeding pairs at the start of the study in the 1970s. The first census of the Italian population was published in 1984, at which time the population of our study area was 82–105 pairs (Fasce & Fasce 1984). The population in the whole Italy in 2007 was estimated at 547 pairs (Fasce & Fasce 2007). Annual surveys were standardized from 1985 onwards, with poorer data quality previously. For this reason, statistical analyses have only been conducted for data from 1985 to 2008, but results are presented graphically for both 1972–2008 and 1985–2008 (see also Table 1).

Table 1. Mean, standard deviation, minimal and maximal value of breeding parameters for 1972–84, 1985–2008 and the whole study period.

Parameter	1972–84				1985–2008				1972–2008			
	Mean	sd	Min.	Max.	Mean	sd	Min.	Max.	Mean	sd	Min.	Max.
Proportion of checked pairs	0.74	0.12	0.60	1.00	0.91	0.06	0.76	0.99	0.85	0.06	0.60	1.00
Proportion of checked pairs at incubating stage	0.61	0.14	0.44	1.00	0.75	0.09	0.57	0.92	0.70	0.08	0.44	1.00
Proportion of incubating pairs	0.68	0.13	0.44	1.00	0.52	0.10	0.41	0.69	0.58	0.08	0.41	1.00
Proportion of successful pairs	0.63	0.13	0.32	1.00	0.36	0.10	0.23	0.49	0.46	0.08	0.23	1.00
Breeding success	0.91	0.08	0.73	1.00	0.70	0.09	0.54	0.83	0.78	0.07	0.54	1.00
Average productivity	0.81	0.39	0.40	2.00	0.42	0.08	0.27	0.57	0.55	0.30	0.27	2.00
Mean number of young fledged by successful pairs	1.25	0.27	1.00	2.00	1.13	0.08	0.98	1.26	1.17	0.18	0.98	2.00

Annual population growth rate (r) between year t and $t + 1$ was estimated as $r = \log_e(N_{t+1}/N_t)$, with N being the total number of territorial pairs. Density dependence was assessed by fitting a regression of r on either population size (total population size of the original area; Caughley 1980) or the various breeding parameters. Trends were first inspected visually to assess whether linear or quadratic terms should be modelled. Non-parametric Spearman rank correlation was used when the parameter of interest was in the form of a frequency value (e.g. total productivity). When it was in the form of a percentage (e.g. proportion of incubating pairs, proportion of pairs with at least one fledgling), we used a generalized linear model (GLM) with the frequencies of each of the two classes, corrected for overdispersion with a quasi-binomial error distribution, which also accounted for unbalanced sample sizes among years. For average productivity, given the unbalanced samples between years, a weighted linear regression model was used. We applied Ripley's K function, which tests for point pattern distribution departure from randomness towards aggregation or regularity (Ripley & Kelly 1977) to analyse the spatial distribution of nests. Data are presented with the value of the L function, a linearized form of the K function, and a confidence envelope, which can be considered significance bands (i.e. these are not confidence intervals), computed with 200 simulations of a random Poisson point process of similar size (in our case, the same number of nests distributed under complete spatial randomness). A value of the $L(r)$ function is iteratively computed around each point (nests) at different distances r. If the L function value lies below the lower limit of the envelope, points are over-dispersed at the consid-

ered distance (repulsion between points leading to a regular distribution of nests), whereas if lying above the upper limit, they are aggregated (for an example, see Cornulier & Bretagnolle 2006).

Ferrer *et al.* (2006) proposed comparing the skewness of the distribution of productivity with changing mean productivity to assess density dependence. Contrary to mean values of productivity that can decrease similarly under both the habitat heterogeneity and individual adjustment hypotheses, changes in the skewness of the distribution of productivity indicate the process by which this decrease occurs. If skewness becomes more positive with decreasing productivity, it suggests that the shift in mean value of a particular fecundity parameter comes from a shift in the distribution of fecundity and that a buffer effect is responsible for the observed pattern of density dependence. Data were analysed using R 2.10.0 (R Development Core Team 2009).

RESULTS

Nests, territories and spatial distribution

Over the study period, each territory held between one and 12 eyries (mean = 4.9 ± 2.6, n = 107 territories, excluding the Cuneo region (Fig. 1) from the analysis because data were not available). Of the 513 observed nests, only seven (1.3%) were located in trees, all others were on cliffs. Nest altitude was on average 1676 ± 350 m (n = 505), and ranged from 350 to 2650 m asl. Using the spatial distribution of territory centroids in 2007 (mean location calculated from the position of all known nests for each territory), we found that Eagles
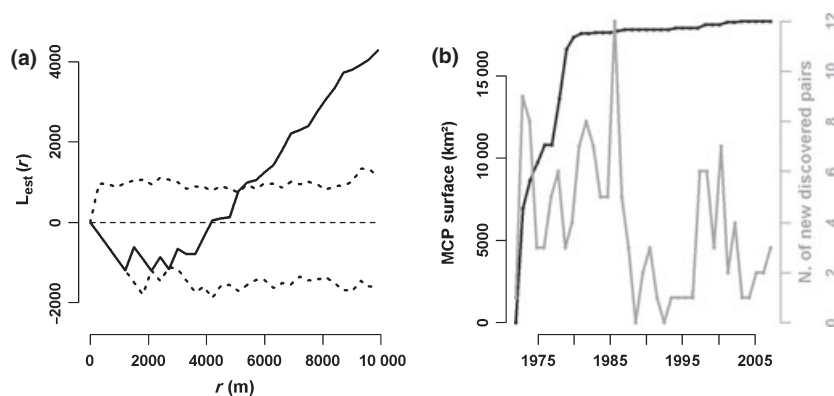
Figure 2. Spatial distribution of Golden Eagle territories in the western Italian Alps. (a) L_{est} of Ripley's K function (black line). Dashed lines enclose the confidence envelope based on 100 simulations assuming a Poisson distribution. (b) Surface of the minimum convex polygon (MCP 100%) for all known territories and number of discovered territorial pairs.

showed a strong tendency to over-dispersion at a small scale (up to 3 km, especially so below 1800 m), as expected for a territorial species, but at a larger scale, their distribution became significantly aggregated over 6 km (Fig. 2a). The average distance between territory centroids was 5492 ± 201 m in 2007.

Age structure

We knew the age category for both members of the pair in 2405 pair/year combinations. Most pairs comprised two adult birds ($n = 2296$, 95.5%), 104 involved one sub-adult/immature bird with an adult bird and five pairs were formed by two sub-adult/immature birds. Of the 104 pairs with one adult and one sub-adult bird, only 11 laid eggs, seven of them fledging one chick. The proportion of pairs formed by two adult birds was stable over the period 1985–2008 (GLM with quasi-binomial family, $F_{1,22} = 0.08$, $P = 0.78$).

Population size and trends

In the western Italian Alps, the knowledge of the population increased from one pair in 1972 to 144 in 2008 (Fig. 3a), and the number of newly discovered territories started to stabilize in 1981, declining after 1985, an indication that from that year a newly discovered pair was most certainly a new settled pair (Fig. 2b). The proportion of pairs surveyed annually gradually increased and varied from 74 ± 2% between 1972 and 1984, to 91 ± 2% after 1984 (see values, according to breeding stage, in Fig. 3a). The annual rate of population increase

over the whole study period was between 1.3 and 1.9%, depending on starting population size (respectively 70 vs. 90). Using data only from 1985 slightly increased the estimate of population growth to 2.8%. Currently and for the period 2003–2008, the rate of increase itself increased (respectively 0.7, 0.7, 1.5, 2.1 and 2.1%), indicating either that carrying capacity has yet to be achieved, or that it is increasing. Similarly, the total productivity of the entire population increased slightly (Fig. 3b; $r_s = 0.58$ for 1985–2008), again suggesting that carrying capacity may not have been reached yet.

Population breeding parameters and trends since 1972

Average breeding population parameters are shown in Table 1. Over the 37 years of monitoring (1972–2008) we were able to check 2775 pair/year combinations (2072 at the egg-laying stage; Fig. 3a). Overall, 72.4% of pairs laid eggs. However, this fell to 58.0% if the proportion of breeding attempts is calculated separately for each year, and a mean calculated from these annual values. This proportion was variable between years (Fig. 3c) and showed a strong decreasing trend (GLM, $F_{1,22} = 15.7$, $P < 0.0001$; Fig. 3c), with no more than 50.1% of territorial pairs laying eggs in 2003–2008. Similarly, the yearly proportion of territorial pairs raising at least one young, for 1972–2008 (Fig. 3c), was on average 45.7% (33.7%, 2004–2008) and showed a negative trend over the study period, although this was not significant when considering only data from 1985–2008
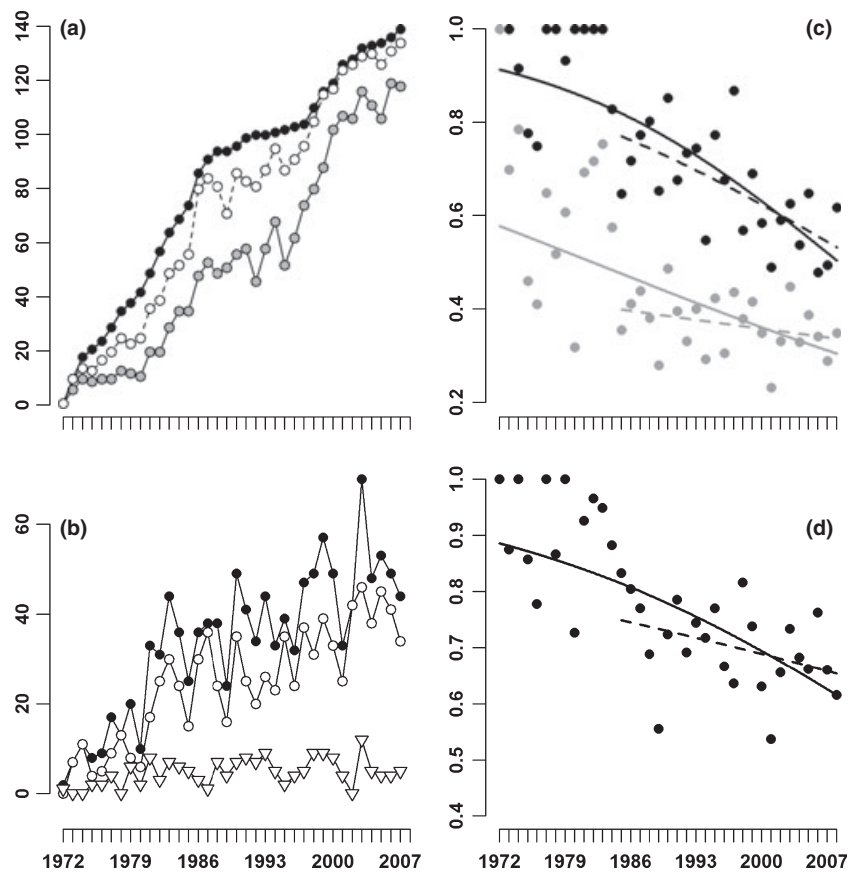
Figure 3. Trends in breeding parameters in Golden Eagle from the western Italian Alps. (a) Numbers of territories (black dots: number of known territories, white dots: number of territories surveyed at fledgling stage, light-grey dots: number of territories surveyed at incubating stage). (b) Total number of fledging (black dots), pairs with one fledgling (white dots) and pairs with two fledglings (triangles). (c) Proportion of pairs laying (black dots) or having chicks (grey dots). The continuous line indicates trend over the whole study period (1972–2008), while the dashed line indicates trend restricted to 1985–2008. (d) 'Apparent' breeding success (see Methods). The continuous line indicates trend over the whole study period (1972–2008), and the dashed line indicates trend restricted to 1985–2008.

($F_{1,22} = 2.23$, $P = 0.14$; Fig. 3c). This was not simply due to a decreasing proportion of laying pairs, as breeding success (on average 77.6%, $n = 1501$; Table 1) also declined but only marginally significantly (1985–2008 data: $F_{1,22} = 3.94$, $P = 0.06$; Fig. 3d). On average, 15% of successful nests produced two fledglings (Fig. 3b), a percentage variable between years (range 0–26%), decreasing for the whole period but not significantly since 1985 (Fig. 3d; $F_{1,22} = 2.1$, $P = 0.16$). Consequently, average productivity showed a marginally significant decline between 1985 and 2008 ($t_{22} = -1.9$, $P = 0.07$). However, the number of young per successful pair (overall average = 1.17 ± 0.17) did not show any significant trend with time for the 1985–2008 period ($F_{1,878} = 2.43$, $P = 0.12$).

Density dependence in population growth rate, and breeding parameters

There was no negative relationship between population growth rate (PGR) at year $t + 1$ and population size at year t (Fig. 4a; $F_{1,22} = 2.9$, $P = 0.10$). PGR has never been negative (Fig. 4a), as, up to now, no territory has ever been deserted, even temporarily. In contrast, two of three breeding parameters (percentage of incubating pairs and breeding success) showed evidence of density dependence, significantly decreasing with increasing total population size (Fig. 4b–d). This was the case in particular for the proportion of incubating pairs (Fig. 4c; $F_{1,22} = 45.565$, $P < 0.0001$). Negative relationships between fecundity parameters
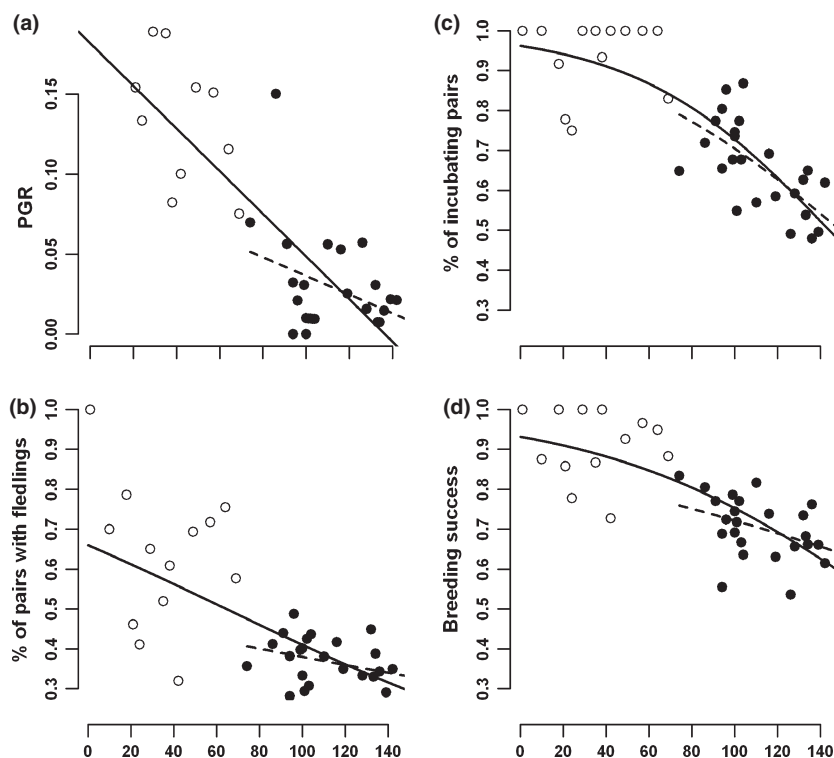
Figure 4. Density dependence in fecundity parameters. White dots refer to the period before 1985, black dots after 1985. The two regression lines indicate respectively trends over 1972–2008 (continuous line) or restricted to 1985–2008 (dashed line). PGR, population growth rate.

and density may equally result from interference competition or the buffer effect (Brown 1969) whereby, as the population approaches carrying capacity, poorer territories are used, resulting in lower breeding success, thus reducing average population fecundity. We also followed Ferrer *et al.* (2006) and used the relationship between skewness of productivity and mean productivity (Fig. 5) to test for evidence of density-dependent processes. We found a clear and significant negative relationship ($F_{1,22} = 18.9$, $P < 0.0001$, adjusted $R^2 = 0.43$).

DISCUSSION

Spatial distribution and average breeding parameters of this population of Golden Eagle are largely consistent with those of other published studies. The average distance between territory centroids was around 5.5 km, closely matching the suspected potential hunting range of the resident pair (5 km; Watson *et al.* 1992, Pedrini & Sergio 2001). Average productivity (number of fledglings per pair surveyed) was consistent with published
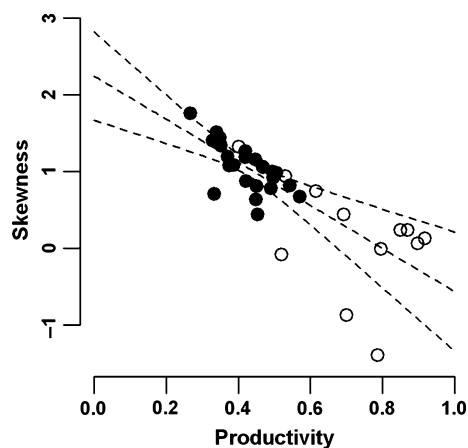

Figure 5. Relationship between average yearly productivity and skewness of productivity, white dots before 1985, black dots after 1985. Regression line and confidence interval are shown.

productivity, which ranges from 0.34 (Estève & Matérac 1987) to 0.76 (Mathieu & Choisy 1982), both estimated from populations in the French Alps, but is usually between 0.4 and 0.6 (Watson 1997, Pedrini & Sergio 2001, Fasce & Fasce 2009).

The same is true for apparent breeding success (see Fasce & Fasce 2009 for values from the entire Alps). However, comparing those results with values from other populations is only meaningful if populations are at the same level with respect to local carrying capacity. This is unlikely because Golden Eagle density and productivity have changed in recent decades all over Europe (e.g. Dennis *et al.* 1984, Jenny 1992, Haller 1996, Watson 1997), although the closest population to ours that has been studied, in the eastern Italian Alps, has not shown such changes in density (Pedrini & Sergio 2001). The latter authors reported no change over a period of 10 years, although the surveyed area was comparable in size (7600 km^2) and landscape (alpine and pre-alpine). The breeding density was lower, suggesting a lower carrying capacity, especially as productivity, which was evaluated on a sub-sample of the 46 territories, was comparable with that observed in this study.

Although there was no evidence that the surveyed population extended its distribution after 1985, and assuming that 70–90 pairs were breeding in the early 1970s, the population density of Golden Eagles across the study region roughly doubled in 37 years. This population was still increasing at the end of this period but there was no evidence of density-dependent regulation on population growth rate or on total productivity. Many Golden Eagle territories were located in protected areas, where populations of wild ungulates and marmots, the main prey of Golden Eagles breeding in the Alpine range (Fasce & Fasce 1984, Pedrini & Sergio 2001), have recovered. This certainly increased carrying capacity, at least for the western Italian Alps (see Pedrini & Sergio 2001 for a comparison of Golden Eagle prey availability in the eastern Italian Alps).

On the other hand, whereas the total number of young fledged each year increased slowly, average productivity per pair declined, suggesting density-dependent processes acting negatively upon breeding parameters. Interestingly, productivity in successful pairs remained constant over the study period, suggesting that the regulation acted on early stages of reproduction, either through interference by local pairs or floating individuals, or competition for food. Thus, there was a clear and significant negative trend in the number of pairs incubating with increased density, although the very high values found at the early stages of the study (Fig. 4a) may result from an over-representation of successful (and more easily detectable) pairs in early data. The same trend was not found for successful pairs, suggesting that brood reduction was no more common in later years than in earlier years. We have no data on adult survival, which may also be related to population density (Altwegg *et al.* 2003, Nicoll *et al.* 2003) or local density (Serrano *et al.* 2005). This could be an important factor in population regulation of a long-lived species such as the Golden Eagle, but this could not be evaluated in our study.

A negative relationship between fecundity and density in a territorial species may result either from interference competition ('individual adjustment' in Both 1998) or from habitat heterogeneity (Ferrer *et al.* 2006), also termed the buffer effect (Sutherland 1996, Soutullo *et al.* 2006). In the latter case, at low density, only the best habitats are occupied (Ferrer & Donazar 1996, Krüger & Lindström 2001, Krüger *et al.* 2010), but when population size increases, new territories will be of ever-poorer quality. Territory occupancy may then reflect either the arrival order of pairs or the quality of individuals according to their capabilities in monopolizing resources (Sutherland & Norris 2002, Ferrer *et al.* 2006). In that case, however, the birds in good habitats (e.g. often those breeding on territories that were colonized first) would show a relatively constant breeding performance, as has been found in some colonial seabirds (Harris *et al.* 1997) and raptors (Mearns & Newton 1988, Ferrer & Donazar 1996). We tested this latter hypothesis using the relationship between skewness of productivity and mean productivity. The negative relationship found between those two variables suggests regulation by habitat heterogeneity (Ferrer *et al.* 2006, 2008). Further analyses at the territory level will be needed to identify the mechanisms involved in regulation processes.

Negative density dependence in breeding success has been found repeatedly in other raptor species (Houston & Schmutz 1995, Carrete *et al.* 2006, Ferrer *et al.* 2006), and has been explained in terms of competition for prey resources (Houston & Schmutz 1995), habitat heterogeneity and the increased use of territories of lower quality (Ferrer *et al.* 2006), or interference competition (i.e. a negative impact of non-breeding, floating individuals on the performance of breeding birds) (Carrete *et al.* 2005, Bretagnolle *et al.* 2008). Adaptive restraint has also been suggested to occur

in populations at high densities where natural selection could favour the raising of fewer young of higher quality (Simmons 1993). Those individuals would live longer and thereby enjoy greater lifetime reproductive success. Golden Eagle populations breeding in the western Italian Alps have potentially reached the carrying capacity of the habitat, at least in terms of breeding sites and potential territories. Even if all potential breeding cliffs are still not used by territorial pairs, it is doubtful that such a territorial species will indefinitely bear the costs associated with high density; in other words, direct interference competition (i.e. agonistic interactions) will almost certainly affect breeding success.

The rate of increase in this Golden Eagle population was rather low when compared with other large colonial or semi-colonial raptors of the western Palaearctic whose populations have recovered over the last 30 years from near extinction. For example, Ospreys in Corsica showed a 10-fold increase over the last 30 years with a PGR of 15% (Bretagnolle *et al.* 2008, see also Thibault *et al.* 2001 for a review of increase rate in Osprey populations) and Griffon Vultures *Gyps fulvus* PGR reached 13% (Sarrazin & Lecuyer 2004). Because lifespan and age of first reproduction are rather similar for these other raptor species compared with Golden Eagle, we suggest that the reason why PGR is substantially lower in the Golden Eagle may be related to its territorial behaviour in comparison with semi-colonial (Osprey) or colonial (vulture) species. Thus, reproductive rates of Osprey did not decrease in studies where populations were increasing (Witt 1996, Steen & Hansen 2001, Dennis & McPhie 2003), except in the Corsican population, which is constrained by breeding habitat availability (Bretagnolle *et al.* 2008). Interestingly, recovering populations of territorial species such as the White-tailed Eagle *Haliaeetus albicilla* or the Bearded Vulture *Gypaetus barbatus* presented weaker population growth rate: respectively 6.7% (Krüger *et al.* 2010) and 3.4% (calculated from Carrete *et al.* 2006) and more similar to PGR in this study. Territorial behaviour may thus be a characteristic of prime importance when considering the regulation of population and can potentially explain interspecific differences of population growth rate of endangered or recovering raptor populations.

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