# Density dependence in Golden Eagle *Aquila chrysaetos* fecundity better explained by individual adjustment than territory heterogeneity

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Density-dependence effects acting on fecundity can be explained by two competing hypotheses. The individual adjustment hypothesis (IAH) states that, as population density increases, interference among individuals negatively affects their breeding performance. The second hypothesis, the habitat heterogeneity hypothesis (HHH), proposes that, as more individuals occupy the space available, lower quality habitats are increasingly used, causing average population fecundity to decline. In territorial species, it is often predicted that interference mechanisms (IAH) should be of less importance than spatial heterogeneity (HHH). Here, we test this prediction in Golden Eagles, using 35 years of reproduction monitoring data from a population that has been recolonizing the grounds of a French National Park (Ecrins) in the Alps. During the study period, the Eagle population increased from *c.* 11 to 41 territorial pairs, providing a good opportunity to explicitly assess fecundity across a gradient of densities. Under the IAH, we expect the fecundity of all territories to diminish as density rises. Under strict HHH, older territories should maintain higher fecundity across time, and a positive relationship between fecundity and the seniority of a territory should be observed. A density-dependent pattern was clearly detected at the population level. At the territory level, the decrease of fecundity was strongly related to population size but not to territory seniority. Fecundity decreased similarly in all territories, suggesting that the IAH better explains the observed pattern. Two alternative mechanisms, related to the IAH, could be at play in this population: (1) negative interference by neighbours and non-territorial Eagles and (2) the contraction of individual territories over time. Our results provide new insights into density dependence in territorial raptors, suggesting that, in addition to habitat heterogeneity, interference mechanisms might actually also play an important role.

**Keywords:** breeding output, cohort effects, interference hypothesis, population dynamics, population regulation, productivity, territorial raptors.

Density dependence is defined as a decrease of population growth rate due to lowered survival and/or fecundity as the population density increases (Nicholson 1933). It is a key process of population regulation that has historically attracted much interest from ecologists (Lack 1954, Murdoch 1994, Turchin 1995). The relative importance of regulation and limitation of wild populations has been the source of intense debate (White 2001, 2004, Berryman *et al.* 2002), mostly because we still do not fully understand the

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underlying mechanisms of negative density-dependent feedbacks (Carrete *et al.* 2008, Krüger *et al.* 2012). Two non-exclusive competing hypotheses are often put forward to explain patterns of density dependence observed in wild populations (Krüger *et al.* 2012): the individual adjustment hypothesis (IAH) and the habitat heterogeneity hypothesis (HHH). Under the IAH (Nicholson 1957, Both 1998), density dependence is directly explained by competitive mechanisms. As density increases, competition for limited resources (food, space, mates, etc.) becomes more intense. Higher competition results in lower resource intake per capita and/or higher rates of aggressive behaviours among conspecifics (e.g. territorial defence, food pre-emption). With fewer resources available and more energy spent on defensive and aggressive behaviours, vital rates are negatively affected. Under this hypothesis, all individuals of the population are equally affected, as they are all exposed to competition. Under the HHH (Dhondt *et al.* 1992, Ferrer & Donazar 1996), vital rates decrease because sites of increasingly lower quality (i.e. lower reproductive value) are being occupied as the population becomes more crowded. This mechanism, also referred to as 'site dependence' (Sergio *et al.* 2007, Nevoux *et al.* 2011) or 'buffer effect' (Gill *et al.* 2001), supposes the existence of (1) spatial heterogeneity in site quality and (2) pre-emptive selection of sites based on their quality (Rodenhouse *et al.* 1997). In contrast, under the HHH, increasing density does not affect individual vital rates (McPeek *et al.* 2001). Animals that acquire high- (or low-) quality sites, maintain high (or low) vital rates at all densities. The negative relationship observed at the population level, as density increases, occurs because the proportion of low-quality sites, and hence low vital-rate individuals, increases. In other words, only the population's average vital rate value shows a negative trend (McPeek *et al.* 2001), whereas its variance is expected to increase (Ferrer *et al.* 2006).

Site dependence (HHH) has been reported for a wide range of taxa, including arthropods (e.g. Desert Spiders *Agelenopsis aperta* (Riechert 1981), Yellow Jackets (wasps) *Vespula maculifrons* (Lord & Roth 1985)), small mammals (Red Squirrels *Sciurus vulgaris*; Wauters & Lens 1995)), passerines (Great Tits *Parus major* (Krebs & Perrins 1978), Blue Tits *Cyanistes caeruleus* (Dhondt *et al.* 1992), Eurasian Jays *Garrulus glandarius* (Andren 1990), Black-throated Blue Warblers *Setophaga caerulescens* (Holmes *et al.*

1996)) and seabirds (European Shags *Phalacrocorax aristotelis* (Potts *et al.* 1980), Common Murre *Uria aalge* (Kokko *et al.* 2004)). Strong evidence for the occurrence of interference competition (IAH) also exists from studies in the wild (e.g. Pale-headed Brush Finch *Atlapetes pallidiceps*; Hartmann *et al.* 2017) and experimental work (e.g. Pied Flycatcher *Ficedula hypoleuca*; Alatalo & Lundberg 1984 and Common Lizards *Zootoca vivipara*; Mugabo *et al.* 2013). Both mechanisms can also interact. For instance, studies on Red-breasted Geese *Branta ruficollis* and Ravens *Corvus corax* found that the strength of interference mechanisms is greater at low-quality sites (Prop & Quinn 2003, Grünkorn *et al.* 2014).

Because it relies on territoriality, the HHH is often assumed to be more important than interference competition in territorial species (Ferrer & Donazar 1996, Fernandez *et al.* 1998, Grünkorn *et al.* 2014). A growing body of literature provides empirical support for this prediction (e.g. Sergio & Newton 2003, Carrete *et al.* 2006, Krüger *et al.* 2012). In birds of prey in particular, assessment of the HHH has attracted a great deal of attention (Carrete *et al.* 2008). The current state of knowledge suggests that, in birds of prey, site dependence is more prominent than interference competition. Support for the HHH has indeed been reported in Northern Goshawks *Accipiter gentilis* (Krüger & Lindström 2001, Krüger *et al.* 2012), Imperial Eagles (Ferrer & Donazar 1996), Black Kites *Milvus migrans* (Sergio & Newton 2003), Bearded Vultures *Gypaetus barbatus* (Carrete *et al.* 2006a), Golden Eagles *Aquila chrysaetos* (Fasce *et al.* 2011), as well as Eurasian Sparrowhawks *Accipiter nisus*, Common Buzzards *Buteo buteo* and White-tailed Eagles *Haliaeetus albicilla* (Krüger *et al.* 2012). There are, however, several reasons to question the absolute prominence of the HHH in raptors. First, several empirical examples highlight the relevance of interference mechanisms in raptors of varying degrees of territoriality (from colonial to fully territorial species). In a colonial species, the Cinereous Vulture *Aegypius monachus*, Fernández-Bellon *et al.* (2016) showed that individual interference (IAH) density-dependent mechanisms were actually more prominent than site dependence (HHH). In Ospreys *Pandion haliaetus*, a semi-colonial raptor, decreasing hatching success was related to increasing behavioural interference by conspecifics as the population density increased (Bretagnolle *et al.* 2008). For a population of Bearded Vultures, a territorial species,

breeding depression over time was explained by both the HHH and IAH (Carrete *et al.* 2006a). Another mechanism at play in that population was the recruitment of a third (unpaired) bird into territories already occupied by a pair, thus forming a polyandrous trio, which resulted in lower productivity (Carrete *et al.* 2006b). For Golden Eagles and Bonelli's Eagles *Aquila fasciata*, two territorial species, Carrete *et al.* (2006) found a pattern of breeding success consistent with the HHH, but deeper investigation allowed them to reject site heterogeneity as the primary mechanism. Instead, the trend was explained by the fact that some nests had high turnover (due to increased adult mortality) and were thus increasingly occupied by young birds, which have less experience and thus lower fecundity.

Second, investigation of the HHH has raised analytical concerns (Carrete *et al.* 2008). Indeed, several studies (e.g. Ferrer & Donazar 1996, Ferrer *et al.* 2006, Fasce *et al.* 2011) that reject the IAH in favour of the HHH draw conclusions from correlations between fecundity averages and variances (and/or skewness), a simplistic approach that is unreliable and can produce spurious results (Beja & Palma 2008). Such spurious evidence might have biased our understanding of density-dependent mechanisms and partially diverted research efforts from testing alternatives to the HHH (Carrete *et al.* 2008).

In this paper, we investigated density-dependent effects on fecundity, defined as per-pair fledgling productivity, in a population of Golden Eagles living in the French Alps. First, to test for the existence of negative density dependence, we assessed whether population fecundity decreased with population size. As this population has been growing at a steep rate since the 1970s, the dataset to hand provides an excellent opportunity to test this feature. Indeed, in the Alps and other areas of southwestern Europe, populations of Golden Eagles have experienced a steady growth over the last 50 years thanks to protection of the species. We then assessed and compared the relative importance of the two mechanistic hypotheses, the HHH and IAH, which could underlie such a negative density-dependent pattern. The Golden Eagle, which displays strong territoriality, is an excellent study species with which to tackle this question. In this species, large territories (*c.* 50 km$^2$) are held and ardently defended by breeding pairs to secure nesting sites and food resources

(Sergio *et al.* 2006, Watson 2010). As territories probably vary in habitat quality, we can expect site dependence to be the most prominent mechanism at play. To avoid spurious relationships that could occur when using simple population statistic summaries (Ferrer *et al.* 2006), we followed recent studies (Carrete *et al.* 2008, Nevoux *et al.* 2011, Grünkorn *et al.* 2014) and used a generalized linear mixed modelling (GLMM) approach to assess the hypotheses of interest.

## METHODS

### Species, study area and data collection

Golden Eagles are territorial raptors usually encountered between *c.* 400 and 2000 m asl. They often inhabit alpine environments with open landscapes but can also be found in forested areas. Breeding pairs, which are monogamous, actively defend a breeding territory, where they select between one and ten or more nesting sites, often located on cliffs and sometimes in trees (depending on availability), which can be used alternatively between years (Watson 2010). The size of Golden Eagle territories is not well documented in continental Europe, but it is thought to be anywhere between 25 and 120 km$^2$ (i.e. ~3–6 km in radius, McGrady *et al.* 2002, McLeod *et al.* 2002, Sergio *et al.* 2006). In addition to nesting sites, a territory also provides a hunting habitat for the breeding pair, thus securing food resources for themselves and their offspring. The population of Golden Eagles of the Parc National des Ecrins lives in an area of 2700 km$^2$ located in the Alps between 44.4488°–45.1647°N and 5.9235°–6.6069°E (Fig. 1). Elevation varies between 700 and 4100 m. This population of Eagles has been surveyed by the National Park rangers since the 1970s and is known to have increased from *c.* 11 to 41 territorial pairs during the 1981–2015 study period, providing an ideal situation to assess density-dependent effects. Data prior to 1981 exist, but because surveys were not intense and regular at that time, they were not included in the analyses presented in this paper.

Population monitoring has historically proceeded as follows. Each year, starting around February–March, territories and active nesting sites of known territorial pairs were searched for. The study area was also actively surveyed to detect potential new pairs and their nests. Once found,
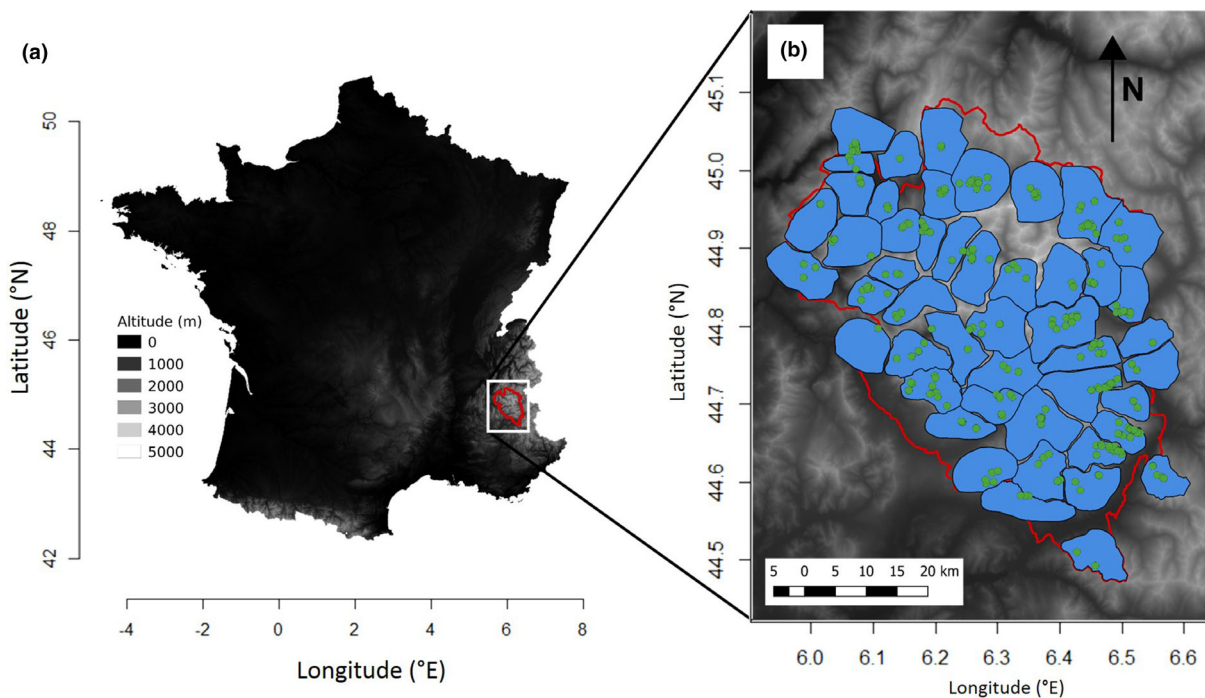
**Figure 1.** (a) Map of France, showing the limits of the Parc National des Ecrins (red line). (b) Location of known territories (blue polygons) and known nesting sites (green dots), as of 2015, within the Park (delimited by the red line). On both maps, the grey colour gradient represents altitude variation (the lighter the grey, the higher the altitude).

an active nesting site was subsequently surveyed at least twice more within the breeding season, between March and August, to detect the presence of eggs (March–April), chicks (May–June) and fledglings (July–August). Because breeding pairs often changed nesting sites between years, finding the current active nest of a given territory was the most time-consuming activity. It was also the greatest source of uncertainty in the data, as nests could remain undetected in some years. For nests that were detected, subsequent surveys were straightforward and required relatively little effort. There was no strict protocol for nest detection because the constant presence of park rangers on the field (for various missions) ensured continuous observation pressure. For most pairs (either new or formerly known), their presence and the location of their nest could thus be ascertained thanks to opportunistic observations made by rangers during their routine work. However, this was usually not sufficient to find all active nests, especially in the presence of new territorial pairs. Some specific work time of rangers (~1500 h/year) was thus dedicated to searching for nests that remained unidentified. These formal surveys often proceeded

as follows. A team of two to eight observers would stand at strategic locations (high observing points) visually to survey a large area of a presumed territory. When an observer detected a Golden Eagle (or a pair) in flight, its current position and movement direction was communicated to the entire team, by radio, so that the Eagle could be tracked, sometimes for several hours, until it reached its nest. Sometimes, visual contact was lost before Eagles reached their nest. Observation sessions were usually reiterated until an active nest was found or until there was enough evidence to conclude that the pair had not attempted to reproduce that year (e.g. non-breeding pair or abandoned nest). Occupancy by a pair was determined through observations of specific behaviours such as courtship flights, territorial defence and nest refurbishment. The absence of breeding was ascertained when nest refurbishment had clearly been stopped (abandoned nest). The effort devoted to each pair for nest detection and breeding surveys varied between 8 and 75 h (average 29.8 h; Couloumy 1996), and mostly depended on how quickly and easily the active nesting site was found early in the season. Failure to detect an

active nest could be due either to the fact that a pair skipped reproduction that year (true absence of breeding attempt/event) or to the failure to find the nesting site (false negative, due to imperfect detectability).

For the analysis below, we defined productivity as the number of young, per territorial pair, successfully raised to the fledgling stage. The outcome of a pair that hatched some chicks but failed to raise at least one of them to the fledgling stage was assigned a productivity of 0. Any other form of known breeding failure (e.g. no attempt to breed (ascertained), unhatched egg(s)) was also considered a productivity of 0 offspring produced that year. All available behavioural cues (nuptial displays, mating signs, old nests attendance, presence/absence of eggs, etc.) were used to determine a pair's reproductive outcome in a given year. When there was not enough evidence to ascertain the absence or failure of breeding (e.g. failure at an early stage), we treated that data as unknown status ('NA'; instead of '0 offspring') to avoid biasing estimates of annual fecundity.

## Data analysis

We used generalized linear (mixed) models (GL (M)M) to test for density dependence and assess the HHH and IAH, as well as heterogeneity across territories. We first investigated evidence for density dependence at the population level. The response variable was the population's annual average productivity ($\bar{y}_t$), which corresponded to the average number of fledglings produced, per pair, in a given year ($t$). Using linear regressions, we tested the relationship between average productivity and the number of occupied territories ($N_t$, hereafter annual population size) and assessed the gross temporal trend in productivity from 1981 to 2015, as population size increased.

Next, we investigated the HHH and IAH, using GLM approaches. Here, the response variable ($y_{st}$) was still annual productivity, but instead of the population average, it was now defined at the level of territories. These data, i.e. number of fledglings produced by a given territory ($s$) in a given year ($t$), were integer values between 0 and 2. The data adequately fit a Poisson distribution ($\chi^2 = 718$, df = 915, $P > 0.99$), with a mean of 0.57 and a variance of 0.45 fledglings per pair, and there was no evidence of overdispersion ($\hat{c} = 0.78$). We followed the recommendations of McDonald and White (2010) for small count data (mean < 2) and analysed the fecundity data assuming Gaussian errors. For the sake of comparison, we also ran the analysis using a Poisson distribution (Appendix S1), and the conclusions remained unchanged.

As explained above, the interference processes driving the IAH are density-dependent mechanisms acting at the individual level. To test this hypothesis, we directly investigated the effect of annual population size ($N_t$) on individual territories' productivity. We emphasize the difference between the non-specific test presented above, which was simply aimed at assessing the presence of a density dependence pattern at the population level ($\bar{y}_t \sim N_t$), and this hypothesis-specific test, carried out on individual territories' productivity ($y_{st} \sim N_t$). Whereas the former pattern could be equally explained by the IAH or the HHH, or a mixture of both, the latter test is more specific to the IAH (although not exclusive of the HHH) as it focuses on the link between density and productivity at the level of individual territories. Under strict HHH, a negative trend in the population-level fecundity would instead be due to younger (low-quality) territories having lower productivity compared with older (high-quality) ones. Thus, under the assumption that the quality of territories has not dramatically changed over time (see Discussion), the HHH predicts a positive correlation between a territory's productivity and its seniority. We defined seniority (covariate: $Sen_s$) as the time elapsed, as of 2016, since a territory's first recorded occupancy. For instance, a 'young' territory that was first occupied in 2014 has a seniority value Sen = 2, whereas an 'old' (senior) territory first occupied in 1986 has a value Sen = 30. Because the sample size (i.e. number of breeding events observed) available for a territory is linked to its seniority, we decided to censor data to territories at least 10 years old to avoid skewing results. We remind the reader that we do not have information about individual turnover on territories (Eagles were unmarked). We also analysed data restricted to territories at least 5 years old to check for potential differences. Results remained unchanged (Appendix S1). Finally, because the first occurrence of a territory's occupation might not always have been detected, seniority might have slightly been undervalued for some territories. However, given the intensity of monitoring devoted to that species within the National Park, we were

confident that most territories were discovered quickly after their first establishment.

We first evaluated the following models using GLM analyses: M1: $\{y_{st} \sim N_t\}$; M2: $\{y_{st} \sim Sen_s\}$; M3: $\{y_{st} \sim N_t + Sen_s\}$. Model M1 considered only IAH mechanisms, M2 only HHH mechanisms and M3 considered both (additive model). Using a GLMM approach, we then added individual random effects to these models to control for potential confounding effects due to the non-independence of observations coming from the same territory. Random effects ($\varepsilon_s$), applied to each territory ($s$), were modelled with a normal distribution centred on zero, as $\varepsilon_s \sim N(0, \sigma)$. The corresponding models were: M4: $\{y_{st} \sim N_t + \varepsilon_s\}$; M5: $\{y_{st} \sim Sen_s + \varepsilon_s\}$; M6: $\{y_{st} \sim N_t + Sen_s + \varepsilon_s\}$.

The test of the HHH based on seniority only holds if the relative quality of territories did not change dramatically over time. If habitat quality is an important driver but has evolved differentially among territories, the expected correlation between seniority and fecundity weakens but we would still expect the relative variance of fecundity to increase over time, due to the increasing number of poor quality sites being occupied (Ferrer et al. 2006). This prediction of increasing variance is in contrast to the IAH, for which the decrease in average fecundity is expected to occur relatively uniformly across territories (Ferrer & Donazar 1996). We performed a non-parametric Fligner–Killeen test (hereafter 'test of variance') to compare the variance of fecundity between the first and the last 10 years of the study. This test of variance is not sufficient on its own to draw strong conclusions but it provides useful information to further discriminate between the two hypotheses of interest.

Finally, as an ultimate way of investigating the relative importance of habitat quality differences in terms of offspring productivity, we assessed the level of inter-territory heterogeneity across the entire study timeframe. We investigated inter-territory heterogeneity using the random effect models (GLMMs) described above, but also with a finite mixture components approach, in which heterogeneity was modelled as a discrete feature (groups of territories) instead of a continuous normal distribution. The relative support for heterogeneity was assessed in several ways: first, using a formal model selection procedure; second, by comparing the amount of variability observed in the data with that expected under the models with and without

heterogeneity; and, finally, by means of visual inspection of the amount of variability displayed by the raw data. For model selection, we used the Bayesian information criterion (BIC), which, with its strong penalty, is more robust than other criteria when dealing with unobserved heterogeneity (Brewer et al. 2016). All analyses were performed in the program R (R Core Team 2018), using packages *lme4* for GL(M)M models (Bates et al. 2015), and *flexmix* for finite mixture models (Gruen & Leisch 2008).

## RESULTS

We found clear evidence for a negative density-dependent effect on population productivity ($\beta$ = –0.014, se = 0.004, 95% confidence interval (CI) –0.022 to –0.007, $P$ = 0.001). Overall, population size explained 27.5% of the variance in productivity (Fig. 2). This result was confirmed by a strong negative temporal trend between 1981 and 2015, when the population grew from 11 to 41 territorial pairs (simple linear regression: $\beta$ = –0.010, 95% CI –0.015 to –0.005, $P$ = 0.001; Fig. 3).

Contrary to our expectations, we did not find any evidence supporting the HHH (Fig. 4). Nor was the seniority covariate supported in either of the models (Table 1, Fig. 4). These results remained virtually unchanged when we included individual heterogeneity in the models (Table 1). The IAH, on the other hand, was strongly supported in both models that included the effect of population density on a territory's fecundity ($\beta$ = –0.017, se = 0.04, 95% CI –0.025 to –0.008, $P$ = 0.001). Model selection through Akaike's information criterion (AIC; Table 1) led to the same conclusion: model M1 (IAH) was clearly better supported than M2 (HHH; $\Delta AICc$ = 13.8) and M3 ($\Delta AICc$ = 2.0). At the territory level, productivity showed a progressive decline over the years as the population became more crowded (Fig. 3). These results suggest the existence of interference mechanisms acting at the individual territory level.

These conclusions were also supported by the tests of variance. We found no difference in the variance of fecundity between the first and the last 10 years of the study, which suggests that fecundity has decreased homogeneously, as predicted by the IAH but not by the HHH. This result held when we used data for all territories (first 10 years: coefficient of variation (CV) = 0.92; last
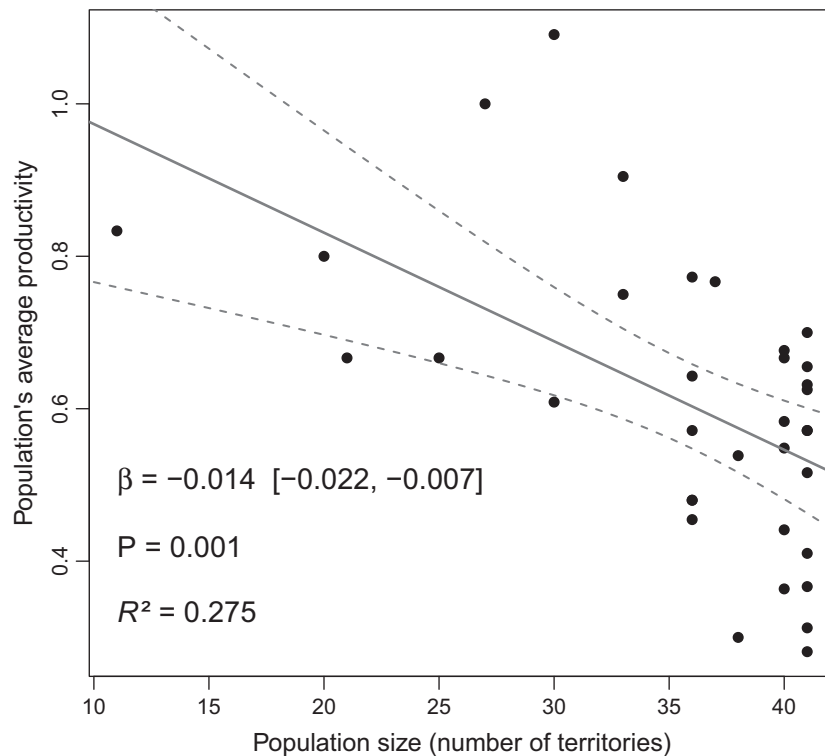
**Figure 2.** Relationship between a population's average fecundity and population size (number of territorial pairs). Black points represent values of average fecundity for years between 1981 and 2015. The grey line is the regression line, with the 95% CI shown as dotted lines. The estimated parameter value (β) is shown with the 95% CI in square brackets.

10 years: CV = 1.21; Fligner–Killeen test: $\chi^2 = 0.015$, df = 1, $P = 0.90$), as well as when we used only the oldest territories to increase statistical power (first 10 years: CV = 0.92; last 10 years: CV = 1.23; Fligner–Killeen test: $\chi^2 = 0.14$, df = 1, $P = 0.70$).

Finally, investigation of individual heterogeneity over the entire study timeframe did not provide much evidence for consistent differences across territories. In the finite mixture approach, the model considering a single ($k = 1$) mixture component (i.e. homogeneous fecundity across all territories) received much more support than models considering $k = 2$ (ΔBIC = 4.6) or $k = 3$ (ΔBIC = 17.2) groups of heterogeneity. The same conclusion was reached when we modelled inter-territory heterogeneity as a continuous latent variable, as the model without heterogeneity (M1) was slightly better supported than the model including heterogeneity (M4; ΔBIC = 1.9). Moreover, comparison of the observed reproductive outputs with the reproductive outputs predicted by each model did not reveal a higher predictive accuracy compared with the model including heterogeneity (M4: root

mean square error (RMSE) = 0.99; M1: RMSE = 0.40). Finally, a visual inspection of the data (Fig. 5) did not reveal any conclusive level of heterogeneity among territories. In addition, there was no apparent trend related to seniority in terms of either average fecundity or its variability.

## DISCUSSION

We conducted analyses to assess density dependence on offspring productivity in a population of Golden Eagles from the French Alps that has shown a steady growth over the last 35 years. Based on the temporal pattern of the productivity of Eagle territories, we tested two competing, but non-exclusive hypotheses: the individual adjustment hypothesis (IAH) and the habitat heterogeneity hypothesis (HHH). Because Golden Eagles are highly territorial, we anticipated more support for the latter hypothesis (HHH).

We found clear evidence for negative density dependence acting on productivity; however, contrary to our predictions, we found more support for interference mechanisms (IAH) than for the
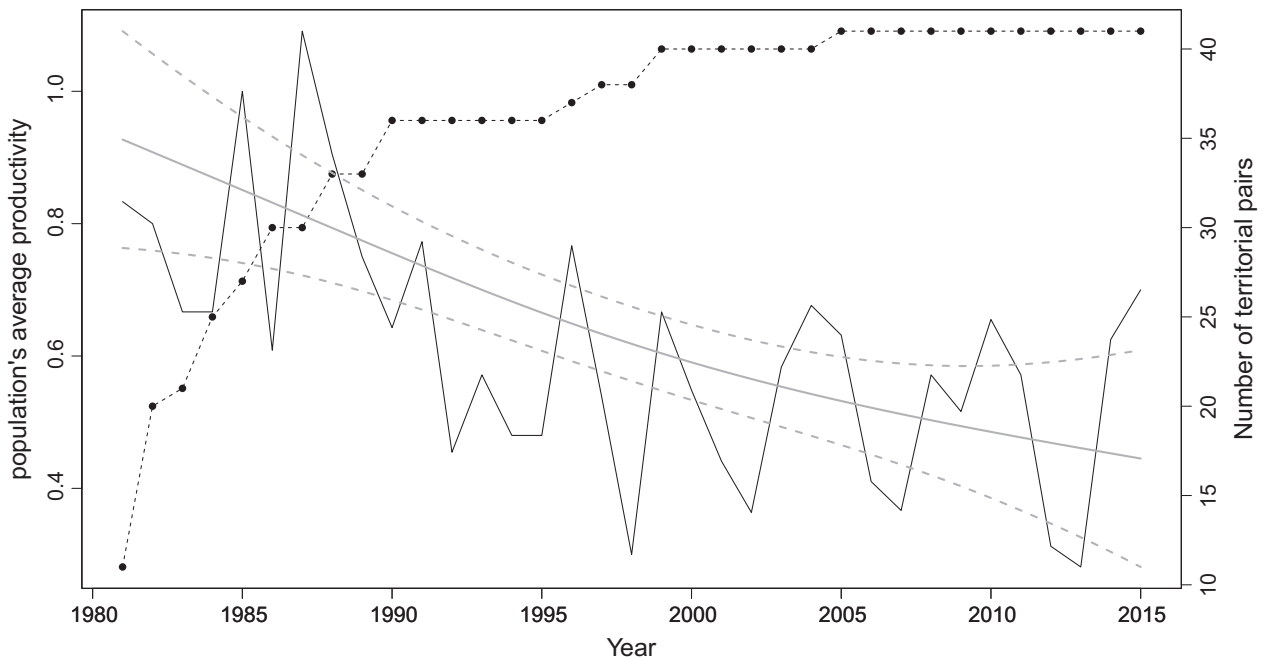
**Figure 3.** A population's average productivity and population size from 1981 to 2015. The black solid line represents observed annual values of productivity. The estimated temporal trend is shown as a grey curve with 95% CI dashed lines. The dash-dot line represents the number of territorial pairs, each year.

HHH. Indeed, at the territory level, productivity was strongly related to population density but not to seniority. We acknowledge that the negative result for the test on seniority could be due on a lack of statistical power. We also failed to find any increase in fecundity variance over time, which suggests that fecundity has decreased in a similar fashion for all territories. Finally, we found very weak levels of heterogeneity in productivity among territories. However, we cannot totally rule out differences in habitat quality as an important factor in this population, because our analyses did not focus on mechanisms that potentially underlie habitat quality (e.g. prey availability). Instead, we focused on predictive patterns (correlation productivity/seniority, homogeneity in productivity) related to the two hypotheses of primary interest. To extrapolate further and conclude that quality differences among sites are negligible, we would need to assume that seniority is a reliable proxy of habitat quality. Although it is fair to expect that Eagles did not select their territory at random, site selection might not exactly follow the expectations of an ideal free distribution (Fretwell & Lucas 1970), particularly if the information on site quality is not perfect or fully available. Finally, it is

important to keep in mind that the IAH and HHH are not necessarily mutually exclusive, and that both mechanisms could act in parallel.

Our results are in contrast to the conclusions of a previous study (covering 37 years, 1972–2008) done on a nearby population of Golden Eagles living in the Western Italian Alps (Fasce *et al.* 2011). That study also found decreasing breeding success at the population level as density increased, but the authors suggested that this pattern is mainly due to HHH mechanisms (buffer effect). Here, we bring new insights regarding density dependence in this species by highlighting the importance of negative interferences occurring at high density. Although we cannot directly extrapolate our results to other populations of Golden Eagles, we suspect that similar mechanisms exist elsewhere. Considering that, in Western Europe, most Golden Eagle populations have experienced quick growth over the last 40–50 years, it would be interesting to investigate, in some of these other populations, temporal trends in fecundity and to assess whether the same density-dependent processes are at play.

In the population studied here, we suspect that density has had a negative effect primarily because of competition for territorial space. Over time, as
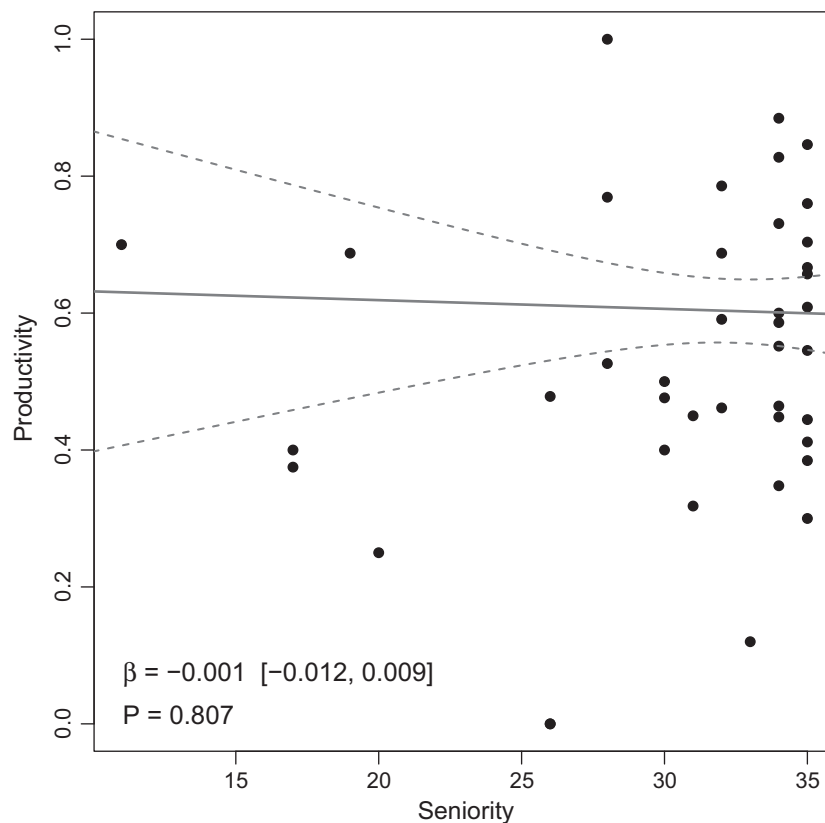
**Figure 4.** Observed productivity of territories (points), averaged across years, and estimated seniority effect (solid grey line) from model M3, with 95% CI (grey dashed lines). The estimated parameter value (β) is shown with the 95% CI in square brackets.

**Table 1.** AIC table of the GLM and GLMM analyses.

| Model | Covariate effect | df | AICc | ΔAICc |
|---|---|---|---|---|
| *Analysis without random effects* | | | | |
| M1 | Population size | 2 | 1853.5 | 0.0 |
| M3 | Population size + Seniority | 3 | 1855.4 | 2.0 |
| M2 | Seniority | 2 | 1867.3 | 13.8 |
| *Analysis with random effects* | | | | |
| M4 | Population size | 3 | 1851.9 | 0.0 |
| M6 | Population size + Seniority | 4 | 1858.6 | 6.7 |
| M5 | Seniority | 3 | 1866.0 | 14.1 |

the population became more crowded, individual territories may have shrunk to a suboptimal size (Ebersole 1980, López-Sepulcre & Kokko 2005), reducing the amount of food, shelters and/or breeding sites secured by each territorial pair. Territory shrinkage is expected to occur because, as less total space becomes available, new recruits try to acquire breeding space by encroaching on the boundaries of existing territories. Eventually, the expansion of these newly established territories will reduce the size of neighbouring territories. This process has been described in other species, such as Oystercatchers *Haematopus ostralegus* (Heg *et al.* 2000), Red-winged Blackbirds *Agelaius phoeniceus* (Beletsky 1992) and bronze anole lizards *Anolis aeneus* (Stamps & Krishnan 1995). With the contraction of territory sizes, competition for resources inevitably becomes more intense. Competition can affect fecundity and/or survival through exploitative competition (indirect interferences) and/or direct interferences among individuals. For instance, with less hunting space, a territorial pair might need to spend more time and energy hunting to fulfil their feeding requirements. This means that, on average, an individual's food intake per unit of effort is reduced through indirect competition among eagles. Such exploitative competition induced by territory contraction seems to occur in many taxa (Adams 2001) and it has been demonstrated experimentally in some fish
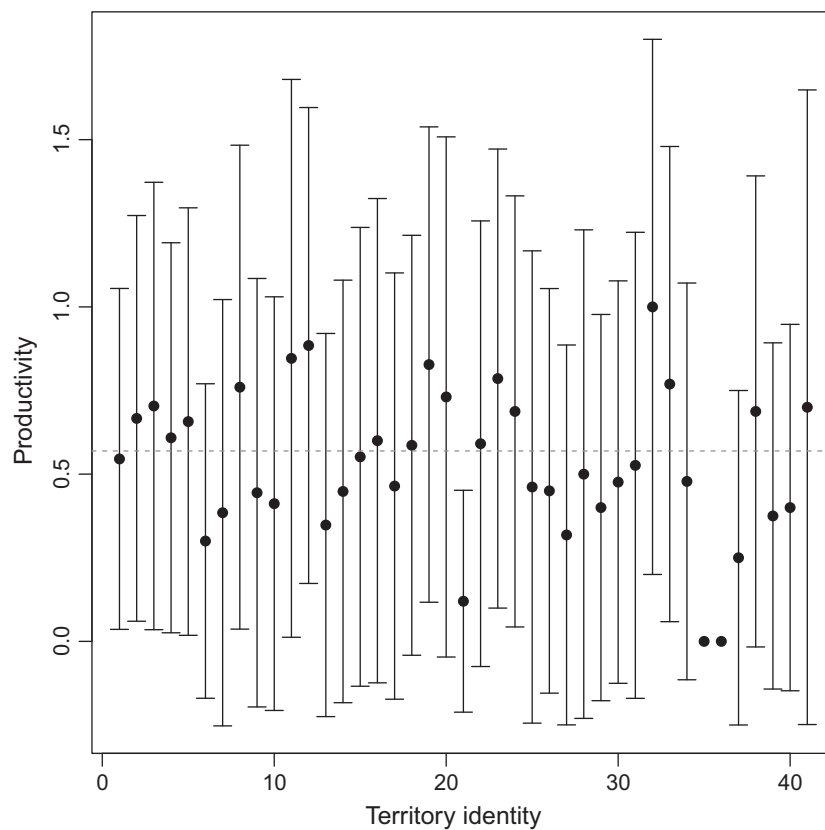
**Figure 5.** Visualization of inter-territory heterogeneity. Territories are ordered by decreasing values of seniority (oldest on the left-hand side). The average value (black dots) and standard deviation (error bars) of annual productivity are shown for each territory. Only territories older than 10 years are displayed to allow sufficient data. The overall average productivity (mean value across territories) is shown (horizontal dashed grey line) as a point of reference.

(Iguchi & Hino 1996, Keeley 2000) and passerine birds (Beletsky 1992, Both & Visser 2000). Individual fecundity might also be negatively impacted by an increase of aggressive interference (Hansen 1987, Jenkins & Jackman 1993, Carrete *et al.* 2006a, Bretagnolle *et al.* 2008, Grünkorn *et al.* 2014), as a result of higher density and smaller territories. In raptors, aggressive behaviours can occur between neighbouring territorial pairs, but these occurrences are not common and they are usually limited to brief interactions at the borders of adjacent territories (Gargett 1975, Haller 1982, Bergo 1987). On the other hand, aggression by non-breeding individuals (floaters), which are attempting to evict existing breeders and seize their territories (Moreno 2016), seem much more frequent (Brooker 1974, Gargett 1975).

Overall, the relative contribution of IAH vs. HHH mechanisms in raptors and other territorial species is far from being fully understood, as evidenced by the diversity of findings found in the literature (e.g. Ferrer & Donazar 1996, Carrete *et al.* 2006a, Sergio *et al.* 2007, Nevoux *et al.* 2011, Ferrer *et al.* 2015, this study). This lack of convergence among different studies might, in part, be due to the fact that both types of processes are actually at play in most populations (Nevoux *et al.* 2011).

## DATA AVAILABILITY STATEMENT

Data used in this paper: Annual reproductive output of Golden Eagles (*Aquila chrysaetos*). These

data are available in a Zenodo repository (https://doi.org/10.5281/zenodo.3601479).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Results of the complementary analyses