

Population regulation by habitat heterogeneity or individual adjustment?

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Summary

1. The habitat heterogeneity (HHH) and individual adjustment (IAH) hypotheses are commonly proposed to explain a decrease in reproduction rate with increasing population density. Higher numbers of low-quality territories with low reproductive success as density increases lead to a decrease in reproduction under the HHH, while more competition at high density decreases reproduction across all territories under the IAH.

2. We analyse the influence of density and habitat heterogeneity on reproductive success in eight populations of long-lived territorial birds of prey belonging to four species. Sufficient reliability in distinguishing between population-wide, site-specific and individual quality effects on reproduction was granted through the minimal duration of 20 years of all data sets and the ability to control for individual quality in five of them.

3. Density increased in five populations but reproduction did not decrease in these. Territory occupancy as a surrogate of territory quality correlated positively with reproductive success but only significantly so in large data sets with more than 100 territories.

4. Reproductive success was always best explained by measures of territory quality in multivariate models. Direct or delayed ($t-1$) population density entered very few of the best models. Mixed models controlling for individual quality showed an increasing reproductive performance in older individuals and in those laying earlier, but measures of territory quality were also always retained in the best models.

5. We find strong support for the habitat heterogeneity hypothesis but weak support for the individual adjustment hypothesis. Both individual and site characteristics are crucial for reproductive performance in long-lived birds. Proportional occupancy of territories enables recognition of high-quality territories as preferential conservation targets.

Key-words: birds of prey, intraspecific competition, long-term studies, population density, territory quality

Introduction

In many animal and plant populations, reproductive success decreases with increasing population density. This density dependence of reproduction has been known since the dawn of modern animal ecology (Lack 1954), but the main mechanism that facilitates it and the proper methods for its recognition have become the subject of a heated debate in recent years (Balbontín & Ferrer 2008; Beja & Palma 2008; Carrete *et al.* 2008; Ferrer, Newton & Casado 2008). Two main

mechanistic hypotheses may explain how increasing density leads to lower reproductive success.

1 The *habitat heterogeneity hypothesis* (HHH) is based on early studies documenting a relationship between territory occupancy and reproductive success (Newton & Marquiss 1976; Møller 1982; Newton 1991; Rodenhouse, Sherry & Holmes 1997). Rodenhouse, Sherry & Holmes (1997) proposed it under the name of site-dependent regulation. It assumes that at low population densities, mainly territories of high quality are occupied. Abundant resources there allow territory holders to maintain good body condition and raise comparatively large broods.

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Furthermore, high territory quality may confer territory holders with superior survival prospects. When population densities increase, new breeders take territories of increasingly worse quality. Resource scarcity limits these individuals to low provisioning rates and decreases their chances of successful reproduction (Rodenhous, Sherry & Holmes 1997).

- 2 Alternatively, the *individual adjustment hypothesis* (IAH) proposes that with an increase in population density, the intensity of competition rises. High levels of intraspecific aggression and competition are experienced by all breeding individuals and lead to a reduction in reproductive success throughout the population (Ferrer & Donazar 1996). The term individual adjustment is slightly misleading as it suggests that individuals adjust their reproduction at high density. More appropriate would be to talk about individuals being constrained in their reproduction by high density, so that a better label would be *individual constraint hypothesis*.

Even though the influences of habitat heterogeneity and interference on reproductive success have been opposed in the context of density dependence and population regulation, it should be recognized that both can have a negative impact on reproduction even if density dependence is not evident. Both mechanisms are not mutually exclusive, but in a given species probably one will be far more influential in shaping the distribution of reproductive success than the other. Originally, trade-offs between fecundity and its coefficient of variation or skewness were supposed to deliver support for HHH (Ferrer & Donazar 1996). Eventually, this was shown to be true only when brood sizes in the saturated population are left-skewed. In fact, the same trade-offs could support IAH when brood size is normally distributed (Beja & Palma 2008; Ferrer, Newton & Casado 2008). The main distinction between the two hypotheses therefore tends to get reduced to an assessment of whether the distribution of reproductive success is normal or left-skewed and whether density *per se* is important or not. Under IAH, the whole histogram representing the distribution of reproductive success shifts towards zero when density is high, while under HHH, the left-hand side of the histogram increases excessively. Examining these hypotheses has been further obstructed by habitat quality not being easily measurable as perceived by study species and potentially interacting with individual quality in a complex way (Sergio & Newton 2003; Sergio *et al.* 2009).

While the distinction between the possible underlying mechanisms of density-dependent reproductive success is not trivial, a resolution of the issue is by far not only of academic concern. Every conservation programme aimed at a particular species has to deal with the essential questions where, when and how to support the target population. The answers could be very different, depending on the mechanism limiting population growth. In populations where reproductive success depends highly on territory quality, efforts should first protect high-ranking territories where most recruits would

originate (Evans *et al.* 2009). However, the conservation of a few desired sites could even harm the population, if they become centres of intraspecific competition that diminish reproductive success. Particularly, competition-sensitive species can be harmed even by conservation measures apparently reducing competition, such as supplementary feeding, because it temporarily increases focal density at feeding sites (Carrete, Donazar & Margalida 2006). Thus in populations where the IAH applies, conservation management programmes should cover the entire habitat used by the species and further measures should aim to minimize intraspecific encounters.

Although density dependence has been examined in different taxa (Sibly *et al.* 2005), the specific decrease in individual reproductive success is most easily studied in large territorial species. Despite the generality of the question, many of these species are of conservation concern and normally not available for experimental testing. One particularly prominent group used for disentangling hypotheses about density-dependent reproductive success have been birds of prey. The predatory habit could amplify the occurrence of strong density dependence and make them especially suited for studies of the underlying mechanisms (De Roos & Persson 2002). Territoriality allows both habitat heterogeneity and density effects to be examined in detail, while this possibility could be impaired in classically colonial species. The charismatic nature, conspicuousness and relatively high vulnerability of birds of prey not only increase their conservation value, but also make recording of their reproductive success and population dynamics attractive and relatively common.

The apparently straightforward life histories of long-lived territorial species, however, also hide some pitfalls. While many studies of density dependence encompass only around 10 years of data, a few very successful individuals in many species can have a significantly longer life span and systematic changes in vital rates have been documented (Krüger & Lindström 2001b; Krüger 2005; Blumstein & Møller 2008; Sergio *et al.* 2011). Therefore, most studies at best take the reproductive success of one generation of territory holders into account. This does not allow a firm distinction between effects of the quality of breeding individuals and territory quality. In such setups, high reproductive success could originate from the high quality of a territory under HHH or from high resilience to interference of the territory holders under IAH.

In this study, we address this problem by analysing territory-specific reproduction over much longer time spans that exceed the reproductive lifetime of even the most persistent individuals. For four long-lived, territorial bird of prey species, we use eight data sets longer than 20 years, the longest reaching 62 years, which encompass several to many generations of territory holders. These exceptionally long time series additionally allow for consideration of both direct and delayed density dependence. The recognition of individuals in five of these data sets further permits a clear distinction between the effects of territory and individual quality.

Materials and methods

STUDY SPECIES

The goshawk (*Accipiter gentilis* L.) is a medium-sized (48–68 cm body length, 517–1509 g body weight) avian predator breeding across the Holarctic (del Hoyo *et al.* 1994). It opportunistically feeds on birds and mammals.

The closely related sparrowhawk (*Accipiter nisus* L.) is much smaller (28–38 cm body length, 110–342 g body weight) and breeds across the Palaearctic (del Hoyo *et al.* 1994). Its main prey consists of passerine birds.

The common buzzard (*Buteo buteo* L.) is medium-sized (50–57 cm body length, 525–1364 g body weight) and breeds across the Palaearctic (del Hoyo *et al.* 1994). Its main prey consists of microtine rodents.

The white-tailed eagle (*Haliaeetus albicilla* L.) is a large bird of prey (69–92 cm body length, 4100–5500 g body weight), breeding across the Palaearctic and south-western Greenland (del Hoyo *et al.* 1994). It opportunistically feeds on fish, birds and mammals.

STUDY SITES

The *goshawk 3816* study site measures 250 km² and is located in Eastern Westphalia, Germany (52°12'N, 8°20'E), and has been under study between 1975 and 2008, with a total of 377 breeding attempts in the data base. The area is a mixture of forest and cultivated areas and has been described in more detail in Krüger & Lindström (2001b).

The *goshawk 3916* study site measures 175 km², is also located in Eastern Westphalia, Germany (52°05'N, 8°25'E), and data have been collected between 1989 and 2009. The data base holds 204 breeding attempts. The area is a low-mountain terrain with larger forest patches and cultivated areas and has been described in more detail in the study by Krüger & Lindström (2001b).

The *goshawk Schleswig* study area measures 2000 km², is located in northern Germany (54°20'N, 9°15'E) and has been studied between 1968 and 2008, with a total of 1833 breeding attempts. The flat terrain is a moraine landscape with large forest patches and extensive cultivated areas. It has been described in more detail in Looft (2000).

The *goshawk Denmark* study area measures 2417 km² and is located in Vendsyssel, Denmark (57°19'N, 10°11'E) and has been monitored between 1977 and 2005, with a total of 1527 breeding attempts. The study area has been described by Nielsen & Drachmann (2003).

The two *sparrowhawk study sites* come from the same area in Denmark. The *sparrowhawk small* site is located in Sindal (57°28'N, 10°10'E) and measures 68 km². Sparrowhawks have been studied there from 1977 to 1997, with 268 breeding attempts included. The *sparrowhawk large* site is located in Vest (57°25'N, 10°E) and measures 436 km². Sparrowhawks have been studied between 1978 and 1997, and the data base includes 553 breeding attempts.

The *common buzzard study site* measures c. 300 km² and is located in Eastern Westphalia, Germany (52°06'N, 8°25'E). It overlaps partially with the goshawk 3816 and 3916 sites and has been described in more detail elsewhere (Chakarov, Boerner & Krüger 2008). Buzzards have been studied between 1989 and 2009 and data include 1498 breeding attempts.

The *white-tailed eagle study site* covers the entire federal state of Schleswig-Holstein in Germany (15 800 km², centre of the study

area at c. 54°10'N, 9°50'E), and the white-tailed eagle has been studied there continuously since re-colonization of the state began in 1947, yielding a total of 687 breeding attempts so far up to 2008. The species mainly breeds around freshwater lakes in the eastern part. This core area covers c. 6600 km² or 42% of the area of the state and is a young moraine landscape with hills up to 168 m in height and more than 300 eutrophic lakes, fishponds and coastal brackish lagoons. It has been described in more detail in the studies by Struwe-Juhl & Schmidt (2003) and Krüger, Grünkorn & Struwe-Juhl (2010).

DATA COLLECTION

Data for this study were collected from these eight study areas in a very similar way. Each year, all forest patches were visited and checked for activity of the study species. This includes breeding pairs (occupying a nest and showing signs of egg-laying activity) as well as non-breeding pairs that just occupy a territory. Each active nest was visited at least three (normally 5–10) times a year to determine breeding success (success or failure) and brood size (number of chicks fledged) for successful breeding attempts. Data were either collected through careful and intensive observation from the ground (goshawk 3816, goshawk 3916, common buzzard 1989–2001), whereas nests were regularly climbed in the goshawk Schleswig, goshawk Denmark, both sparrowhawk studies, common buzzard (2002–2009) and white-tailed eagle studies. Observation from the ground allows reliable data collection (Krüger & Lindström 2001a; Nielsen & Drachmann 2003). Those studies where nests were regularly climbed also collected data on chick age that allows a laying date to be estimated.

In goshawks, sparrowhawks and white-tailed eagles, the individual colour pattern on the primary and tail feathers is a reliable way of identifying individual birds and has been used repeatedly (Opdam & Müskens 1976; Newton & Marquiss 1982; Kühnapfel & Brune 1995; Bezzel, Rust & Kechele 1997; Nielsen & Drachmann 2003; Krüger 2005, 2007). Breeding females start moulting while incubating, so moulted feathers can be found below or near the nest tree. Age at first breeding was also determined from moult feathers, as they allow for a distinction between ages 1, 2, 3 and 3+ years based on colour pattern and the degree of fading of the bars of the feather (goshawk and sparrowhawk). White-tailed eagle ages allow for a distinction between ages 1, 2, 3, 4 and 5+. Several other studies have used this technique in *Accipiter* and *Haliaeetus* species to age individuals and study age-specific patterns in vital rates (Opdam & Müskens 1976; Kühnapfel & Brune 1995; Rust & Kechele 1996; Bezzel, Rust & Kechele 1997; Nielsen & Drachmann 2003; Krüger, Grünkorn & Struwe-Juhl 2010).

Individual buzzards were drawn or photographed, because the high variation in plumage pigmentation pattern (Glutz von Blotzheim, Bauer & Bezzel 1971; Ulfstrand 1977; Cramp & Simmons 1980; Boerner & Krüger 2009) allows for individuals to be recognized from year to year without artificially marking them. As plumage in buzzard species varies only marginally over its lifetime (Briggs 2010), data on complete life histories can be collected. Since 2002, many individuals have also been colour-ringed or wing-tagged as chicks, which simplifies individual recognition and allows validation of the first method of individual identification.

The studied species show a very high territory fidelity (Cramp & Simmons 1980); movements between territories are very rare. Because birds of prey occasionally skip a breeding attempt, individuals were only classified as dead if they were not found breeding in the study area for at least 2 years (Newton 1989).

DATA ANALYSIS

Variation in reproductive output was analysed using either a linear model or a generalized linear mixed model (GLMM), where female identity was included as a random factor. Depending on the distribution of reproductive output as the dependent variable, either a Poisson error structure and log link function (Nielsen & Drachmann 2003) or a normal error structure with identity link function was used. We used population density (breeding pairs per 100 km²) and the population density in the previous year, territory quality (no. of years a territory was occupied), territory proportional occupancy (proportion of time a territory was occupied since it was first used), and the first year a territory was used as covariates in the analyses. We have used three different surrogate variables for territory quality because they capture different aspects: number of years of occupation is an overall surrogate of territory quality, but it underestimates that newer territories, for whatever reason, can be of high quality, too. Proportional occupancy takes this into account by using the first year of occupancy as the starting point. For example, if, over 20 years, a territory was occupied for 10 years during the last 10 years, the territory occupancy variable would be scored as 0.5, whereas the proportional territory occupancy variable would be scored as 1.0. First year of territory occupancy is a very crude measure but is often used if data are incomplete; hence, we also included it here to see whether this crude measure might be significant and might hence provide a simple surrogate measure of territory quality.

One potential problem with analyses using surrogate variables for territory quality is that in studies lasting several decades, territories change as forest patches become older or might even get felled. In line with earlier studies (Krüger & Lindström 2001a), we excluded the very few territories where a major abrupt change occurred. However, our approach of using occupancy as a surrogate measure of territory quality next to proportional territory occupancy enables us to deal with the problem of changes within territories. If a territory deteriorates in quality over time for an unknown reason, this should affect our surrogate measures of territory quality as such territories are not used any more. Hence, both our surrogate measures of territory quality decrease in their value.

Because our data sets cover many decades, large-scale environmental changes could affect reproductive success. We therefore also included weather variables, precisely annual mean temperature and annual cumulative rainfall, in the analyses (mean temperature of April–June and cumulative rainfall of April–June for the Danish time series, because of missing data for other months). Weather data were obtained from the nearest meteorological station from the German and Danish meteorological offices. To test for delayed effects of weather, we also included the weather data from the previous year in the analyses.

For those data sets where we had information on individual identity, age and laying date, these were added as a random factor (identity) and as covariates (age and laying date) in the GLMM analyses. The random factor individual identity was always kept in the model.

To select the model best fitting the reproductive output data, we used an information theory approach, the Akaike Information Criterion (AIC), which penalises a model for every additional parameter used and hence avoids overfitting (Burnham & Anderson 2002). We started with univariate models and then added more variables one by one with all possible variable combinations. We checked for variable redundancy by including collinearity statistics, and 0.1 was used as a lower threshold, as recommend by Hair *et al.* (1995). The relative importance of each model was estimated through ranking the models by $\Delta\text{AIC} = \text{AIC}_i - \text{AIC}_{\min}$ (where AIC_{\min} is the best model in the

model subset). Model weight was estimated through the normalized Akaike weights, $\exp(-0.5 \times \Delta\text{AIC}) / \sum_{r=1}^R \exp(-0.5 \times \Delta\text{AIC}_r)$. Differences in AIC between models above two suggest less support (Burnham & Anderson 2002), and this was used as a threshold for presentation. This model selection approach seems preferable to stepwise regression models (Whittingham *et al.* 2006).

Results

DESCRIPTION OF THE TIME SERIES

All observed populations showed substantial fluctuation in density over time (Fig. 1). Density did not show a directional change over time in the goshawk 3916 and Schleswig populations (Table 1). However, there was a positive trend in the goshawk Denmark and a significant increase in density over time in the goshawk 3816 population. The large Denmark sparrowhawk population also increased significantly, while the adjacent small sparrowhawk population decreased significantly over the study period. The common buzzard and white-tailed eagle populations increased strongly (Table 1). There was significant heterogeneity among the correlation coefficients between time and density between the eight populations ($\chi^2_7 = 74.436$, $P < 0.001$). Duration of the time series, latitude, longitude or species as explanatory variables were not significantly associated with the variation in correlation coefficients (*all* $P >> 0.05$). Reproductive rate, measured as mean number of juveniles per breeding pair, did not correlate with population density in most study populations. Exceptionally, white-tailed eagles showed a significant increase in reproductive rate with density, probably due to abandonment of DDT since the 1970s (Krüger, Grünkorn & Struwe-Juhl 2010), ageing of the recolonizing population and the associated higher reproductive rate. The goshawk 3916 population also showed a negative trend between reproduction and population density (Table 1). There was significant heterogeneity among the correlation coefficients between density and reproductive rate between the eight populations ($\chi^2_7 = 20.516$, $P < 0.01$). Duration of the time series, latitude, longitude or species as explanatory variables were not significantly associated with the variation in correlation coefficients (*all* $P >> 0.05$).

To better visualize the potential influence of density on breeding success, we separated years having the highest or lowest population densities for each population, as recommended by Ferrer, Newton & Casado (2008). The brood size histograms differed significantly or showed a strong trend between low and high population densities for three of the eight data sets (Fig. 2: goshawk 3916: $\chi^2_3 = 7.57$, $P < 0.06$; goshawk Denmark: $\chi^2_4 = 8.737$, $P < 0.07$; common buzzard: $\chi^2_3 = 44.22$, $P < 0.001$). Five data sets showed no significant shift in distribution of brood size (Fig. 2: goshawk 3816: $\chi^2_3 = 4.011$, $P > 0.25$; goshawk Schleswig: $\chi^2_4 = 2.359$, $P > 0.75$; sparrowhawk large: $\chi^2_6 = 5.659$, $P > 0.25$; sparrowhawk small: $\chi^2_6 = 3.908$, $P > 0.5$; white-tailed eagle: $\chi^2_2 = 0.004$, $P > 0.99$). The frequency of failed broods increased during high population densities in five of

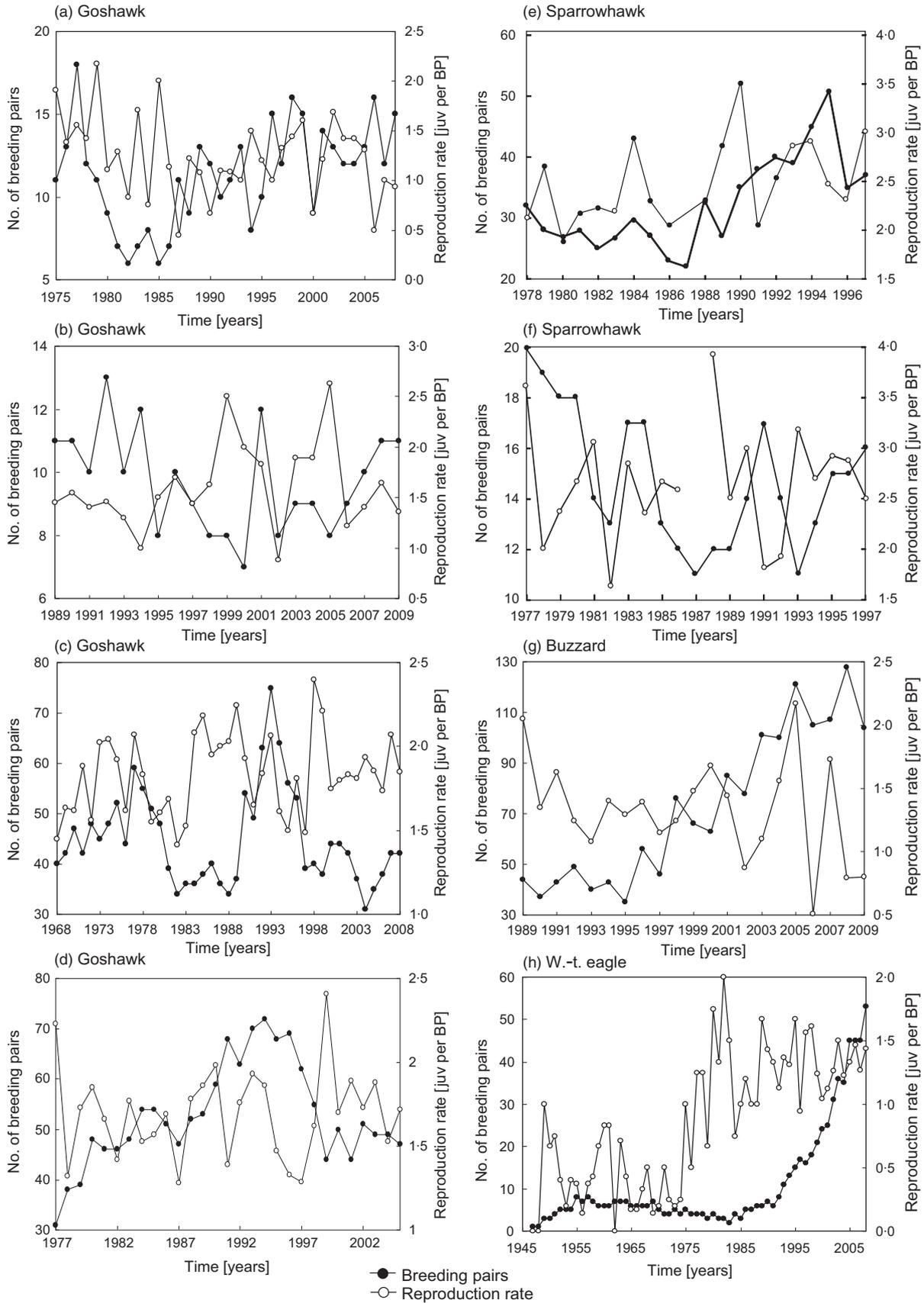


Fig. 1. Population dynamics and reproductive rate dynamics (juveniles per breeding attempt) for the nine populations (goshawk 3816 = a, goshawk 3916 = b, goshawk Schleswig = c, goshawk Denmark = d, sparrowhawk Denmark large = e, sparrowhawk Denmark small = f, common buzzard = g, white-tailed sea eagle = h).

Table 1. Correlation coefficients between population density and time and between population density and reproduction rate across the eight studies. The final column provides the duration of the time series in years

Study	Time	Reproduction	Study length [years]
Goshawk 3816	0.393	-0.151	34
Goshawk 3916	-0.259	-0.369	21
Goshawk Schleswig	-0.135	-0.070	41
Goshawk Denmark	<i>0.342</i>	-0.262	29
Sparrowhawk Denmark L	0.698	0.337	20
Sparrowhawk Denmark S	-0.475	-0.137	21
Common Buzzard	0.939	-0.194	21
White-tailed eagle	0.701	0.418	62

Significant relationships ($P < 0.05$) are highlighted in bold, trends ($P < 0.1$) in italics.

the eight populations. The populations notably changing their distribution of brood size between high and low densities were those of common buzzard and goshawk 3916. Reproductive success shifted from a normal, tentatively right-skewed distribution at low densities to a left-skewed one in high density years (Fig. 2).

CROSS-TERRITORY ANALYSES

Reproductive rate was positively correlated with territory quality in four of the eight studied populations. Reproductive rate was not correlated with the number of times a territory was occupied by the end of the study period, i.e. territory quality in the goshawk 3816 and 3916 and in the small Denmark sparrowhawk and the white-tailed eagle populations. A significant correlation between reproductive rate and territory quality was evident in the goshawk Schleswig and Denmark, and in the buzzard populations. Notably, correlations were evident in all populations where more than 100 territories were studied (Table 2). Reproductive rate in a territory decreased with first year of use only in two instances – the Schleswig goshawk and the common buzzard populations. These represented two of the three largest territory samples considered in our study.

MULTIVARIATE ANALYSES

Proportional occupancy of the territory appeared in the best models of seven of eight data sets of reproductive success in the study populations (Table 3). Additionally, territory quality entered the best models explaining reproduction in the goshawk 3816 population. Reproduction increased with proportional occupancy of a territory and territory quality. Population density in the previous year of breeding joined the explanatory models for reproductive output in the goshawk 3916 and common buzzard populations, while density joined the best models for common buzzard. The effect of density of reproductive output was positive for white-tailed eagles. This

strong increase in both reproductive output and density can be traced back to an overall re-colonization of Schleswig–Holstein, analysed in more detail by Krüger, Grünkorn & Struwe-Juhl (2010). Since territories occupied only in later years might indicate low-quality territories, start year of territory use was supposed to enter models as a negative predictor, but it only entered as a positive predictor in white-tailed eagles (Table 3). Annual mean temperature of the previous year entered best models for three of eight data sets with higher temperatures being associated with higher reproductive success.

Models incorporating individual identity of the breeding female were very similar. In most cases, there was significant variation among individual females (random factor individual identity was significant at $P < 0.05$ except for the goshawk 3816 data set). In three of five data sets, laying date entered the best models as a negative predictor (early laying coinciding with higher reproductive success) and age of the breeding female entered best models as a positive predictor of reproductive output in two out of five extended data sets. Laying date entered the best models of reproduction in the goshawk Denmark, the small sparrowhawk Denmark and the buzzard populations (Table 3). Age became part of the best extended models for reproduction in the goshawk 3816 and the large Denmark sparrowhawk populations. Nevertheless, proportional occupancy of the territory entered the best models in all five extended data sets, whereas density entered only the best models for the common buzzard extended data set, and delayed density was never included. Annual mean temperature of the previous year entered best models for three of five data sets (goshawk 3816 and both Denmark sparrowhawk populations).

Discussion

Our results show most clearly a higher reproductive success in high-quality territories. At the same time, we found very limited support for a negative influence of direct or delayed density *per se* on reproduction in the spectrum of long-lived birds of prey that we analysed. These results strongly favour the habitat heterogeneity hypothesis, while we found weak support for the individual adjustment hypothesis.

Site-dependent reproductive success is common in raptors. Similar results have been obtained for other species of birds of prey (Carrete *et al.* 2006; Sergio *et al.* 2007, 2009) and for other bird species such as mute swans *Cygnus olor* L. (Nummi & Saari 2003) and great tits *Parus major* L. (Dhondt, Kempenaers & Adriaensen 1992), although the mute swan study did not analyse interference in combination with effects of habitat heterogeneity. Studies showing intra-specific interference at higher densities to induce a decrease in reproductive success are less common (Ferrer & Donazar 1996; Haller 1996). Two of the examples come from old-world vultures, a small group of particularly large birds of prey foraging on a very unpredictable resource (carcasses). Reproductive success of griffon vultures (*Gyps fulvus* Habl.) was explained by nest-site characteristics and by regional

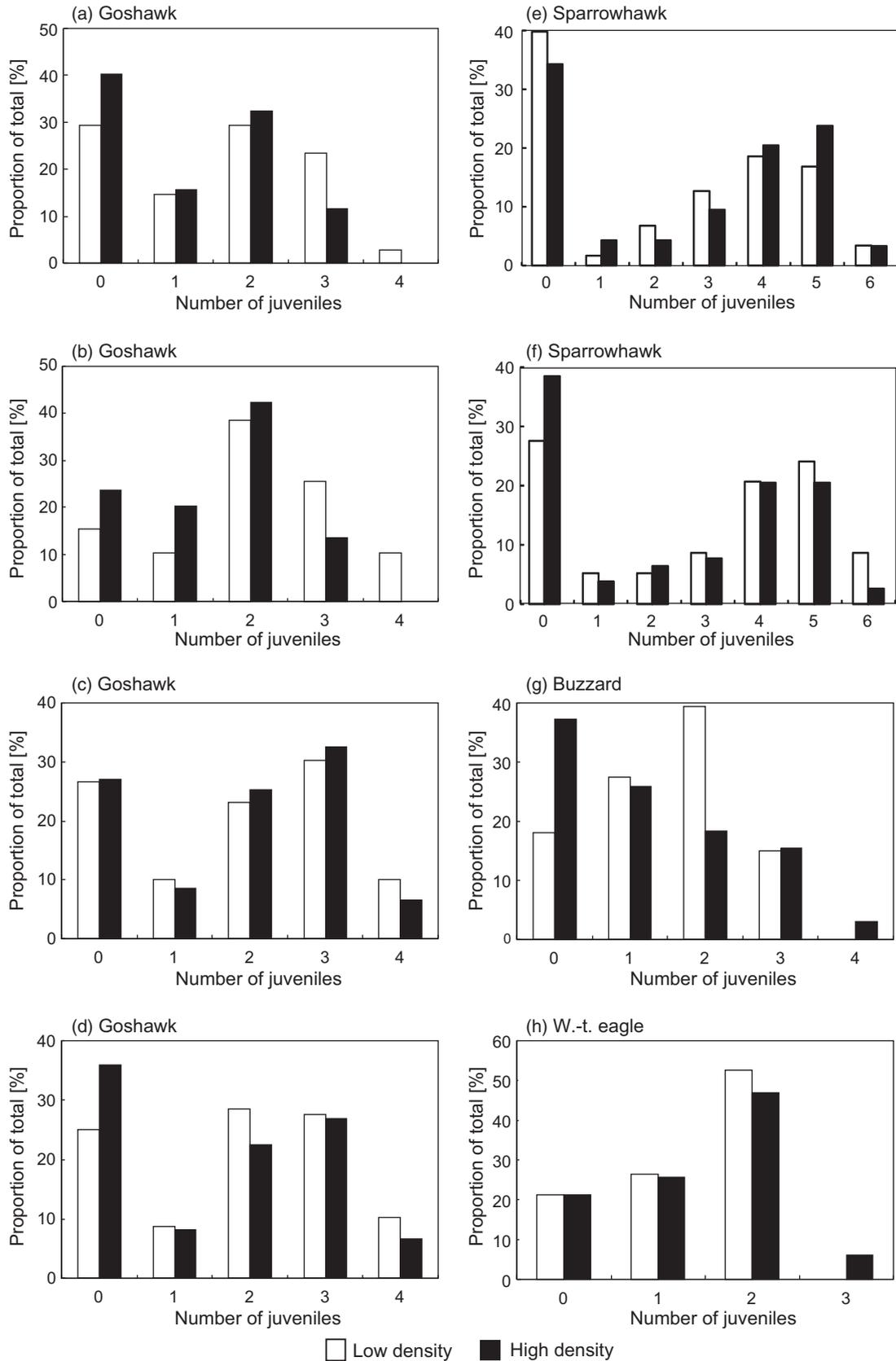


Fig. 2. Differences in the frequency distribution of reproductive success between years with low population density (white bars) and years with high population density (black bars). For each study, the 5 years with the lowest and highest population density were included, respectively. Letters refer to goshawk 3816 = a, goshawk 3916 = b, goshawk Schleswig = c, goshawk Denmark = d, sparrowhawk Denmark large = e, sparrowhawk Denmark small = f, common buzzard = g, white-tailed sea eagle = h.

Table 2. Correlation coefficients between territory quality, first year of use and mean reproduction rate per territory for the eight studies. Entries provide the correlation coefficient. Territory quality was estimated by territory occupancy

Study	Territory quality	First year of use	No. of territories
Goshawk 3816	0.017	-0.235	34
Goshawk 3916	0.187	0.022	19
Goshawk Schleswig	0.276	-0.168	143
Goshawk Denmark	0.359	-0.135	113
Sparrowhawk Denmark L	0.152	0.056	290
Sparrowhawk Denmark S	0.066	-0.095	63
Common Buzzard	0.174	-0.244	209
White-tailed eagle	0.122	-0.137	53

Significant relationships ($P < 0.05$) are highlighted in bold.

density. The latter best described the probability of meeting severe competition at the next carcass (Fernandez, Azkona & Donazar 1998). Similarly, fecundity in bearded vultures (*Gypaetus barbatus* L.) decreased with density, but much more drastically when nest sites were close to a small supplementary feeding point. There, food attracted many non-breeding individuals and probably caused higher stress from interference for local breeders (Carrete, Donazar & Margalida 2006). The foraging and feeding behaviour of old-world vultures clearly predisposes them for high sensitivity to scramble competition and individual adjustment of fecundity to higher densities. In addition, Haller (1996) found clear effects of density on golden eagle (*Aquila chrysaetos* L.) reproduction in a long-term study.

Individual adjustment can also arise when food is not necessarily clumped but simply scarce. Both (1998) found an indistinguishable decrease in individual and population reproductive success at higher densities in great tits (*Parus major* L.), concluding that most individuals experienced similar clutch reduction. This reduction was thought to be an adaptation to higher competition for food (Both, Tinbergen & Visser 2000). As an experimental density manipulation was not able to reproduce the pattern, the main pressure has been reasoned to occur outside the nestling stage (Nicolaus *et al.* 2009). Experimental support for the prerequisites of individual adjustment to density comes from a study showing better provisioning rates and enhanced fledgling production when density of black-throated blue warblers (*Dendroica caerulescens* Gmel.) was artificially decreased. This pattern, however, appeared only under poor conditions (Sille, Rodenhouse & Holmes 2004). Although small birds are more likely to be influenced by poor environmental conditions, most animal species respond to fluctuations in food abundance. Among the species used in our study, the common buzzard is the most specialized, and its microtine prey shows significant population fluctuations (Mebs 1964). Prey abundance strongly determines and couples annual buzzard density and brood size (Lehikoinen *et al.* 2009), as shown by the disparate distributions of buzzard brood size at different densities (Fig. 2). Nevertheless even in this species, territory quality

Table 3. Multivariate modelling of reproduction for each study. Model selection was based on Akaike's Information Criterion (AIC). Models where information on identity, age and laying date was included are referred to as 'extended'

Model description	Δ AIC	Model weight
Goshawk 3816		
Terr quality + Terr proportion	0.0	0.263
Terr quality	0.3	0.227
Goshawk 3816 extended		
Terr proportion + Age + Temp T-1	0.0	0.115
Terr qual + Terr proportion + Age + Temp T-1	0.0	0.115
Terr qual + Terr proportion + Age	0.1	0.109
Goshawk 3916		
Terr proportion + Density T-1	0.0	0.535
Terr proportion	1.4	0.266
Goshawk Schleswig		
Terr proportion	0.0	0.735
Goshawk Denmark		
Terr proportion + Temp T-1	0.0	0.846
Goshawk Denmark extended		
Laying date	0.0	0.428
Terr proportion + Laying date	1.1	0.247
Sparrowhawk Denmark L		
Terr proportion + Temp T-1	0.0	0.197
Terr proportion + Temp + Temp T-1	0.3	0.170
Terr proportion + Temp	0.5	0.154
Sparrowhawk Denmark L extended		
Age + Temp T-1	0.0	0.256
Age + Terr proportion + Temp T-1	0.2	0.231
Age + Temp + Temp T-1	0.4	0.209
Sparrowhawk Denmark S		
Terr proportion + Temp T-1	0.0	0.164
Terr proportion	0.6	0.122
Temp T-1	0.8	0.110
Sparrowhawk Denmark S extended		
Terr proportion + Laying date	0.0	0.330
Laying date	0.4	0.271
Laying date + Terr proportion + Temp T-1	0.5	0.123
Common buzzard		
Terr proportion + Density + Density T-1	0.0	0.314
Terr proportion + Density + Density T-1 + Temp	1.2	0.172
Terr proportion	1.3	0.164
Common buzzard extended		
Terr proportion + Laying date + Density	0.0	0.711
White-tailed eagle		
Start year + Temp	0.0	0.259
Density + Temp	0.6	0.192

Start year, year of first territory occupancy; Terr quality, territory quality (no. of years of occupancy); Terr proportion, proportional occupancy (proportion of occupancy since first year of use); Age, age of the breeding female in years; Density, population density at time t ; Density, population density at time t ; Density T-1, population density at time $t-1$; Temp T-1, mean annual temperature at time $t-1$.

plays an equally important role as population density in explaining reproductive success. Overall scarcity and/or distribution of food, along with factors such as food

specialization, can lead a species to being substantially more sensitive to competition.

Density in the previous breeding season did have a negative effect on reproductive success in two of the eight analysed populations. Such an effect could appear if many individuals are able to produce only small broods after a successful breeding season at high densities. Our analyses probably underestimate this effect, because nonbreeders could not be considered in all data sets, while weakened individuals in long-lived species can easily skip a breeding attempt. Still, food abundance is likely to be one of the main factors determining density and reproductive investment in the examined species (Krüger 2002; Rutz & Bijlsma 2006; Millon *et al.* 2009). Because most of them are opportunistic predators, being buffered against fluctuations of a single prey species might be adaptive. The relative scarcity of direct or delayed density dependence in our results are seemingly contradictory to the pattern found in a semi-desert raptor community, where direct density dependence played a significant role in explaining population dynamics (Krüger, Liversidge & Lindström 2002), probably due to most species feeding on the same food resource. Moreover, in that population-level study, territory quality was not accounted for and could still represent the most influential determinant of reproductive success.

The proportion of time a territory was occupied since its first use was a better predictor of reproductive success than the number of years it has been occupied. While the distribution of territory quality is commonly slightly left-skewed (Sergio & Newton 2003), the proportional territory occupancy was constantly slightly right-skewed. Hence high-quality territories can also be established late in population history. Nevertheless, once occupied, they will support frequent breeding and high reproductive success. In support of this notion, the year of territory establishment had an influence on reproductive success only in one of the inferior models for one study. This could indicate that local environmental characteristics favourable for breeding are hard to detect not only for researchers, but also for their study species. Prime territories are not necessarily the first to be established but are used more often. Thus, for a species that has not reached carrying capacity of a study area, the number of years a territory has been used should not always *a priori* be interpreted as higher-quality habitat compared to a site that has never been occupied (Cianfrani *et al.* 2010).

We detected a strong influence of habitat heterogeneity on reproductive success in all populations, although there was only a significant left-skewed distribution of reproductive success at high population densities in the common buzzard. In all goshawk populations, the distribution of fecundity was quasi-normal, while in the cases of sparrowhawk and white-tailed eagle, it was right-skewed, irrespective of density (Fig. 2). The logical expectation of the HHH is an increasing frequency of small and failing broods at high density (Ferrer, Newton & Casado 2008). However, when density does not influence reproductive success significantly as in most of our study populations, there should be no *a priori* expectation for

the distribution of reproductive success in the population. Thus if there are many often used, high-quality territories and few seldom-used, low-quality territories, neither a normal nor a left-skewed distribution of reproductive success should occur in the population. While this example is extreme, it is possible that many potential breeding sites are not particularly suboptimal (Pagan, Martinez & Calvo 2009). Hence, we would argue that several test procedures should be employed to disentangle the two competing hypotheses rather than relying on brood size histograms alone.

Although many studies found an association between habitat heterogeneity and reproductive success, some failed to find such a relationship (e.g. Pagan, Martinez & Calvo 2009). In our case, the effect of habitat heterogeneity became obvious in all populations only after multivariate modelling. Bivariate correlations of territory quality and reproductive rate were only significant in data sets encompassing more than 100 territories. Similarly, a correlation between reproductive rate and start year of territory use appeared only in two of the three largest populations, the third being by far the largest data set. Unfortunately, such large sample sizes are extremely rare, although their use in generalized linear (mixed) models may help remedy the current heterogeneity in results among studies.

A word of caution is also warranted at this point because our data sets cover almost seven decades and both climatic and abiotic changes have occurred over these time spans. This might well explain the large variation observed in the importance of habitat heterogeneity for reproductive output. Especially for sparrowhawks, territories systematically change in their quality over time as young stands of conifer which is prime nesting habitat, mature and become progressively unsuitable (Newton 1991). While we included weather variables to address the issue of long-term changes in the environment, the abiotic environment is just one part of this, although a very important one for birds of prey (Newton 1986; Kostrzewa & Kostrzewa 1990; Steenhof, Kochert & McDonald 1997; Krüger 2002). Temperature in the previous year was important for three of eight data sets, with higher temperatures coinciding with higher reproductive success. Such an association has been found before (Kostrzewa & Kostrzewa 1990; Krüger 2002, 2004), and the most likely mechanism is that warmer years provide subsequently more food for birds of prey.

Considering traits that reflected individual quality in the models did not substantially change conclusions. Age and laying date were important factors explaining female-specific reproductive success, as previous analyses of some data sets have established (Nielsen & Drachmann 2003; Krüger 2005; Krüger, Grünkorn & Struwe-Juhl 2010). The main reason for the increase in fecundity with age most probably is the improving experience of breeders in subsequent breeding attempts (e.g. Balbontín *et al.* 2007). Foraging skills commonly improve with age (MacLean 1986), increasing the probability of raising large broods. A recent study of black kites (*Milvus migrans* L.) has shown additional selection

against low-output breeders (Blas, Sergio & Hiraldo 2009), although previous analyses point out that this is not the case in at least two of our study populations (Nielsen & Drachmann 2003; Krüger 2005). Laying date is an important component of reproductive timing and can occur earlier under favourable conditions, then coinciding with larger broods (e.g. Nielsen & Møller 2006). A calendar effect, where individuals in prime condition start breeding earlier and are more successful, should be expected if timing is adaptive (Sockman & Schwabl 2001). This pattern is indeed found in many species (Verhulst & Nilsson 2008).

The comparatively low reproductive rates of long-lived species such as birds of prey increase their extinction risk (Owens & Bennett 2000; Krüger & Radford 2008) and make precise targeting of conservation efforts even more crucial. We have shown that reproductive success in long-lived birds of prey is commonly determined mainly by individual quality and habitat characteristics rather than population density *per se*. These findings support the approach of primarily conserving high-quality territories (Krüger & Lindström 2001a; Sergio & Newton 2003). The recognition of such sites could be problematic as some of the relationships became obvious only in the most long-term data sets with large sample sizes. Territory quality can be estimated using reproductive success once they have been used for breeding for a number of years. However, unused sites should not automatically be dismissed as being of low quality and rejected for conservation.

Acknowledgements

We are indebted to M. Boerner, S. Kalinski, U. Ostermüller and U. Stefener who helped with data collection. We are also grateful to F. Trillmich and F. Sergio for comments on the manuscript. This study was funded by a Royal Society Research Fellowship and a Heisenberg-Professorship of the German Science Foundation (DFG) to O.K. (KR 2089/2-1). N.C. was supported by the Volkswagen Foundation within its Evolutionary Biology initiative, grant I/84-196.

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Received 8 March 2011; accepted 17 August 2011

Handling Editor: Peter Bennett