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Hunting behaviour and breeding performance of northern goshawks *Accipiter gentilis*, in relation to resource availability, sex, age and morphology

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Abstract Animal territories that differ in the availability of food resources will require (all other things being equal) different levels of effort for successful reproduction. As a consequence, breeding performance may become most strongly dependent on factors that affect individual foraging where resources are poor. We investigated potential links between foraging behaviour, reproductive performance and morphology in a goshawk *Accipiter gentilis* population, which experienced markedly different resource levels in two different parts of the study area (rabbit-rich vs. rabbit-poor areas). Our analyses revealed (1) that rabbit abundance positively affected male reproductive output; (2) that age, size and rabbit abundance (during winter) positively affected different components of female reproductive output; (3) that foraging movements were inversely affected by rabbit abundance for both sexes (for females, this may mainly have reflected poor provisioning by males in the rabbit-poor area); (4) that younger breeders (both in males and females) tended to move over larger distances than older individuals (which may have reflected both a lack of hunting experience and mate searching); and (5) that male body size (wing length) showed some covariation with resource conditions (suggesting possible adaptations to hunting agile avian prey in the rabbit-poor area). Although we are unable to establish firm causal relationships with our observational data set, our results provide an example of how territory quality (here, food abundance) and individual features (here, age and morphology) may combine to shape a predator's foraging behaviour and, ultimately, its breeding performance.

Keywords *Accipiter gentilis* · Age · Breeding performance · Foraging movements · Goshawk · Habitat heterogeneity · Phenotypic traits

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Introduction

Habitat heterogeneity is a key driver of the demographics and dynamics of animal populations, with habitat quality often linked to variation in survival and reproductive output (e.g. Ostfeld et al. 1985; Roese et al. 1991; Blondel et al. 1993; Laaksonen et al. 2004; Penteriani et al. 2004). Territories that differ in food quality or availability are expected to require (all other things being equal) different levels of effort for successful reproduction (Catchpole and Phillips 1992; Ens et al. 1992; Siikamäki 1995); accordingly, breeding performance may be most strongly dependent on foraging ability where resources are poor (Winkler and Allen 1996; Espie et al. 2004 and references therein). Thus, a full understanding of habitat-related population processes requires a detailed investigation of how breeding performance is affected both by territory quality itself (e.g. food availability) and by the features of the individual breeders (e.g. age, physical condition, morphology) (for birds: Hill 1988; Bart and Earnst 1999; Lõhmus and Vali 2004; Sergio et al. 2009; Burgess et al. 2011).

We examined the topic of habitat–individual interactions with unusually detailed data from a population of radio-tagged goshawks *Accipiter gentilis* on the island of Gotland. Importantly, in different parts of our study area, goshawks experienced marked (and stable) differences in resource conditions. While hawks in coastal areas had good access to rabbit *Oryctolagus cuniculus* prey in semi-natural habitats of grassland and scrubby pine, birds breeding inland faced low rabbit densities and had to forage for alternative prey (see below). We systematically compared age and morphology of breeders with foraging movements and breeding performance in these goshawk 'subpopulations' in 'rabbit-rich' and 'rabbit-poor' areas (Kenward et al. 1993a, b, 1999). On the basis of earlier work linking goshawk home range size to habitat structure and food availability (Kenward 1982), we hypothesised an inverse relationship between resource (rabbit) abundance and foraging movements, with ranging patterns in turn inversely correlated with breeding performance. As hunting efficiency and breeding performance tend to increase with age in raptors (e.g. Newton et al. 1981; Penteriani et al. 2003; Rutz et al. 2006a), we examined (and where necessary controlled for) possible age effects.

As a next step, we investigated whether any of these possible effects on ranging behaviour and breeding performance were linked to individual morphology, with its assumed phenotypic component. There is some evidence that goshawk morphology can adapt rapidly to changing environmental conditions (Tornberg et al. 1999; see also Yom-Tov and Yom-Tov 2006), and intense directional selection (Kingsolver et al. 2001) on body size in resource-poor conditions (Hoffmann and Parsons 1997; Nager et al. 1998; Charmantier et al. 2004) may have led to detectable differences in our sample of birds. While goshawks in the rabbit-rich area predominantly killed rabbits during the breeding season, their counterparts in the rabbit-poor area hunted smaller and more agile prey (mainly corvids and thrushes) (Kenward et al. 1993a; for a review of goshawk diet choice across Europe, see Rutz et al. 2006b). These alternative prey species require different hunting and transportation ability, with small- and medium-sized birds selecting for small size and high agility in their predators (Storer 1966; Pennycuick 1975; Newton 1979; Hakkarainen et al. 1996). Therefore, we predicted that (1) because *Accipiter* males are almost solely responsible for hunting from incubation to fledging (Newton 1979; Kenward 2006), the size of males breeding successfully might reflect differences in prey availability between the rabbit-rich area (favouring large males) and the rabbit-poor area (favouring small males) and (2) if small males forage best for the scarce resources in the rabbit-poor area, morphological advantages might be reflected in offspring quantity or quality.

Methods

Study area and species

The study was conducted in a belt of ca. 846 km^2 across the 3,100-km^2 mid-Baltic island of Gotland. The area comprised woodland (54 %, mainly Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*; a total of 48 goshawk nest sites) and open stretches of pasture and arable farmland. Rabbits were especially abundant in the eastern part of the study area (the rabbit-rich area: one goshawk breeding territory per 10.5 km^2; for details, see Kenward et al. 1993a, b), which had extensive areas of grassland on shallow soil and bare limestone. The rich-soiled and more agricultural western area (the rabbit-poor area) had a goshawk breeding density that was about half of that in the rabbit-rich area (one goshawk breeding territory per 20.3 km^2). Rabbits on Gotland were eaten year-round by radio-tagged goshawks (but mostly by females when rabbits were full grown). Young corvids *Corvus* spp. and thrushes *Turdus* spp. were also important among prey recorded during nest visits (Fig. 1). Adult males provide most food during the breeding season, while females incubate and guard the young (Reynolds 1972; Kenward 2006). Previous studies had demonstrated that the different abundance of rabbits between these two areas affected goshawk sociality, dispersal dates and distances, and nest switching of young after fledging (Kenward et al. 1993a,b).

Goshawks show strong reversed sexual size dimorphism: in Sweden, females weigh 60 % more than males (in winter) and have wings that are 13 % longer (Marcström and Kenward 1981). This size dimorphism is associated with differences in breeding roles (see above) and winter diet (i.e. females kill larger prey than males; Kenward et al. 1981). During 1980–1984, morphology and movements were recorded for 131 adult (59 males and 72 females) and 196 juvenile (103 males and 93 females) goshawks that had been equipped with VHF radio tags on full-grown tail feathers. For adults, we also assessed breeding performance. Nest trees were climbed first to count eggs, then again to weigh and measure downy nestlings (wing lengths for ageing), and finally one last time to ring and measure nestlings close to fledging (tarsus width and sternum length from the clavicular notch to the distal end; for sexing and size indication). The latter measures, together with wing lengths, were also taken when older hawks were trapped with hardened feathers for radio tagging. Radio tracking used three-element hand-held

Yagi antennas and six-element Yagis mast-mounted on a vehicle to record bird locations from within 1 or 2 km, respectively, for ca. 100-m accuracy. Each radio-tagged hawk was located routinely one to two times weekly, with additional periods during winter when three foraging locations were recorded daily for 10 days to record kills and to obtain standard-effort 30-location home range estimates. For further details of measuring and radio tagging/tracking procedures, see Kenward et al. (1993a, b, 1999, 2001) and references therein. We estimated home range sizes with ellipses, because samples of as little as 10–12 locations are adequate to achieve stable estimates with this technique (Kenward 2001), and we only had 10–15 location records for adults tracked during incubation and chick rearing. Juvenile movements are those recorded after dispersal.

Statistical analyses

We constructed a set of a priori competing models starting from the simplest null model (intercept only) to a full model that included all of the explanatory variables to examine the effect of different predictor variables on our suite of response variables. Response and predictor variables were grouped into three main topics (for details, see ESM 1): (1) adult breeding performance, (2) adult and juvenile movements and (3) adult body size.

Depending on the response variables we were testing, models were run on different subsamples of birds according to data completeness (not all field data were available for all individuals). Since there was no significant between-year variation in the above-mentioned parameters for each area, sex group and age group (after controlling for rabbit availability) (ANOVA and Kruskal–Wallis tests, $P > 0.1$, and see also Kenward et al. 1993a, b, 1999), data were pooled across years. To reduce collinearity and the number of putative predictor variables, we employed the method of variable reduction proposed by Green (1979) where pairs of intercorrelated variables ($r > 0.6$) are considered as estimates of a single underlying factor; only the variable judged of greatest importance to the study organism is retained for analysis. Of the remaining variables, only those for which high univariate differences ($P < 0.1$) were detected between rabbit-rich and rabbit-poor areas were included in the models.

Depending on whether the error structure of the response variables followed normal, binomial or Poisson distributions, data were modelled using identity, logit and log-link functions, respectively. Detection of the most parsimonious hypothesis was based on model selection procedures using the Akaike information criterion (AIC), which enables comparison of multiple working hypotheses. As the ratio of the sample size to the number of parameters was usually less than 40, we used the second-order AIC derivation, the AICc (Burnham and Anderson 2002). Two AIC statistics were calculated for each model: ΔAIC and weighted AIC, which indicate the probability that the model selected is the best among the different candidates. Values of $\Delta\text{AIC} \leq 2$ were used as the criterion for selecting the best models, i.e. those with substantial support from the data (Burnham and Anderson 2002). All analyses were performed using lme4 (version 0.999375-28) (Bates and Sarkar 2007) in the R software package (R Development Core Team 2009).

For all analyses, means are given ±1 SD, tests are two-tailed, and statistical significance was set at $\alpha \leq 0.05$. For robustness with small samples, *t* tests and Mann–Whitney *U* tests (Sokal and Rohlf 1981) were used both for general comparisons between the rabbit-rich and rabbit-poor areas, and for testing possible relationships between age and morphology. When multiple tests were performed on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989). Pseudo-replication was absent for radio-tracked birds because they carried tags for only one season.

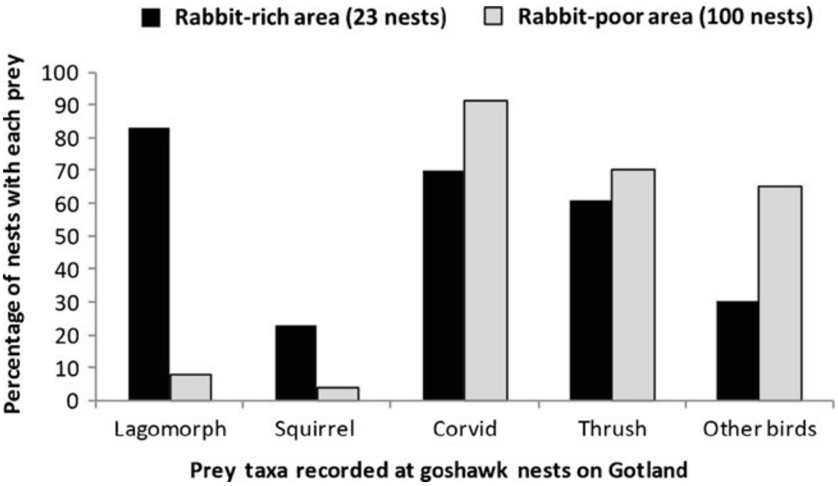

Fig. 1 The percentage of active goshawk nest territories in Gotland at which fur, feathers or bones of lagomorphs, squirrels, corvids, thrushes and other birds (primarily game birds, pigeons and waterfowl) were recorded during one to three visits to count eggs, measure young and ring them shortly before fledging

Results

Reproductive output and sex ratios

Goshawk pairs in the rabbit-rich area had larger clutch sizes (rabbit-rich area=3.0±0.8 eggs; rabbit-poor area=2.1±1.2 eggs; $z_{7,39}=-2.13$, $P=0.03$) and produced more offspring (rabbit-rich area=1.86±0.9 offspring; rabbit-poor area=0.8±1.2 offspring; $z_{10,34}=-2.14$, $P=0.03$) than those in the rabbit-poor area. Including broods from both radio-tagged and untagged adults, there was no difference in brood sex ratio, calculated as the percentage of fledged males, between the two areas (rabbit-rich area=54.9±34.1 %; rabbit-poor area=51.4±32.5 %; $z_{46,126}=-0.66$, $P=0.51$).

Male breeding performance and foraging distances

The six radio-tagged males breeding in the rabbit-rich area produced on average more fledglings than the 23 males in the rabbit-poor area (rabbit-rich area=2.5±0.6 fledglings; rabbit-poor area=0.9±1.3 fledglings; $z_{6,23}=-1.95$, $P=0.05$). Among the total of 29 radio-tracked adult males that bred, most young were fledged by those that had the shortest foraging distances from the nest during courtship (i.e. the month before egg laying; Fig. 2a) and the greatest mass (Table 1, male, result i) when caught pre-breeding. During brood rearing, the older males tended to cover the shortest distances from nests (Fig. 2b; Table 1, male, result ii), and the average distances between consecutive locations of males with and without broods were smallest in the rabbit-rich area (rabbit-rich area=1,367.6±463.2 m; rabbit-poor area=2,678.3±1,909.0 m; $t_{7,51}=3.24$, $P=0.002$).

Remarkably, adult males from the rabbit-rich area were larger in terms of wing length than those from the rabbit-poor area (rabbit-rich area=323.7±3.01 mm; rabbit-poor area=318.2±6.4 mm; $z_{6,49}=-2.38$, $P=0.02$). Moreover, high body mass of male nestlings in the rabbit-poor area was associated with short wing length amongst their fathers ($N=10$ males, chi-square=4.96, $P=0.026$).

Female breeding performance and foraging distances

Among 59 adult females tracked during the breeding season (Table 1, female, result i), older individuals were more likely to lay eggs than younger ones, and egg laying was associated with high numbers of rabbits in the winter before breeding. Similar to the finding for males, adult females with the shortest distances from the nest in the courtship period (before egg laying) fledged more young (Table 1, female, result ii), although in this case the effect was mainly for females whose broods failed (Fig. 2c), so that the 22 females that laid eggs also had smaller home ranges than non-breeding females (Fig. 2e). As for males, the youngest females were also most likely to move far from the nest but, in this case, during the courtship period (Fig. 2d; Table 1, female, result iii) and mostly in the rabbit-poor area. In addition, among the 21 females that laid a known number of eggs, the oldest had the largest clutches (Fig. 2f; Table 1, female, result iv). Although 9 out of these 21 females lacked size measurements, among the remaining 12 subjects, the largest birds fledged most young (Table 1, female, result v); female age and sternum length were not correlated ($t_{22,47}=0.27$, $P=0.79$).

Discussion

Our analyses revealed, among other relationships, (1) that rabbit abundance positively affected male reproductive output; (2) that age, size and rabbit abundance (during winter) positively affected different components of female reproductive output; (3) that foraging movements were inversely affected by rabbit abundance for both sexes (for females, this may mainly have reflected poor provisioning by males in the rabbit-poor area); (4) that younger breeders (both in males and females) tended to move over larger distances than older individuals; and (5) that male body size (wing length) showed some covariation with resource conditions.

Foraging distances during courtship seemed to be associated mainly with the final breeding outcome (i.e. the number of fledglings produced) in both sexes. The fact that reproduction was successful in 75 % of the nests in which eggs were laid (Kenward et al. 1999) indicates that egg failure or nestling mortality was quite low in the study area.

Breeding success of *Accipiter* hawks mainly depends on hunting by males until the young are several weeks old (Newton 1979, 1986; Kenward 2006). In goshawks, several studies have shown strong age dependence in male breeding performance, with young birds not breeding at all, failing their nesting attempts, or raising significantly fewer young than older birds (Kenward et al. 1999; Nielsen and Drachmann 2003; for a review, see Rutz et al. 2006a). We found that the youngest hawks in our sample made the longest foraging movements during brood rearing, possibly indicating a lack of hunting experience. Foraging skills improve with age in many bird species (e.g. Burger 1988; Marchetti and Price 1989; Wunderle 1991) and are particularly important for goshawks, given their reliance on agile prey (Krüger 2005; Rutz et al. 2006a; Rutz 2012). In urban-breeding goshawks, for example, males hone their pigeon-hunting skills (Rutz 2006) over the first few years of life (Rutz et al. 2006a), with gradually increasing selectivity for rare colour variants—a strategy with substantial fitness pay offs (Rutz 2012). Age and territory quality, in combination, have previously been highlighted as key determinants of female breeding performance for goshawks (Krüger 2005; Krüger and Stefener 2000; Krüger and Lindström 2001) and other *Accipiter* hawks

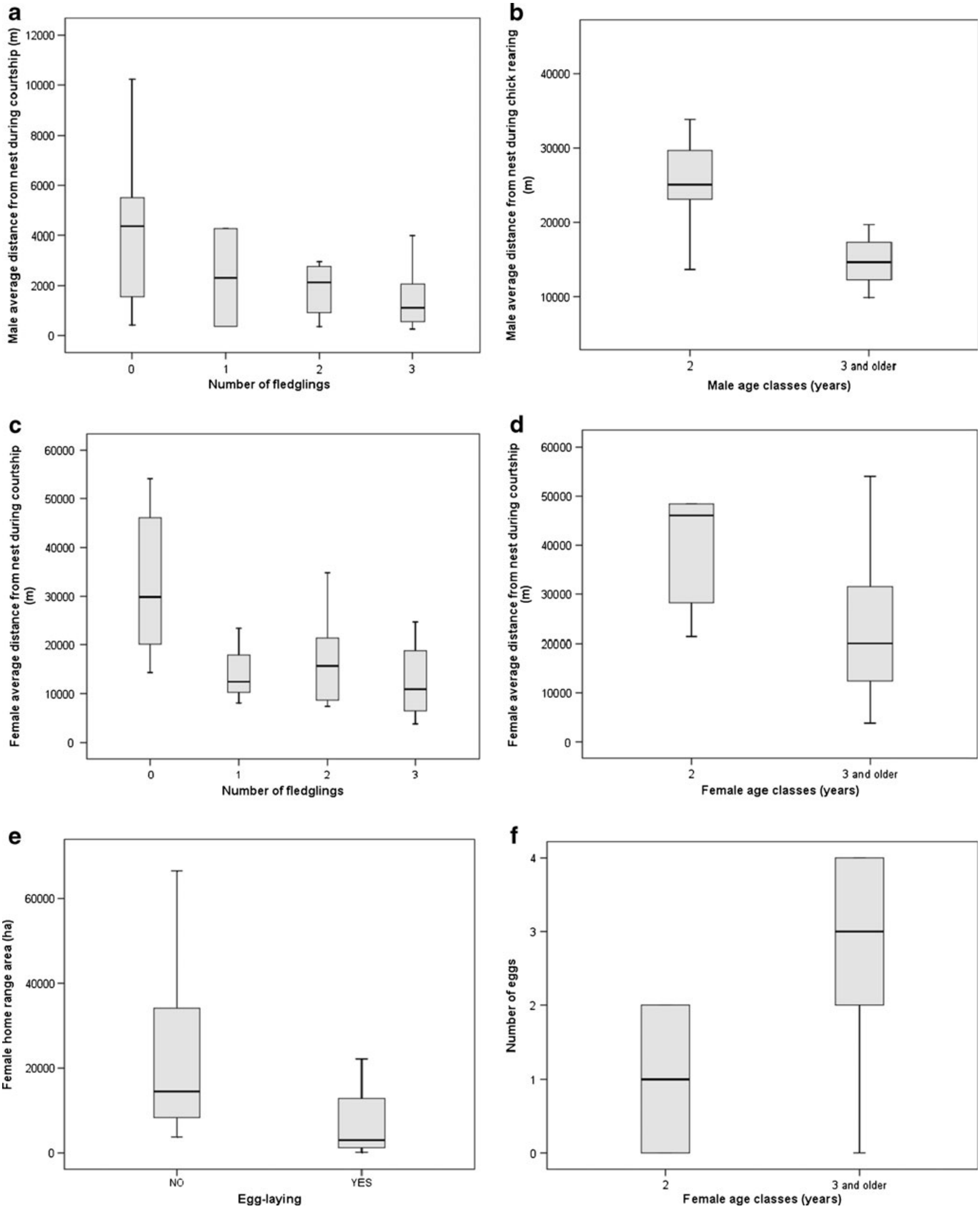

Fig. 2 Key associations between age, breeding performance (in terms of tendency to lay and brood sizes) and foraging movements (distances from the nest and range sizes) in goshawks from the island of Gotland. *Box plots* are for average values with quartiles, with *bars* showing range of values. For statistics, please refer to Table 1 and the main text

Table 1 Summary of models examining relationships between breeding performance, movements, age and adult morphology in male and female goshawks in Gotland. For selected models (ΔAIC≤2), parameter estimates (β±SE); AIC, AICc, ΔAICc, and AICcw values; and deviance are shown

Parameters	β±SE	AIC	AICc	ΔAICc	AICcw	Deviance
Male						
i. Number of fledglings (*N*=29)[a]						
Intercept	−1.523±2.936	77.48	79.40	−16.55	0.25	0.27
Mass of male breeder	0.003±0.003					
Average distance travelled during courtship[b]	−0.628±0.408					
ii. Average distance travelled during young rearing (*N*=28)[c]						
Intercept	4.248±0.394	20.34	20.82	−9.10	0.96	0.34
Age of male breeder	−0.512±0.142					
Female						
i. Whether a given hawk laid eggs[d] (*N*=59)[e]						
Intercept	−8.417±3.256	75.16	75.60	−7.52	0.00	0.23
Age of female breeder	1.959±1.029					
Rabbit density in the winter before breeding	0.001±0.001					
ii. Number of fledglings (*N*=22)[c]						
Intercept	2.431±0.737	60.05	60.68	0.88	0.35	0.26
Average distance travelled during courtship[b]	−0.848±0.283					
iii. Average distance travelled during courtship[b] (*N*=26)[c]						
Intercept	5.435±0.932	56.90	57.99	−1.78	0.53	0.23
Age of female breeder	−0.850±0.328					
Territory in the rabbit-rich or rabbit-poor area[f]	−0.075±0.328					
iv. Clutch size (*N*=21)[a]						
Intercept	−2.117±1.527	71.44	72.11	−3.15	0.48	0.28
Age of female breeder	1.059±0.520					
v. Number of fledglings (*N*=12)[c]						
Intercept	−14.299±6.211	26.46	27.79	−5.29	0.62	0.50
Sternum length of female	0.022±0.007					

[a] Poisson distribution, log-link

[b] March in the study area

[c] Normal distribution, identity link

[d] Categorical variable: 0=no eggs, 1=eggs laid

[e] Binomial distribution, logit link

[f] As defined in Kenward et al. (1993a, b)

(Newton 1991). Kenward et al. (1999) suggested that a few females with poor ability to contribute to brood raising may manage to nest by choosing an efficient male, but then show below-average fledging success, as was observed for some radio-tagged females of more than 2 years old. Females in our study travelled furthest during courtship when they were young, which could have resulted from poor foraging but perhaps most likely was the result of searching for good mates, because they tended to visit different breeding territories (Kenward 2006).

Body size effects observed in our males were in the same direction as long-term morphological changes found in Finnish goshawks, where small body size was associated with decreasing availability of the locally preferred prey (grouse) and consequent dietary shifts toward smaller prey (Tornberg et al. 1999). In contrast to our results, however, this earlier study found that the body size reduction was associated with an increase in male wing length. We currently have no convincing explanation for these opposing trends, although Marcström and Kenward (1981) found that sternum length was much more strongly related to body mass in goshawks than was wing length, which did not correlate strongly with sternum length. Our results suggest that small males enjoyed highest reproductive success in the rabbit-poor area, where small hawks may be more efficient in replacing rabbits by hunting small- and medium-sized birds, and shorter wings may facilitate the pursuit of agile prey in forests or close to woodland edges (Kenward 1982; Beier and Drennan 1997;

Sergio et al. 2007). Diet-related evolutionary changes have been described for a range of bird species (e.g. song sparrow *Melospiza melodia* (Schluter and Smith 1986), Darwin's finches (Grant and Grant 1989)). Although our findings provide a useful comparison to the study by Tornberg et al. (1999), we caution that they are based on small sample sizes and primarily reported here to stimulate future work in this area. An interesting test case for these ideas is the invasion of goshawks into cities across continental Europe (Rutz et al. 2006b; Rutz 2008) where stronger reliance on avian prey compared to non-urban habitats could select for smaller body size in both sexes (C. Rutz, unpublished).

Our analysis of radio-tracking data for both range size and distances travelled within ranges (e.g. from the nest and between locations) highlights the importance of considering a combination of different spatio-temporal factors and individual-level processes when studying animals' ranging behaviour (Campioni et al. 2013; Penteriani et al. 2013). The findings agree with those of recent studies that ascribed intraspecific variation in home range behaviour to both differences among individuals and resource availability (Börger et al. 2006; Saïd et al. 2009; Arlettaz et al. 2010; van Beest et al. 2011). In a range of terrestrial predators, foraging movements and reproductive output are related to the distribution and abundance of prey (e.g. Herfindal et al. 2005; Benson et al. 2006; Fernández et al. 2007; Mitchell and Powell 2007; Loveridge et al. 2009), with individuals in food-rich habitats using comparatively smaller areas to acquire sufficient food for survival and reproduction.

To conclude, although we were unable to establish firm causal relationships among our suite of variables, due to the non-experimental nature of our data, our results highlight how territory quality (here, food abundance) and individual features (here, age and morphology) may combine to shape a predator's foraging behaviour and, ultimately, its breeding performance.

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