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Site-specific variation in partial brood loss in northern goshawks

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While many studies have shown that patterns of partial brood loss often differ with offspring sex, food availability or between years, the question of whether family-size adjustment varies between sites has achieved little attention. I investigated this in Finnish northern goshawks *Accipiter gentilis*, and found that partial brood loss varied considerably between locations. This variation was present both between territories and between two larger regions with different densities of goshawks' main prey, grouse. Partial brood loss was inversely related to natural main-prey densities, but the relationship was far from straightforward: spatial nonlinearities arising from between-territorial differences influenced the results. Brood-loss patterns also differed between years and between initial clutch-size categories. Potential sex-biased post-hatching mortality was not related to grouse density and partial brood loss did not alter the original population-wide egg sex ratio. Between-territory variance in offspring sex ratios was low. The lack of the spatial dimension in earlier studies might have undermined a correct interpretation of the causes and consequences of brood-loss patterns, irrespective of whether sex ratios were biased.

Introduction

The phenomenon of secondary family-size adjustment is taxonomically widespread. Examples have been found in plants, invertebrates and mammals (Mock & Parker 1997). While a majority of studies in this field have focused on birds in the context of Lack's (1954) brood-reduction hypothesis, the diversity in brood-loss patterns observed is considerable. This has produced a wide array of hypotheses as to why broods are reduced (e.g., Magrath 1990, Mock & Parker 1997). Even if much of the observed variation is due to species differing in their biology, it is well-documented that partial brood loss ("some, but not all, members of a sibship dying from any and all causes"; Mock 1994) can vary as a result of morphological size, food availability and sex. For example, in size-dimorphic Tengmalm's owls *Aegolius funereus*, the smaller male nestlings suffered higher mortality when food was limited than when food was abundant, whereas female nestling mortality did not differ in response to food availability (Hipkiss *et al*. 2002). From this and other studies (e.g. Drummond *et al*. 1991, Nager *et al*. 2000, Koenig *et al*. 2001) it is clear that partial brood loss can be related to food availability and that the two sexes can differ in their sensitivity towards variation in food abundance.

From a wider perspective, it is possible that small-scale patterns such as those described above have repercussions for whole populations. Life-history patterns often differ across localities, e.g. in parallel with spatial variation in resource availability or weather. For example, seed production of trees or offspring number and offspring sex ratios of vertebrates do not necessarily vary only when measured between individuals or territories within a single study site, but can also vary between different sites situated hundreds or thousands of kilometres away (Koenig & Knops 1998, Mysterud *et al.* 2000, Przybylo *et al.* 2001, Byholm *et al.* 2002a, 2002b). As natural populations usually are spatially structured, and as dispersal between sites decreases with increasing distance (Clobert *et al.* 2001), spatially variable life history patterns must be quantified because local variations in life history patterns may have important ramifications for population dynamics. In this scenario, patterns of site-specific partial brood loss might play an important role — whether related or not to offspring sex ratios — but studies assessing whether partial brood loss vary between localities are almost absent from the literature (but *see* Valkama *et al.* 2002). More straightforward, in situations when sites are occupied over long periods, and partial brood-loss patterns differ between locations (e.g. territories and larger regions), lack of information regarding such nonlinearities could have consequences for the correct understanding of any brood-loss pattern. This will be the case when partial brood loss varies non-randomly between territories, and ‘territory’ is used as a study unit when trying to derivate factors explaining observed brood-loss patterns in general. Likewise, variation of partial brood loss can have consequences for other life-history events, such as offspring sex ratios.

To evaluate whether patterns of secondary family-size adjustment differ between territories and larger geographical areas, I analysed patterns of brood loss in northern goshawks *Accipiter gentilis* (from here onwards goshawk). Two adjacent areas with different prey densities during a four-year-period and a set of territories were compared. The goshawk is a long-lived, medium-sized and sexually dimorphic (females larger than males) raptor with high mate and territory fidelity (Cramp & Simmons 1980, Squires & Reynolds 1997). Throughout its range, medium-sized birds and mammals are important prey items, with forest grouse being the most important prey (60%–70% by weight) in Finland (Tornberg 1997). Recently it has been shown that the offspring sex ratio of Finnish goshawks is related to grouse density: more males are produced when/where grouse are abundant than when grouse are scarce (Byholm *et al.* 2002b). In addition, albeit the pattern is inconsistent between different regions, the proportion of males in goshawk broods has been observed to vary seasonally; the proportion of males increases, decreases or remains unchanged with advancing date (Byholm *et al.* 2002a).

Here I describe the general patterns of partial brood loss in goshawks and test whether partial brood loss is related to large-scale spatial variation in the density of goshawks’ main prey (grouse), while simultaneously accounting for potential territorial differences in brood loss. Finally, I address the question of whether partial brood losses can explain the seasonal and prey-dependent sex ratio patterns previously reported (Byholm *et al.* 2002a, 2002b).

Material and methods

Study area and partial brood loss monitoring

Goshawk reproduction was monitored during 1999–2002 in the western part of Finland, east from the small town of Närpiö (62°00´–62°55´N, 21°05´–22°40´E). The study area (Fig. 1) covers roughly 6300 km^2 and is dominated by heavily managed coniferous forest and mires (> 80% of the area). Other landscape components (fields, lakes, rivers, built-up areas) are less common. Despite heavy forest management practices, goshawks still nest quite commonly over the study area, the number of active nests ranging from 120 to 133 (mean ± SE: 125.7 ± 3.8) and the number of additionally occupied territories ranging from 28 to 33 (32.7 ± 2.6).

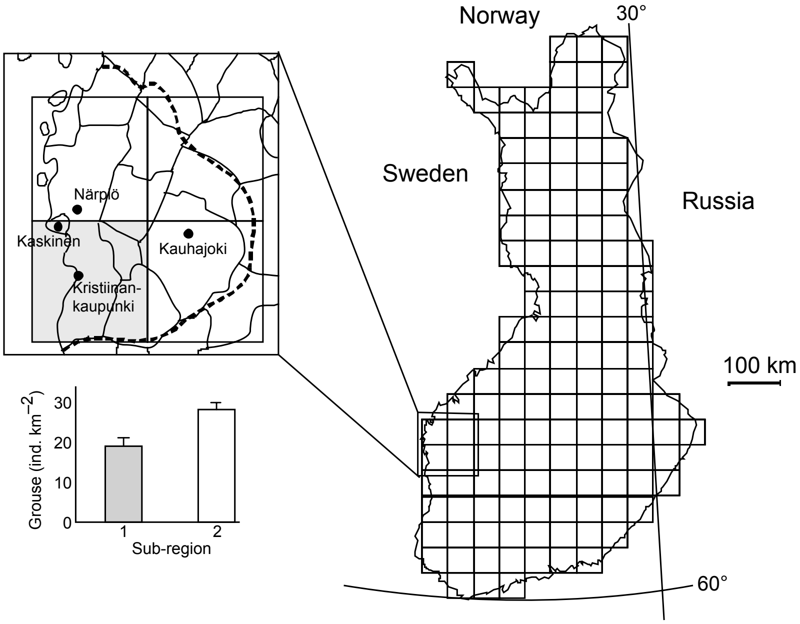

Fig. 1. Map of Finland with 50 × 50 km grids on top and the study area at the west coast. The exact border of the study area is indicated by the dotted line on top of municipality borders in the left side panel of the figure. The south-western most (filled with grey) of the four 50 × 50 km grids approximately laying on top of the study area has a significantly lower grouse density than the remaining three grids (mean + SE), as indicated by the bar-chart inserted with the map (grey bar referring to the SW-most grid, white bars to the remaining grids, *see* text for further details).

Fieldwork was initiated each year in late April–early May by counting the number of eggs in active goshawk nests (a total of 294 clutches in 1999–2002). The fate of the clutches was then followed at least until the nestlings were ringed in the end of June at an age of roughly three and a half weeks (26.1 ± 0.2 days, $n = 645$). As my objective here is to analyse partial brood-loss patterns, 43 nests (containing 129 eggs) failing to produce any young (e.g., due to eagle owl *Bubo bubo* predation, desertion or forest practices) were excluded from all brood-loss analyses. To keep the post-hatching brood-loss measure conservative, nests ($n = 32$) with one or more egg(s) ($n = 36$) failing to hatch (searched from the nest bottom) were also excluded from all analyses of brood reduction. This was done because hatching failure may increase the survival of offspring that may have died in the absence of hatching failure (Smith 1988, Forbes *et al.* 1997, Forbes *et al.* 2002). I used this conservative measure even though the proportion of lost nestlings was not lower in nests with hatching failure as compared with nests where all eggs hatched (GLMM: $F_{1,249} = 0.92$, $P = 0.34$). The remaining data set contained information on egg and nestling numbers from 219 nesting events, containing 768 eggs in 123 different territories, which produced 655 nestlings. Among these, the sex of all nestlings was known (determined either morphologically or by DNA sexing) from 216 nesting events (757 eggs, 123 territories, 645 nestlings). Due to the pronounced reversed sexual size-dimorphism in the goshawk, sexing by morphology is a trustworthy method (*see* Byholm *et al.* 2002b).

At this point, I considered a clutch reduced if the number of nestlings at the time of ringing did not correspond to the number of eggs originally laid. Even if the exact causes of death for the majority of lost offspring is not known, most documented partial brood losses occurred within the first 2–5 days after hatching ($n = 28$), being the result of starvation or physiological instability. Siblicide occurred only in the second half of the nestling period and was quite uncommon ($n = 5$). Partial egg predation was documented only in two nests ($n = 3$ eggs). Both the occurrence (clutch reduced/clutch not reduced) and magnitude (proportion of nestlings lost/clutch) of partial brood loss was then measured. Nest-specific hatching dates were estimated from nestling wing lengths by backdating (information lacking for two nests), all territories were assigned a territory number (territory-id) and brood sex ratios [males/(males + females)] were calculated.

Food supply

Data on the natural densities (ind. km^{-2}) of forest grouse (black grouse *Tetrao tetrix*, hazel grouse *Bonasa bonasia*, willow grouse *Lagopus lagopus* and capercaillie *Tetrao urogallus*) for 1999–2002 were obtained from wildlife triangle census data (Lindén *et al.* 1996) from the Finnish Game and Fisheries Research Institute. It is known that fluctuations in grouse numbers are in rather good temporal match, and that spatial synchrony in grouse population fluctuations diminishes with increasing distance (Lindström *et al.* 1996, Ranta *et al.* 2003). To correctly account for local synchrony of grouse population dynamics, annual grouse densities (adults and juveniles combined) were calculated for four different 50 × 50-km grids roughly matching the study area (Fig. 1). Annually, 3–11 wildlife triangles (median = 6) were censused within each of the grids, corresponding to a total average annual transect length of 78.0 ± 6.3 km (range: 36–132 km). A model including year and grid as factors showed that grouse density did not differ significantly between years (repeated measures GLM: $F_{3,88} = 1.98$, $P = 0.16$), and that the pattern of inter-annual variation did not differ between grids (grid × year: $F_{9,88} = 0.42$, $P = 0.92$). However, over the years the grouse densities in the four grids differed consistently ($F_{3,88} = 3.72$, $P = 0.02$). This effect was due to the southwesternmost 50 × 50-km grid being inhabited by fewer grouse than the others (18.8 ± 2.4 *vs.* 28.2 ± 1.6, Fig. 1; difference between grid 1 and grids 2–4: Tukey's post hoc test: $P = 0.01$). As I was interested in analysing brood reduction patterns in respect to grouse density, the data for the low grouse-density grid were kept as a group of its own ('low grouse-density region'), while the high grouse-density grids were combined to form a second group ('high grouse-density region').

Data analysis

Analyses were performed with the statistical package S-Plus version 6.1 (Insightful Corporation 2001). The use of Generalized Linear Mixed Models (GLMMs) is the best option for much of the present data because these models not only allow for analyses of several fixed independent variables, but also allow inclusion of non-independent information as random variables (Crawley 2002). Subsequently, as the same territories often produce nestlings in more than one year, territory-id was included as a random variable in all models. In order to clarify whether territorial patterns differed between the two larger grouse-density regions, territory-id was nested with grouse-density region in an alternative of the otherwise identical model version. Region, year, nest-specific median egg-laying date, original clutch size and their second order interactions were set as fixed variables. Whether or not a clutch experienced partial brood loss, was then modelled as a binomial response (0 = clutch intact, 1 = clutch reduced) and fitted with a logistic link function. Following the normal procedure in S-Plus concerning proportion data, the absolute number of nestlings lost (number of failures) and the one(s) surviving (number of successes) were united to form the response variable. In models involving sex ratio, the response variable was specified as the number of males and the number of females as joined in a single variable. In these models the distribution was specified as binomial. All models with a binomial error function were analysed with the MASS library (Venables & Ripley 2002). In analyses of clutch size (data normally distributed), I used an identity link with normal errors.

In all models, residuals were visually inspected to assure that the variance in errors was constant. When performing specific model selection, I followed a manual step-procedure by first excluding non-significant fixed terms from the model, starting with interactions, until the model contained only significant factors. At this stage performances of the two alternative mixed models (*see* above) involving the random term (i.e. territory-id nested with region *vs.* territory-id not nested with region) were compared. Using the Akaike Information Criterion (AIC), the most parsimonious model was selected for further analyses. The significance of the random term was then assessed through variance comparisons, first assuring that the approximate 95% confidence interval was not disproportionately wide as compared with the variance estimate. Fixed factors were tested with *F*-statistics.

Results

Clutch size variation

During 1999–2002, the modal clutch size was 3 (3.41 ± 0.04, range 1–5, $n = 294$). A GLMM with no stepwise model selection showed that the two grouse-density regions did not differ in territorial clutch size patterns as the more complex model with territory-id nested with region had no greater explanatory power than the simpler model with only territory-id as a random factor (ΔAIC = 3.80, $P = 0.91$). In general, between-territory differences in clutch size were small ($\sigma^2_{\text{between}} = 0.06$, 95% CI 0.02–0.18) and territory differences explained only 17% of the total residual variance ($\sigma^2_{\text{total}} = 0.36$). There were no regional differences in annual clutch size variation, but clutch sizes differed significantly between years and between regions (Table 1). Clutches were consistently smaller in the low grouse-density region (3.30 ± 0.11, range 2–4) than in the high grouse-density region (3.54 ± 0.05, range 1–5) and larger in 1999 (3.73 ± 0.08, range 1–5) than in 2000–2002 (3.41 ± 0.05, range 2–5). A closer inspection of the data revealed that four-egg clutches were more abundant in 2000 (54.7%) as compared with 1999 and 2001–2002 (45.1%). Clutch size also decreased significantly with advancing date, the pattern of decrease being identical in the two regions and in all four years (Table 1).

Partial brood loss

Excluding complete failures and nests with one or more eggs remaining unhatched, partial brood loss occurred in 39.7% (87/219) of all nesting events. In a model assessing the probability of brood loss, the fit of the model was not improved by nesting territory-id with region (ΔAIC = 0.70, $P = 0.19$), i.e. the two grouse-density regions showed the same patterns of partial brood loss at the territorial level. In the remaining model, however, the overall between-territory variance component ($\sigma^2_{\text{between}} = 7.14$, 95% CI 4.43–11.50) explained 95% of the total residual variance ($\sigma^2_{\text{total}} = 7.54$): territories differed considerably in their probability of experiencing partial brood losses irrespective of in which grouse-density region they were located. Testing the significance of the fixed factors revealed that the proportion of clutches affected by loss varied significantly with clutch size ($F_{1,88} = 27.34$, $P < 0.0001$), but the clutch-specific loss patterns also differed between the two regions (clutch size × region: $F_{1,88} = 6.54$, $P = 0.01$). Subsequently, while clutches of two suffered a higher incidence of partial brood loss in the low grouse-density region than in the high grouse-density region, the pattern was reversed in clutches of four (Fig. 2a). There was no regional difference in the likelihood of partial brood loss among three-egg clutches. In general, the probability for a clutch facing partial brood loss differed over years ($F_{3,88} = 4.52$, $P = 0.005$),

Table 1. GLMM for the variation in clutch size in the study area during 1999–2002 (*n* = 249), using normal errors and an identity link function.

Factor	Parameter estimate	df	*F*	*P*
Hatch date	–0.0477	1	16.74	0.0001
Year	–0.0765[a] 0.0354[b] 0.2845[c]	3	10.54	< 0.0001
Region	0.8130	1	4.15	0.04
Date × Region	0.0172	1	2.69	0.11
Date × Year	0.0031[a] –0.0006[b] 0.0091[c]	3	2.04	0.11
Year × Region	0.0355[a] –0.1026[b] –0.0167[c]	3	1.66	0.18
Error	6939.3	132		

[a] = 2000, [b] = 2001, [c] = 2002

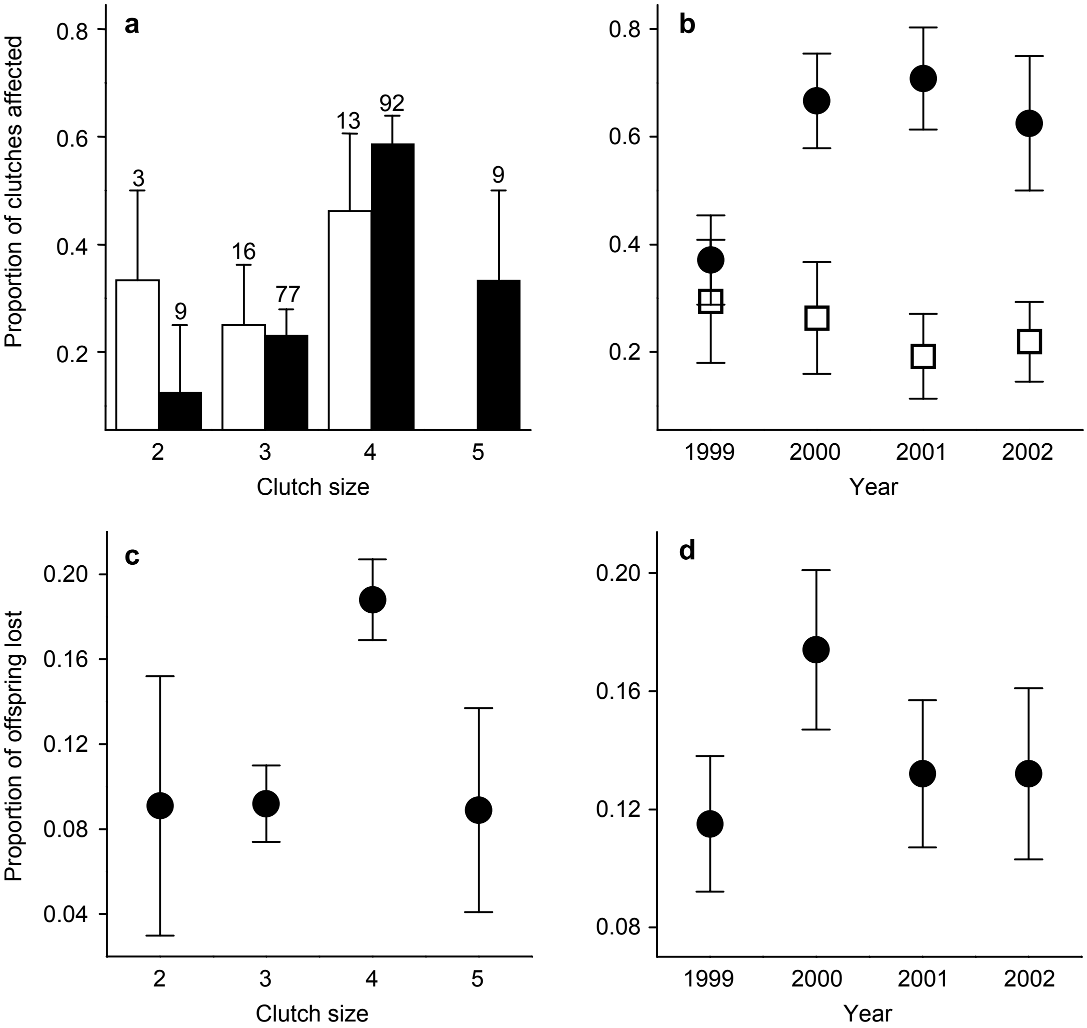

Fig. 2. Proportion of goshawk clutches facing partial brood losses (± SE) in relation to (**a**) clutch size (white bars: low grouse-density region, black bars: high grouse-density region; sample sizes above bars) and (**b**) year (white squares: three-egg clutches, *n* = 93; black circles: four-egg clutches, *n* = 105). The proportion of offspring lost (offspring lost/initial clutch size) due to partial brood loss (± SE) in relation to (**c**) clutch size (*n* = 12, 93, 105, 9) and (**d**) year (*n* = 57, 55, 54, 53). Data for two- and five-egg clutches (*n* = 21) is not shown in panel b.

but at the same time different sized clutches had different probabilities of being affected across years (year × clutch size: $F_{3,88} = 3.25$, $P = 0.03$; Fig 2b).

Overall, 14.7% (113/768) of all offspring were lost due to partial brood losses. While there were no differences between the two regions in territorial brood-loss patterns (ΔAIC = 0.93, $P = 0.22$), the proportion of individuals that were lost differed significantly between territories ($\sigma^2_{\text{between}} = 1.31$, 95% CI 0.79–2.17, 72% of total). The proportion of lost offspring also differed between clutch-size categories ($F_{1,92} = 9.12$, $P = 0.003$) and years ($F_{3,92} = 3.97$, $P = 0.01$), four-egg clutches (Fig. 2c) and year 2000 (Fig. 2d) showing a higher proportion of lost offspring than the other corresponding categories. On average, 19.3% (81/420) of the eggs were lost in four-egg clutches, compared with 9.2% (32/348) in other clutch size categories, and 18.7% (35/187) of the eggs were lost in 2000 as compared with 13.4% (78/581) in 1999 and 2001–2002. Proportion of offspring lost did not vary with hatch date or region ($P > 0.9$).

Partial brood loss and offspring sex ratio

At the population level, males dominated in clutches remaining intact until fledging (54.4% (237/436), Binomial test: $P = 0.04$). Males and females were about equally common (50.2% (105/209), Binomial test: $P = 0.5$) in clutches that faced partial brood losses. The overall sex ratio was 53.0% (342/645) and tended to differ from the 1:1 ratio (Binomial test: $P = 0.07$). As there were no sex-ratio differences between broods facing both partial brood losses and hatching failure as compared with broods facing losses only (GLMM: $F_{1,99} = 1.67$, $P = 0.20$), this suggests that potential sex-biased egg mortality is not powerful enough to alter the initial egg sex ratio. This conclusion must be considered solid, especially as signs of embryonic development lacked from 81% (29/36) of eggs remaining unhatched (egg content was examined by eye as well as by microscope). Three embryos (of the total of seven) that could be sexed by DNA-sexing turned out to be one male and two females. Goshawk brood sex ratios were not found to correlate with any of the fixed factors fitted in a GLMM (laying date, year, region, clutch size, reduced/intact), or with any of their second order interactions (all $P > 0.19$). Thus, even if both grouse density and, to some degree, brood-loss patterns differed regionally, partial brood losses did not alter sex ratios significantly in either of the two regions (Fig. 3). Potential post-hatching sex-biased mortality must be considered weak. Because the confidence interval of the between-territory random effect approached zero, was wide in relation to the variance component estimate (95% CI 0.002–1.24, $\sigma^2_{\text{between}} = 0.05$) and as it explained only 7% of the total residual variance, there were no evidence for territory differences in sex ratio output.

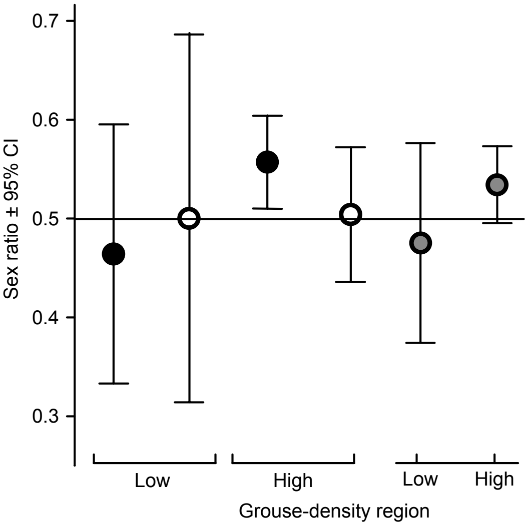

Fig. 3. The average sex ratio (± 95% CI) in goshawk broods not facing partial brood losses (black circles; intact), broods facing partial brood losses (white circles; reduced), and overall (grey circles, intact and reduced combined) in the two regions with different grouse densities (low grouse-density region, high grouse-density region). Total $n = 216$ broods.

Discussion

It is expected that brood loss patterns would have multiple causes (cf. Forbes *et al.* 2002) and be observable at different (inter-connected) organization levels. The patterns of brood loss in Finnish goshawks clearly confirm these views. Partial brood-loss patterns (both occurrence and magnitude) varied between years as well as between clutch-size categories. Although this is the first report in goshawks, both of these results are in concordance with patterns observed in other species (e.g., Howe 1976, Mock & Parker 1986, Wrege & Emlen 1991, Forbes *et al.* 2002). Interestingly, partial brood-loss patterns were also site specific as analysed between territories and between the two regions with different grouse densities.

The fact that brood-loss patterns differ between territories and larger areas clearly has the potential to influence the interpretation of any brood-loss pattern in studies where space has not been considered. If, for example, only a specific subset of territories situated in one region are analysed, conclusions drawn concerning the generality of the results over a wider area might be premature. Certainly this would have been the case in the present study as partial brood loss differed between the two grouse-density regions even if the territorial patterns within the regions were the same. Whether the brood-loss patterns observed at the territorial level originate from a territorial effect *per se*, or if they rather reflect differences in parental quality is a question that is out of the scope of this paper, but intuitively, following the patterns observed regarding breeding parameters in other species (e.g., Przybylo *et al.* 2001), both effects might operate together. For example, as densities of important summer prey species such as corvids, doves and thrushes (cf. Tornberg 1997) differ largely between barren, mire-dominated landscapes and more forest-dominated landscapes (Väisänen *et al.* 1998), this might have repercussions for differences in brood-loss patterns observed in different goshawk territories. Correspondingly, as goshawks have distinctive sex roles during the breeding season — males providing most of the food (Cramp & Simmons 1980) — between-territory differences in brood losses might reflect differences in paternal hunting skills. In any case, as the between-territory differences in clutch size are modest, while the between-territorial differences in partial brood losses are pronounced, the results indicate that partial brood loss, rather than initial clutch size variation, is the prime factor responsible for between-territory differences in breeding performance previously observed in goshawks (Krüger & Lindström 2001, Krüger 2002). Similarly, partial brood loss is an important factor adding to larger-scale (regional) variation in the number of goshawk offspring fledged (P. B. unpubl. data).

Another interesting question is why goshawks lay four eggs even if the production of the fourth egg is clearly linked with increased risks of secondary family-size adjustments. The idea that the fourth egg primarily would be an insurance if some offspring fail ('the replacement hypotheses', reviewed in Mock & Parker 1997) is not directly supported by the fact that there is no difference in the degree of partial brood losses between clutches facing hatching failure *vs.* clutches not facing hatching failure (*see* Material and methods). Instead, it is tempting to suggest that an 'extra' fourth egg is the result of goshawks laying four eggs producing an optimistically large clutch size in order to be able to capitalize on unpredictable favourable conditions (Lack 1954, Temme & Charnov 1987, Pijanowski 1992). This idea is supported by the fact that clutches of four clearly do not face increased brood loss risks in all situations. Clutches of five, on the other hand, are produced probably only in the most extremely favourable situations, which may explain why brood loss is of lower magnitude in this clutch size category than that of four.

It is also important to note that there was little clutch-size variation between territories indicating that clutch size is largely a function of large-scale environmental factors as opposed to within-territory factors (parental and environmental). As shown here and by earlier work (Sulkava *et al.* 1994), local grouse density is one such large-scale element. As clutches of four more often face partial brood losses in the high grouse-density region than in the low grouse-density region, this implies that goshawks are enticed to produce four egg clutches where grouse are abundant. However, grouse population density (with large-scale synchrony in their dynamics; Ranta *et al.* 2003) alone cannot ensure the success of this additional egg. Instead, other more territorial-centred aspects, for example, territorial differences in densities of other prey species (*see* above) can have repercussions for the survival of the fourth egg. Equally, differential parental characteristics, such as parental age, can influence how many young fledge (*see* Nielsen & Drachmann 2003).

Even though patterns of partial brood loss differed between territories and regions, goshawk offspring sex ratios did not differ between the two grouse-density regions. Likewise, on the brood level, sex ratio was not associated with partial brood losses, and there was no clear evidence of territory-specific differences in offspring sex ratio. As the interaction between region and reduction category (brood losses *vs.* no brood losses) is not related to the observed offspring sex-ratio variation, this means that partial brood loss cannot be the main force producing the earlier observed connection between grouse density and goshawk offspring sex ratio (Byholm *et al.* 2002b). Intuitively, especially as potential sex-specific egg mortality is not powerful enough to alter the sex ratio measured at the nestling stage, this indicates that the nestling sex ratio mainly is the result of facultative manipulation of egg sex (cf. Sheldon 1998, Ewen *et al.* 2004). Since the magnitude and occurrence of partial brood losses did not vary seasonally, this furthermore suggests that partial brood losses are not the main agent responsible for the earlier observed patterns of seasonal sex ratio shifts in goshawk broods (Byholm *et al*. 2002a).

Here, I have shown that goshawk territories differ considerably in their brood-loss patterns. In addition, partial brood-loss patterns also differ between two larger regions with different goshawk main-prey abundances. While on the basis of the two regions analysed here it is not possible to tell what the general pattern over a wider scale is, one point becomes clear: partial brood-loss patterns are not necessarily identical even in geographically close locations. There is no reason to believe that this would not be the case in many other species. Unfortunately, territorial and regional nonlinearities have not usually been included or acknowledged in brood-loss studies. When space to some degree has been considered (Wrege & Emlen 1991, Dzus *et al*. 1996, Valkama *et al*. 2002), territory/population has usually been fitted as a fixed factor in conventional statistical models thus violating the assumption of data-independence if data from the same site was used over several years. This is unfortunate, as it may undermine a correct interpretation of brood-loss patterns, including their potential adaptive role (Lack 1954, Mock & Parker 1997). There is thus a need to include space in future partial brood-loss studies, particularly in species that inhabit the same breeding territories for subsequent seasons and are latent in their responses to changing extrinsic ecological factors. The same is true also for sex-ratio studies (Byholm *et al*. 2002b), but even if goshawk nestling sex ratios vary in parallel with local grouse densities, secondary family-size adjustment does not significantly alter the sex ratio initially present in the eggs. In more general terms, as partial brood-loss patterns vary between locations and as natural populations usually are connected to each other by dispersal (e.g., Clobert *et al*. 2001), it is possible that spatial nonlinearities in brood loss could have consequences for the dynamics of whole populations. This is because the occupancy of territories (or sites) of varying quality over long time periods can have consequences for population growth, expansion and viability (Sutherland 1996, Kokko & Sutherland 1998, Krüger & Lindström 2001, Thompson *et al*. 2001, Ambrosini *et al*. 2002).

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