Female offspring desertion and male-only care increase with natural and experimental increase in food abundance

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In species with biparental care, one parent may escape the costs of parental care by deserting and leaving the partner to care for the offspring alone. A number of theoretical papers have suggested a link between uniparental offspring desertion and ecological factors, but empirical evidence is scarce. We investigated the relationship between uniparental desertion and food abundance in a natural population of Tengmalm's owl *Aegolius funereus*, both by means of a 5-year observational study and a 1-year experimental study. Parents and offspring were fitted with radio-transmitters in order to reveal the parental care strategy (i.e. care or desert) of individual parents, and to keep track of the broods post-fledging. We found that 70 per cent of the females from non-experimental nests deserted, while their partner continued to care for their joint offspring alone. Desertion rate was positively related to natural prey population densities and body reserves of the male partner. In response to food supplementation, a larger proportion of the females deserted, and females deserted the offspring at an earlier age. Offspring survival during the post-fledging period tended to be lower in deserted than in non-deserted broods. We argue that the most important benefit of deserting may be remating (sequential polyandry).

Keywords: body reserves; food abundance; food supplementation; offspring desertion; parental care; post-fledging

1. INTRODUCTION

Parental care is beneficial because it promotes survival and future fitness of the offspring, but it may be detrimental to self-maintenance and future reproductive output of the parents (Clutton-Brock 1991). Therefore, parents are expected to terminate care when the net benefits of continued care are exceeded by the benefits of deserting (Stearns 1992; Székely *et al.* 1996). In species with biparental care, each parent benefits from the effort invested by its partner, and usually escapes some of the associated costs (Parker *et al.* 2002; Johnstone & Hinde 2006). According to parental investment theory, there is a conflict between male and female parents over how much care to provide for their offspring (Trivers 1972; Kokko & Jennions 2008). This sexual conflict over care has received much interest (e.g. Arnqvist & Rowe 2005; Houston *et al.* 2005; Wedell *et al.* 2006; Hinde & Kilner 2007; Kokko & Jennions 2008; Olson *et al.* 2008), and has been studied in a number of animal taxa, including birds (see Olson *et al.* 2008 and references therein).

Although the majority of bird species show social monogamy and biparental care, many species regularly exhibit uniparental care; that is, one parent deserts the offspring and leaves the partner to provide care alone (Oring 1982; Davies 1991; Cockburn 2006). In most of these species it is the male that deserts, but in some it is the female that deserts and offloads the costs of caring on the

male (Székely *et al.* 1996; Owens 2002). The costs and benefits of biparental care from the female's perspective are addressed in an increasing number of studies (e.g. Wiebe 2005), but which factors influence female parental care strategies remain poorly understood. Emlen & Oring (1977) suggested that when resources are ample one parent may try to escape parental duties and leave the mate to provide for the offspring alone. Indeed, the traditional view has been that high food abundance is one of the main factors promoting the evolution of uniparental care and polygamy (Davies 1991; Andersson 2005). Yet recent theoretical works on mating system dynamics and parental conflict argue that the link between ecological factors and parental care patterns is weak (Arnqvist & Rowe 2005; Olson *et al.* 2008). However, we emphasize that there have been very few empirical studies investigating the potential relationship between offspring desertion and food abundance (but see Beissinger & Snyder 1987).

In this study, we investigated the relationship between uniparental offspring desertion and food abundance in a natural population of the cavity-nesting Tengmalm's owl *Aegolius funereus*. Tengmalm's owls experience large natural variations in food supply as the population densities of their main prey, microtine rodents (Microtidae), vary widely between years (Sundell *et al.* 2004). Food supply to Tengmalm's owl nests can be easily manipulated by experimentally increasing cache size, because the male delivers prey directly to his brooding mate in the nest cavity, where prey items are temporarily cached (Korpimäki 1987). When food is abundant, a female

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Tengmalm's owl that deserts her first brood may readily find a new mate and raise a second brood in the same year (sequential polyandry: Solheim 1983; Sonerud 1988a; Korpimäki 1989; Hakkarainen & Korpimäki 1998). In years of high microtine rodent population densities, 10–20 per cent of the males are simultaneously polygynous (i.e. they remate within the same breeding season without deserting their first brood), but 20–25 per cent remain unpaired even if they possess a territory and nest cavity (Carlsson *et al.* 1987; Carlsson 1991; Korpimäki 1991; Hakkarainen & Korpimäki 1998).

We tested the hypothesis that there should be a positive relationship between offspring desertion by female Tengmalm's owls and population densities of natural prey, employing two different approaches: (i) an observational 5-year study and (ii) a 1-year food supplementation experiment. We predicted that the proportion of females deserting would increase with (i) increasing natural food abundance and (ii) experimental increases in food supply.

2. MATERIAL AND METHODS

(a) *Study site and study species*

Our study took place during 1995–1999 in Hedmark County in southeast Norway (60°45'–61°10' N, 11°15'–12°00' E, altitude 170–580 m). The study area is situated in the boreal zone and is dominated by coniferous forest, primarily Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, interspersed with bogs, and contains only negligible areas of farmland. The forest is heavily influenced by modern forestry, based on clear-cutting of the old forest and replanting, and is a mosaic of stands of all ages. More detailed descriptions of the flora and fauna of this area are given by Sonerud (1986) and Steen *et al.* (1996).

Tengmalm's owls are small (male body mass of approx. 100 g), nocturnal, cavity-nesting owls that reside in the Eurasian boreal forests (Mikkola 1983; Cramp 1985). In Fennoscandia, they feed mainly on microtine rodents and shrews (Soricidae; Mikkola 1983; Cramp 1985). Tengmalm's owls readily accept and breed in nest-boxes (e.g. Korpimäki 1981), and are robust to trapping, handling and radio-tagging; of 105 adult Tengmalm's owls (56 males and 49 females), none have died or subsequently deserted the nest as a consequence of radio-tagging (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). Adult male Tengmalm's owls are territorial and resident, and typically do not breed when food is scarce (Löfgren *et al.* 1986; but see Hipkiss *et al.* 2002). By contrast, adult females are nomadic, concentrating and breeding where prey is abundant, and they may breed every year (Löfgren *et al.* 1986; Korpimäki *et al.* 1987; Sonerud *et al.* 1988). Individuals of both sexes usually (more than 95%) change mates between breeding seasons, even if their previous partner is still alive (Korpimäki 1988, 1989; K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). Biparental care is obligatory until the offspring can keep themselves warm; the female incubates and broods, and the male provides food for the whole family (Korpimäki 1981). Thereafter, the female resumes hunting and may assist the male in providing prey for the offspring (Korpimäki 1981). Duration of the post-fledging dependency period is six to seven weeks (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data).

(b) *Field methods*

We provided nest-boxes and checked them from mid-March each year. As nests were found, they were visited sufficiently often to determine the hatching date (± 1 day) of the first egg in the clutch. The adults and at least one nestling from each of a total of 43 nests were fitted with radio-transmitters (6, 3, 11, 20 and 3 nests in 1995, 1996, 1997, 1998 and 1999, respectively). Adults were weighed (g), measured (mm) and radio-tagged in the late brooding period, and we determined the ages of the adult owls using the method described in Hörnfeldt *et al.* (1988). Nestlings were radio-tagged shortly before fledging. Brood mates keep together until approximately 60 days post-hatching (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data), so it was sufficient to tag one nestling from each nest to keep track of the broods after fledging. Trapping, handling, tagging and follow-up of radio-tagged individuals were done with permission from, and in accordance with the ethical standards provided by, the Directorate for Nature Management and the National Animal Research Authority of Norway.

At around the time of fledging, we visited the nests at least every second day to determine the fledging day of the first-fledged young. We kept count of brood size on the basis of frequent nest inspections, remains of dead nestlings and by X-raying prey remains from the nests in order to reveal leg bands of dead nestlings. In the post-fledging period, brood size was determined from daytime observations of brood mates perching alongside or in the vicinity of the radio-tagged young, and from visual observations and begging calls of young at night.

Each individual adult was studied during one breeding season only. The only exceptions were one female and one male that were studied in two subsequent years, which differed much with respect to natural prey abundance. Owls were located by the use of portable receivers (Telonics, AZ, USA; Televilt, Sweden) and handheld 2- or 4-element Yagi antennas (Televilt). We determined whether each parent provided care or deserted by using daytime localization of roosting parents and offspring, night-time radio-tracking of parents and offspring, and observations of prey deliveries to nestlings and fledglings. We recorded prey deliveries to each brood throughout three nights: in the late nestling stage, and in the early and late post-fledging stages (median 25, 42 and 58 days after hatching). If an individual parent did not deliver food, the use of radio-telemetry enabled us to determine whether it had died or deserted.

The timing of desertion was determined from daytime and night-time radio-tracking of adults and offspring (see the electronic supplementary material for more detailed descriptions of the field methods). If we were unable to detect radio signals from a parent's transmitter from high vantage points in the terrain, we searched intensively within 3 km of the nest (approx. three times the mean home range radius; K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). If we failed to pick up signals within this area we assumed that the parent had deserted and left the area. Only one owl lost its radio-tag. In addition, two adult owls were killed by predators. In all the three cases, the radio-transmitter was easily found, even though it was located on the ground. The range at which signals could be detected from the ground exceeded 10 km (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data), so the owls that we lost track of had moved even further. We endeavoured to keep track of parents that moved more than 3 km from the nest, and to redetect transmitter signals from parents that deserted.

(c) Estimating natural food abundance

Annual estimates of natural food abundance (1995–1999) were based on snap trapping of microtine rodents in May at one site (60°56' N, 11°08' E) in the study area, with approximately 1100 trap nights each time (Sonerud 1988b). This trapping was done with permission from the Directorate for Nature Management as part of a long-term monitoring study. We defined a rodent index as the pooled indices (animals trapped per 1000 trap nights) of bank vole *Myodes glareolus*, field vole *Microtus agrestis*, root vole *Microtus oeconomus* and wood lemming *Myopus schisticolor*. These four species show interspecific temporal population synchrony (Bjørnstad *et al.* 1999), and made up 87 per cent of the mammals ($n=1047$) and 96 per cent of the rodents ($n=950$) recorded stored as surplus prey in the Tengmalm's owl nests used in our study (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). To determine the spatial scale of microtine rodent synchrony in the geographical region of our study, a large-scale transect was sampled in 1990–1994 (Steen *et al.* 1996). Along this transect, which crossed our study area, the local synchrony domain of small rodent populations was approximately 40 km (Steen *et al.* 1996). All our owl nests were within 46 km from our annual trapping site, and 90 per cent of them were closer than 40 km. We therefore regard the annual variation in our rodent index to be representative for our study area.

We backed up the rodent censusing with the assessments of parental body condition. As an estimate of body condition, we calculated the body reserve indices ($[\text{body mass}/(\text{wing length})^3] \times 10^4$) of male and female parents. Both the measures of rodent densities and parental body condition can provide information about food abundance and its effect on the owls.

(d) Food supplementation experiment

In 1998, we supplied 10 nests with extra food from hatching to fledging, and 10 non-supplemented nests were used as controls. In this year, the rodent index in the study area was intermediate; the rodent index was marginally lower in 1999, much lower in 1996, and higher in 1995 and 1997. Of the first and second nests to hatch, we tossed a coin to decide which to assign to the experimental group. The other nest was assigned to the control group. Thereafter, we repeated this procedure of tossing a coin to decide whether the third or the fourth to hatch, the fifth or the sixth, and so forth, should be assigned to the experimental group. This procedure ensured a similar distribution of hatching dates within the two manipulation groups, and prevented a bias towards later hatching dates in one of the groups. Three nests were lost to predators during the first half of the nestling period. Each of these nests was replaced with the first nest available where hatching had not started.

Food supplementation began on the day when the first egg of a clutch hatched (day 0) or a few days later (median day 3, range 0–4). Whole thawed brown and black laboratory-reared mice *Mus musculus* were placed in the supplemented nests during daytime every fourth day for the entire nestling period (eight times per nest). We added approximately 20 g of food *per capita* (female and nestlings) on the first four inspections, and then approximately 30 g *per capita* on the next four inspections. This corresponds to approximately 30 per cent of the average food consumption of Tengmalm's owl nestlings during the nestling period, and approximately 10 per cent of the energy requirements of the brooding female (see Korpimäki 1981). Mimicking natural food provisioning

in the post-fledging period was not practically feasible, therefore the food supplementation experiment was terminated at fledging. Nestlings were weighed and measured for linear body measurements (foot and wing length) in the mid- and late nestling stage (see the electronic supplementary material). At each visit, we recorded the brood size and biomass of stored surplus prey. Supplemental food only rarely lasted from one feeding visit to the next (2% of the cases) and was included in the total cache biomass (g). Control nests were inspected and disturbed in the same way as supplemented nests, except that no extra food was added.

(e) Statistical analyses

Data were analysed using SAS (v. 9.1 TS Level 1M3, SAS Institute, Inc., Cary, NC, USA) and SIGMASTAT (v. 1.0, Jandel Scientific GmbH, Erkrath, Germany) statistical softwares. We performed exact logistic regression, using the PROC LOGISTIC procedure in the SAS system, to analyse how the rate of offspring desertion varied with changes in natural food abundance (as estimated by the rodent trapping index, and the body reserve indices of males and females). Exact logistic regression was chosen because our datasets were rather small ($n=18$ –30). The usual asymptotic methods may be unreliable when sample sizes are small or the data are sparse, skewed or heavily tied (see Derr 2000 for details on the analytical technique). Exact conditional inference remains valid in such situations (Derr 2000). We report test statistics and exact p -values for two-tailed tests.

We had to use different calculations of timing of desertion to fit the particular circumstances of each desertion, but this did not affect the outcome of our statistical analysis of effects of food supplementation on the timing of desertion (see the electronic supplementary material). Even when we used the most 'conservative' estimates of time of desertion (i.e. the smallest possible difference between females of supplemented and control nests), this did not cause a qualitative change in the results of the analysis.

3. RESULTS**(a) Observational study**

The female deserted in 70 per cent of the non-supplemented Tengmalm's owl broods in which we were able to determine whether the parents deserted the offspring ($n=30$). Of the initial 33 non-supplemented broods in which both parents were radio-tagged, the male deserted in only one case. In this case, the female deserted shortly afterwards, and all the nestlings died. This nest is not included in the analyses below. In addition, the female's strategy (desert or not desert) could not be determined in two other nests; one because of nest predation and the other because the female lost the radio-tag. These two nests are not included in the analyses.

Desertion rate among Tengmalm's owl females increased with increasing rodent index (table 1a; figure 1). The estimated effect of rodent index for the probability of desertion was $\hat{\beta} = 0.40$. The multiplicative effect on the odds of a one-unit increase in rodent index equals ($e^{0.40}$) = 1.49. We infer that each unit increase in rodent index has a 49 per cent increase in the odds that a female will desert (table 1a). All the 1-year-old females deserted, irrespective of rodent index. Therefore, we reanalysed the data and included female age as a cofactor with two possible levels: young (1 year old) or old (more than 1 year old)

Table 1. (a) Desertion rate among female Tengmalm's owls *A. funereus* increased with increasing natural food abundance (rodent index). (b) After including female age as a categorical predictor variable, there was still a positive relationship between desertion rate and rodent index, and young females (1-year-olds) were more inclined to desert than older females (more than 1 year old). (Results of exact conditional logistic regression analyses. Analyses were done on the basis of the data shown in figure 1. The binary response variable had two possible outcomes: $Y=1$, if the female deserted the offspring, and $Y=0$, if the female did not desert. Rodent index (animals trapped per 1000 trap nights) is the pooled index of all the trapped rodent species (bank vole *M. glareolus*, field vole *M. agrestis*, root vole *M. oeconomus* and wood lemming *M. schisticolor*). Asterisk indicates a medium unbiased estimate.)

		95% CI	<i>p</i> -value
(a)			
<i>exact conditional scores test statistic</i>			
rodent index	4.07		0.047
<i>exact parameter estimate</i>			
rodent index	0.40	0.00011 to 0.91	0.050
<i>exact odds ratio estimate</i>			
rodent index	1.49	1.00 to 2.47	0.050
(b)			
<i>exact conditional scores test statistic</i>			
rodent index	4.63		0.035
female age	5.44		0.036
<i>exact parameter estimate</i>			
rodent index	0.45	0.021 to 0.999	0.037
feme age: more than 1 year	−1.17*	−infinity to −0.041	0.041
<i>exact odds ratio estimate</i>			
rodent index	1.57	1.021 to 2.71	0.037

(table 1b). When controlling for the effect of female age, there was a slightly stronger effect of rodent index on desertion rate, and the probability of desertion was significantly smaller for old when compared with young females (table 1b).

Desertion rate tended to increase with body reserve index of both males and females (males: $\hat{\beta}=89.2$, $p=0.015$; females: $\hat{\beta}=28.0$, $p=0.16$). Yet, for the females, the p -value for the estimated slope indicated only marginal influence. Therefore, we fitted a simpler model with only male body reserve index as predictor (scores test statistic = 5.32, $p=0.019$, $n=30$; parameter estimate = 81.5, 95% CI 9.98–165.2).

The proportion of offspring surviving from the late brooding to the late post-fledging stage was on average 0.58 (s.e. 0.11) in broods that were deserted and 0.87 (s.e. 0.054) in broods that were not deserted by the female (95% CI for difference of means −0.014 to 0.61, $t=1.98$, d.f. = 22, $p=0.060$).

Median (interquartile range) number of prey delivered per hour in the post-brooding nestling stage was 1.23 (0.80–1.45) for male and 0.40 (0.0–0.80) for female parents (Wilcoxon signed-rank test: $W=-257.0$, $n=26$, $p<0.0001$).

On average, deserting females left 30.0 (s.d. 8.7) days after hatching of the first egg in the brood ($n=21$), and the first-fledged offspring fledged 32.9 (s.d. 1.9) days after hatching ($n=18$). Hatching date did not differ between deserted and non-deserted broods (Student's t -test: $t=-0.12$, d.f. = 28, $p=0.91$, 95% CI for difference of means −14.4 to 12.8 days).

(b) Food supplementation experiment

Five out of nine females from supplemented broods deserted their offspring during the experimental period (i.e. during the nestling stage) compared with only 1 out of 10 females from non-supplemented control broods

Figure 1. Parental care decisions (desert or not desert) of female Tengmalm's owls *A. funereus* in relation to natural food abundance and age (1-year-olds versus older birds). All 1-year-old females deserted. Natural food abundance was estimated by annual snap trapping. Rodent index (animals trapped per 1000 trap nights) is the pooled index of all the trapped rodent species (bank vole *M. glareolus*, field vole *M. agrestis*, root vole *M. oeconomus* and wood lemming *M. schisticolor*).

(Fisher's exact probability test: $p=0.057$; figure 2a). This difference between supplemented and control nests in the proportion of females deserting was neutralized after food supplementation was terminated. By the end of

Figure 2. (a) Proportion of female Tengmalm's owls *A. funereus* deserting their nest in relation to food supplementation (suppl, supplemented; con, unsupplemented control). (b) Desertion dates of female Tengmalm's owls from nests where food was supplemented or unsupplemented.

the post-fledging period, there was only a negligible difference between supplemented and control broods with respect to the proportion of females deserting (five versus six out of nine females). However, deserting females from suppl broods deserted earlier than females from control broods (suppl: median = 25.0 (interquartile range, i.q.r. 23.8–28.0) days after hatching, $n = 5$; con: median = 33.5 (i.q.r. 33.0–36.0) days after hatching, $n = 6$; Mann–Whitney rank sum test: $T = 17.5$, $p = 0.017$; figure 2b).

Mean $\pm$ s.e. body reserve index was higher for females of supplemented nests than for females of control nests (suppl: 0.284 ± 0.026 ; con: 0.250 ± 0.012 ; $t = 3.75$, d.f. = 18, $p = 0.0015$), and higher for males of supplemented nests than for males of control nests (suppl: 0.213 ± 0.013 ; con: 0.197 ± 0.011 ; $t = 2.91$, d.f. = 18, $p = 0.0093$). In the female brooding stage, median (interquartile range) number of prey delivered per night by the male was lower in supplemented than in control nests (5.5 (5.0–7.0) versus 8.0 (6.0–11.0), $T = 134.5$, $n_{\text{suppl}} = 10$, $n_{\text{con}} = 10$, $p = 0.028$).

There was no difference in cache size between supplemented and control nests. Median (interquartile range) cache biomass was 22.1 (17.0–74.0) g for supplemented and 45.5 (31.6–89.5) g for control nests in the brooding period (average of all nest inspections; $T = 86.0$, $p = 0.16$, $n = 10$ in both groups), and 8.3 (0–22.3) g for supplemented and 12.3 (0–27.0) g for control nests in the post-brooding period (average of all nest inspections; $T = 86.0$, $p = 0.77$, $n_{\text{suppl}} = 9$, $n_{\text{con}} = 10$).

There was no difference in hatching date or clutch size between supplemented and control nests (hatching date: $t = -0.49$, d.f. = 18, $p = 0.63$, 95% CI for difference of means -24.9 to 15.5 days; clutch size: $t = -0.67$, d.f. = 18, $p = 0.51$, 95% CI for difference of means -1.24 to 0.64 eggs). Food supplementation had no effect on brood size, body mass or linear body measurements of nestlings (see the electronic supplementary material).

(c) Desert, and then what?

Despite the fact that we put much effort into tracking down and relocating deserting females, we lost radio-contact with all that moved more than 3 km from their first nest ($n = 20$; supplemented and control broods pooled). Night-time radio-tracking revealed that deserting females most often moved rapidly out of the area in one direction during the course of one night, and without exception we lost track when trying to follow them. Among the six females (supplemented and control pooled) that abandoned their offspring but remained within 3 km of their first nest, one remated and renested 1.7 km from her first nest, while her original partner continued providing for her first brood. Median hatching date of the five females that remained within 3 km of the first nest without renesting was later than that of the renesting female (149 (i.q.r. 146–162) versus 111 days after 1 January), and also significantly later than median hatching date of the females that moved more than 3 km from their first nest (120 (i.q.r. 110–133) days after 1 January, $T = 112.0$, $p = 0.0016$). There appeared to be a tendency among females of non-supplemented nests that those that remained within 3 km had lower median body reserve index than those that moved out of the area (remained within 3 km ($n = 4$): 0.239 (i.q.r. 0.230–0.248); moved more than 3 km ($n = 16$): 0.257 (i.q.r. 0.246–0.271); $T = 24.5$, $p = 0.11$).

4. DISCUSSION

The prevalence of offspring desertion among female Tengmalm's owls increased with increasing natural food abundance (rodent index). Furthermore, in response to food supplementation, a larger proportion of the females deserted during the experimental period (i.e. in the nestling stage). Our results are in accordance with those of Beissinger & Snyder (1987), who found that snail kite *Rostrhamus sociabilis* parents responded to high natural food abundance by deserting their mates. By contrast, Kosztolányi *et al.* (2006) argued that favourable food conditions constrained female desertion in the Kentish plover *Charadrius alexandrinus*, but emphasized the need for experimental studies to establish whether the parental care changes they observed were driven by changes in food abundance.

We also found that the rate of female offspring desertion increased with increasing body condition (body reserve index) of their mate. There was a positive, although non-significant, relationship between desertion rate and the female's own body condition. Body condition of both male and female parents increased in response to food supplementation. Altogether, these results corroborate the positive relationship between desertion rate and natural food abundance, and suggest that the females did not desert because of exhaustion. Bleeker *et al.* (2005) found that male and female penduline tit *Remiz pendulinus* parents in good body condition deserted their offspring more often than those in poor condition. Our results are also in accordance with the single-sex model of avian parental care presented by Webb *et al.* (2002), which predicts that parents with high body reserves early in the season should desert, with the intention of remating. Barta *et al.* (2002) suggested that females may be able to manipulate males into providing care by strategically

reducing their own energy reserves available for care, but we found no support for this hypothesis.

Deserting Tengmalm's owl females apparently paid a cost in terms of reduced offspring survival in the late nestling and post-fledging stages. The question is what benefits the females get from deserting, and how these benefits are related to the abundance of food. Beissinger & Snyder (1987) presumed that deserting snail kite parents attempted to renest, although this proved difficult to ascertain. Although we were unable to document more than one case of renesting in our study, we suspect that many of the females deserted with the intention of remating. Breeding seasons were lengthy (March–August), and 20–25 per cent of the territorial Tengmalm's owl males remain unpaired even in years when food is abundant (Hakkarainen & Korpimäki 1998). Therefore, females deserting early in the season were likely to find a new mate and raise a second brood in the same year (Solheim 1983; Sonerud 1988a; Korpimäki 1989). A male's chances of successfully raising the offspring alone, and a female's chances of remating and succeeding with a second brood, are probably higher when food is abundant than when food is scarce (Hakkarainen & Korpimäki 1998). A number of theoretical and empirical studies have demonstrated the importance of remating probabilities for the parental care strategies adopted (e.g. Székely 1996; Székely *et al.* 1999; Pilastro *et al.* 2001; Owens 2002; Webb *et al.* 2002; Wiebe 2005; Kokko & Rankin 2006). While female Tengmalm's owls must desert to remate (sequential polyandry), males may remate without deserting their first brood (simultaneous polygamy; Carlsson *et al.* 1987; Carlsson 1991; Korpimäki 1991, 1992). We suggest that the differences between the sexes, not only in the availability of potential partners but also in the type of polygamy exhibited (i.e. sequential or simultaneous), determine which parent is more inclined to desert.

Parental care decisions can be viewed as the outcome of negotiations within the family over the supply of parental care (Hinde & Kilner 2007). Cues that have been found to affect parental effort include brood size, chick vocalizations and provisioning rates of the partner (see Hinde & Kilner 2007). In our study, brood size and nestling condition, which presumably affect chick vocalizations, did not differ between supplemented and control broods (see the electronic supplementary material). Furthermore, the results of our study do not indicate that high provisioning rates by the male, or large cache sizes, were perceived as signals of high male parental quality or food abundance; males of supplemented nests actually had lower prey delivery rates than males of control nests, and cache size did not differ between supplemented and control nests. However, male Tengmalm's owls, which were left to care for the offspring alone, increased their provisioning rates after the female deserted (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). This suggests that female Tengmalm's owls were somehow able to identify those males that would later be capable of increasing their effort if 'forced'. The question is whether a Tengmalm's owl female can assess the body condition of her partner, either directly or through his behaviour. During the course of one night, the mates interact when the male delivers food, either briefly at the cavity entrance, or more long-lastingly if the male enters

the nest cavity (K. Eldegard & G. A. Sonerud 1983–1999, unpublished data). Based on the results of an experimental study of mate choice in the kestrel *Falco tinnunculus*, Hakkarainen *et al.* (1996) suggested that female kestrels use relative body mass of males as a cue in mate choice. We suggest that body condition is a link between food abundance and parental behaviour of female Tengmalm's owls, and that a female can assess the body condition of her partner through his physical appearance and behaviour.

Because female Tengmalm's owls brood the offspring alone, while males provide food for the whole family (Korpimäki 1981), females are probably better informed than males about offspring need. This puts the female in a position to decide on a level of effort before the male (see Johnstone & Hinde 2006), and this may also partly explain why females, rather than males, desert the offspring when food is ample. Indeed, prey delivery rates of males were approximately three times the delivery rates of females in the post-brooding nestling stage. This suggests that after the offspring reach thermal independence, offspring condition and survival rely more strongly on male than on female care, and that the costs of deserting may be lower for females than for males. To sum up, the results of our study are in agreement with the view that offspring desertion in birds originates through a combination of evolutionary predisposition (sex roles and competence) and ecological facilitation (Owens & Bennett 1997; Owens 2002).

We endeavoured to relocate deserting females, but the task was made nearly impossible because of the distances travelled by females, and the limitations of our equipment. Based on the controls of ringed birds, Tengmalm's owl females have been documented to renest up to 12 km from the first nest within the same breeding season, but it is likely that renesting even takes place much farther away (see Sonerud 1988a). The methodological challenge in relocating deserting Tengmalm's owl females is also illustrated by the fact that, even in extensive long-term field studies of Tengmalm's owls, the mobility of adult females has made the calculation of lifetime reproductive success for females an impossible task (Korpimäki 1992). Tengmalm's owls are relatively small, and this limited the size of the radio-transmitters that could be used (3–4 g). GPS/satellite tags for birds were not available at the time of our study, and the tags that are currently available are too heavy to be applicable on Tengmalm's owls. More data on the whereabouts of deserting Tengmalm's owl females cannot be provided until smaller GPS/satellite tags are available.

In response to food supplementation, female Tengmalm's owls deserted the offspring at an earlier age. Among double-brooding parents, there is probably a trade-off in the allocation of time between broods (see Gruebler & Naef-Daenzer 2008). Roulin (2002) showed that double-brooding barn owl *Tyto alba* females that deserted their first brood started their second brood two weeks earlier compared with females that did not desert. Also, as the breeding seasons advanced, deserting females left their first brood at an earlier stage (Roulin 2002). The pay-off from parental care generally decreases over the breeding season, and there may be fitness benefits from reducing the time invested in the first brood and starting the second breeding attempt earlier (Székely & Cuthill 1999).

The fact that some Tengmalm's owl females deserted their broods, even though it was too late to reneest, indicates that females may also derive other benefits from desertion. Deserting Tengmalm's owl females, which definitely did not reneest, tended to have lower body reserves than females that deserted and left the study area. In the migrating Cooper's hawk *Accipiter cooperii*, more than 50 per cent of the females deserted, and none of them reneested (Kelly & Kennedy 1993). All the females that deserted were in poor physical condition, and Kelly & Kennedy (1993) assumed that they deserted to save energy before the autumn migration. By terminating care earlier, a female can increase her chances of surviving to reproduce in the next breeding season (Székely *et al.* 1996). Over-winter survival of Tengmalm's owl females has not been estimated, but Hakkarainen *et al.* (2002) found that annual survival in adult males ranged from 25 to 76 per cent, depending on food abundance. If they survive through the winter, female Tengmalm's owls have a good chance of breeding every year, in contrast to males, who typically do not breed every year (Löfgren *et al.* 1986; Korpimäki *et al.* 1987; Sonerud *et al.* 1988). We suggest that the late deserting females, with low body reserves, deserted to increase their own chances of survival to the next breeding season.

All the 1-year-old Tengmalm's owl females deserted, so older females were less likely to desert than 1-year-olds. By contrast, among double-brooding female barn owls, Roulin (2002) found no effect of age on the females' decision to provide care until independence or to desert the first brood. Younger females usually have a longer expected lifespan than older females (Székely *et al.* 1996). Furthermore, clutch size has been found to increase with age within individual female Tengmalm's owls (Laaksonen *et al.* 2002). We therefore suggest that 1-year-old females were more inclined to desert than older females because the value of their current brood was lower, and because their residual reproductive value was higher.

Although we suspected that offspring desertion by female Tengmalm's owls was more common than previously recognized from anecdotal reports, it was surprising that as many as 70 per cent of the non-experimental females deserted. Parental behaviour of Tengmalm's owls has been investigated in a large number of field studies (e.g. Korpimäki 1991; Hakkarainen & Korpimäki 1995, 1998 and references therein), yet the prevalence of desertion has remained unknown. This gives reason to suspect that female offspring desertion may be more common than previously recognized in other birds as well (see Eldegard *et al.* 2003). As pointed out by Wells & White (2007), even though the post-fledging period is considered to be one of the most hazardous phases in the avian breeding cycle, crucial aspects, including parental behaviour and interactions, are poorly represented in the post-fledging literature. In conclusion, we assert that there is a great need for more field studies, especially experiments, to investigate the relationship between ecological factors, such as food, and parental care strategies. Future studies should aim at documenting parental care strategies adopted by both parents throughout the whole offspring dependency period.

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