

Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl

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Abstract Within a family there are conflicts of interest between parents and offspring, and between male and female parents, over the supply of parental care. The observed pattern of parental care is the outcome of negotiations within the family, and may be influenced by environmental factors such as food abundance. We experimentally increased food supply to ten Tengmalm's owl (*Aegolius funereus*) nests from hatching to fledging, mimicking natural cached prey. Ten un-supplemented nests served as controls. Parents and offspring were fitted with radio-tags. Food provisioning by parents was measured both in the (1) mid- and (2) late nestling stage and in the (3) early and (4) late post-fledging stage. In response to food supplementation, both males and females reduced food provisioning, but the effect was more pronounced in females. Females generally contributed much less to food provisioning than males, and food supplementation increased the difference between the sexes. Mass loss during the brooding stage was substantially lower for supplemented than for control females. Food supplementation did not improve offspring survival, and had no effect on body measurements of nestlings. In conclusion, parents of both sexes used the increased food supply to reduce the costs of caring for their current offspring, but females responded more strongly than males.

Keywords Body mass · Food provisioning · Food supplementation · Parent–offspring conflict · Sexual conflict · *Aegolius funereus*

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Introduction

Parental care promotes survival and fitness of current offspring, but is costly to the parents in terms of increased mortality and reduced future reproductive output (Clutton-Brock 1991). This gives rise to a conflict of interest between parents and offspring over the supply of parental care. In animals with bi-parental care, such as the large majority of birds, each parent benefits from the effort invested by its partner and usually escapes some of the associated costs (e.g. Lessells and Parker 1999; Cockburn 2006). This leads to a conflict between male and female parents over how much care to provide for their joint offspring (Trivers 1972; Parker et al. 2002; Houston et al. 2005; Olson et al. 2008). Within-family conflicts over care have received much theoretical and empirical interest (e.g. Hinde and Kilner 2007). Early models of bi-parental care explored the sexual conflicts over parental investment on an evolutionary timescale (Chase 1980; Houston and Davies 1985). More recently, parental care models have been extended to incorporate negotiations within the family on a behavioural timescale (McNamara et al. 1999, 2003; Johnstone and Hinde 2006). Indeed, a number of field experiments have provided support for the notion that parents adjust their behaviour to their mate's behaviour as well as to their brood's need in real time (e.g. Hinde 2006; Hinde and Kilner 2007; Kosztolányi et al. 2008).

Providing food for the offspring constitutes a substantial part of the costs of parental care in most birds (Clutton-Brock 1991). A parent's allocation of food to current offspring versus self-maintenance is a manifestation of the underlying trade-off between current and future reproduction (Stearns 1992). It has been hypothesised that the availability of resources, such as food, influences parental care levels (e.g. Orians 1969; Emlen and Oring 1977). If

food supply is experimentally increased, parents may maintain a constant foraging effort and use the supplemental food to improve conditions for the current offspring. At the other extreme, parents may reduce foraging efforts in order to engage in polygamy, or to improve their own survival prospects, without using the additional food to improve offspring fitness. Many previous studies have investigated whether experimentally increased food supply has a positive effect on body measurements or survival of offspring (e.g. Wiehn and Korpimäki 1997; Dawson and Bortolotti 2002; Hipkiss et al. 2002; Brommer et al. 2004; González et al. 2006). However, to our knowledge, only one previous study has measured the effects of food supplementation on both provisioning behaviour of male and female parents, parental body condition and growth and survival of offspring (Wiehn and Korpimäki 1997). We assert that measuring the effects on all these aspects simultaneously is important to increase our insights into how sexual and parent–offspring conflicts are resolved, and how they are influenced by changes in food supply.

In birds of prey (hawks, falcons and owls), bi-parental care is obligatory at least until the nestlings can keep themselves warm (Newton 1979; Mikkola 1983). Bird of prey parents exhibit a marked duty division, with females brooding and males providing food for the whole family (Newton 1979; Mikkola 1983). Brooding females must either rely on their mates to bring them food, or draw on their own body reserves, and typically lose much of their body mass from hatching to fledging (Brodin et al. 2003). Brodin et al. (2003) argue that brooding female birds of prey should build up fat reserves to hedge against uncertain food availability, but emphasise the need for more manipulative studies that modify body reserve status of bird of prey parents. In contrast to the females, male birds of prey are not expected to build up body reserves, as this is assumed to impair hunting success (Korpimäki 1990). After bird of prey females terminate brooding, they resume hunting, but empirical data on the relative contribution of males and females to food provisioning in the late nestling, and especially the post-fledging period, is scarce even in otherwise well-studied species (Eldegard et al. 2003; Sunde et al. 2003).

Here we report the effects of experimentally increased food supply on provisioning behaviour and body mass of Tengmalm's owl (*Aegolius funereus*) parents, and on body measurements and mortality of their offspring. The study is unique in that it measures both (1) food provisioning behaviour of the parents repeatedly throughout the offspring dependency period, (2) body mass changes of brooding females, (3) body mass of male parents, (4) body size of nestlings and (5) offspring survival in the nestling and post-fledging period. Measuring and collating all these responses in the same study provides novel insights into

how changes in food supply may influence within-family conflicts over parental care.

Materials and methods

Study site and study species

The study took place in Hedmark County in southeast Norway within 60°45'–61°10' N and 11°15'–12°00' E at altitudes of 170–580 m. Relevant descriptions of this area are given by Sonerud (1986) and Steen et al. (1996).

Tengmalm's owls are small (male body mass ≈100 g), nocturnal, cavity-nesting owls that reside in the Eurasian boreal forests (Mikkola 1983; Cramp 1985). They readily breed in nest boxes (Korpimäki 1981), and are robust to trapping, handling and radio-tagging (see Eldegard and Sonerud 2009). In Fennoscandia, Tengmalm's owls feed mainly on microtine rodents (Microtidae) and shrews (Soricidae; Mikkola 1983; Cramp 1985). Population densities of microtine rodents fluctuate widely in Fennoscandian boreal forests, usually with peaks every 3–4 years, in a regionally asynchronous manner (Steen et al. 1996; Sundell et al. 2004; Hörmfeldt et al. 2005).

In Tengmalm's owls, only the female incubates and broods, whereas the male provides all the food for his mate and offspring until the late nestling period (Korpimäki 1981; Cramp 1985). The male delivers prey directly to his brooding mate in the nest cavity, where surplus prey items are temporarily stored (Korpimäki 1987). After the nestlings can keep themselves warm, the female resumes hunting (Korpimäki 1981). The relative contribution of male and female parents to food provisioning in the late nestling and post-fledging periods has not previously been documented, but Eldegard and Sonerud (2009) found that a majority of the females deserted their mate and offspring before the offspring reached independence. Duration of the post-fledging dependency period is 6–7 weeks (own unpublished data).

Adult male Tengmalm's owls are territorial and resident, and typically refrain from breeding when food is scarce (Löfgren et al. 1986). In years of high food abundance, 10–20% of the breeding males are simultaneously polygynous, i.e. they re-mate within the same breeding season without deserting their first brood, whereas 20–25% of the males remain unpaired even if they possess a territory and nest cavity (Carlsson et al. 1987; Carlsson 1991; Korpimäki 1991; Hakkarainen and Korpimäki 1998). In contrast to the resident males, adult females often disperse long distances between breeding attempts, concentrate and breed where prey is abundant and may breed every year (Löfgren et al. 1986; Korpimäki et al. 1987; Sonerud et al. 1988). When food is abundant, a female Tengmalm's owl that deserts her

first brood may readily find a new mate and raise a second brood in the same year (Solheim 1983; Sonerud 1988a; Korpimäki 1989; Eldegard and Sonerud 2009). Individuals of both sexes usually (>95%) change mates between breeding seasons, even if their previous partner is still alive (Korpimäki 1988a, 1989; own unpublished data).

Food supplementation experiment

We put up nest boxes and inspected them from mid-March and onwards. As nests were found, they were visited sufficiently often to determine the hatching date (± 1 day) of the first egg in the clutch. We took advantage of the fact that Tengmalm's owls cache prey temporarily in the nest cavity, and supplied 10 nests with extra food (laboratory-reared mice *Mus musculus*) from hatching to fledging, mimicking naturally stored surplus prey. We used 10 non-supplemented nests as controls. 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). We only moderately increased food supply by adding c. 20 g food per capita (female and nestlings) every fourth day in the brooding period, and c. 30 g per capita every fourth day in the post-brooding period. This corresponds to c. 30% of the average food consumption of Tengmalm's owl nestlings, and c. 10% of the energy requirements of the brooding female (see Eldegard and Sonerud (2009) for details on the food supplementation experiment). At each food supplementation visit, we recorded biomass of cached prey. Remains of previously supplemented food were only found in 2% of these cases. Food supplementation was terminated at fledging of the first-fledged offspring in each brood. Control nests were inspected and disturbed in the same way as supplemented nests, except that no extra food was added. There was no difference in hatching date or clutch size between supplemented and control nests (Eldegard and Sonerud 2009).

The relative density of microtine rodents and shrews in the study area has been estimated by annual snap trapping of small mammals in May since 1981, following the method described by Sonerud (1988b). Our food supplementation experiment was done in 1998, which was a year of intermediate population densities of these mammals (see Eldegard and Sonerud (2009) for details).

Trapping and body measurements of adult owls

Adult females were caught by hand in the nest box. Adult males were captured at night in a swing-door trap mounted in front of the nest box entrance, or in mist-nets in front of the nest tree. Females were weighed at around the time of hatching (median day 3, range 0–4), when food supplementation started and in the late brooding stage (median

day 17, range 16–18). Wing length was recorded at the first or the second weighing. Body mass and wing length of males were recorded in connection with radio-tagging (median day 14, range 11–16). Body mass was measured to the nearest 0.5 g using a 300 g Pesola spring scale. Note that body mass of adults was recorded before the birds were radio-tagged, and thus the radio-tags did not influence the observed effects of food supplementation on body reserves of parents. Wing lengths used in statistical analyses are average of both wings, each measured to the nearest millimetre as the maximum length of the flattened wing by use of a wing chord ruler (method 3 in Svensson 1992).

Body measurements and sex of nestlings

Body mass and foot length of nestlings were recorded in the late brooding stage (median day 17, range 16–19) and in the late nestling stage (median day 29, range 27–30). Wing length of nestlings was measured in the late nestling stage. Nestlings were ringed for individual recognition at the first weighing. Body mass and wing length were recorded using the same methods as for the adults. Foot length was measured to the nearest millimetre as the distance from the intertarsal joint to the tip of the claw on the longest toe, placing the intertarsal joint in the angle of a wing chord ruler and measuring the stretched tarsus and toe.

In order to control for the effect of sex in analyses of effects of food supplementation on body measurements of nestlings, we collected blood samples from nestlings for molecular sex determination. Blood sampling and DNA extraction procedures followed Krokene et al. (1996). Sex determination was done according to the methods of Fridolfsson and Ellegren (1999), using the parents as controls.

Radio-tagging

Radio-transmitters (type TW-4, Biotrack, UK, with a life expectancy of c. 3 months) were mounted as backpacks and attached with a tubular Teflon tape (Bally Ribbon Mills, PA, USA). The total backpack (including harness) weighed 4.7 g, which amounted to 4.4% of average adult male body mass and 3.0% of average adult female body mass. Adult males were captured and radio-tagged at night in the female brooding stage (see above). Adult females were radio-tagged at the end of the brooding stage, in connection with the second weighing (see above). The males were allowed at least one full night for habituation to the tag before recording of food provisioning started. Food provisioning by females was not monitored until at least 3 days after they had ceased brooding. One nestling from each nest was radio-tagged as close to fledging as possible. In each brood, the nestling that was assumed to fledge first (judged from

behaviour and wing length) was tagged. Brood mates keep together until about 4 weeks after fledging (own unpublished data), so it was sufficient to tag one nestling in each brood.

Food provisioning by parents

For each brood, food provisioning (i.e. prey deliveries) by the parents was observed throughout four nights: (1) in the mid-nestling stage, when the female brooded constantly and only the male provided food (median day 16, range 15–18), (2) in the late nestling stage, when the female no longer brooded (day 25, range 23–27), (3) in the early post-fledging stage (day 42, range 40–44) and (4) in the late post-fledging stage (day 57, range 55–58).

Prey deliveries by parents in the nestling stage were monitored automatically using a data-logging receiver (RX-900, Televilt, Sweden), which recorded time and transmitter-frequency of the visiting parent. The receiver was connected to two fixed two-element Yagi-antennas (Televilt). Minimum monitoring time was from just before sunset until just after sunrise. This equipment made it possible to count the number of times each parent arrived at the nest following a period of weak or non-detectable radio signals. Other methods for automatic nest monitoring, like camera or other recording devices placed in the nest, do not discriminate between returns from long-distance foraging trips and non-foraging movements in the nest vicinity. The reliability of our method was tested by carrying out visual observations simultaneously with the automatic monitoring at five nests. The results from the visual and the automatic monitoring were always consistent with respect to number and timing of nest visits.

We assumed that all nest visits by males in the mid-nestling (female brooding) stage, and by males and females in the late nestling stage, were prey deliveries. During visual observations at 20 Tengmalm's owl nests for a total of 50 nights in 1995–1997, males were never observed arriving at the nest without prey during the female brooding stage and none of the parents were observed entering the nest box without prey during the late nestling stage (own unpublished data). Furthermore, video monitoring of prey deliveries at six Tengmalm's owl nests throughout 18 nights revealed no visits by males without prey, and no post-brooding visits by females without prey (own unpublished data). However, according to Korpimäki (1981), Tengmalm's owls may visit their nest without prey, particularly the females. For the females, such visits were least frequent the first week post-brooding (0.5 per night; calculated from data in Korpimäki (1981)). For the males, such visits occurred only in the early nestling period (0.35 per night; calculated from data in Korpimäki (1981)). In our present study, prey deliveries in the mid-nestling stage were

recorded for the males only (on average 5.4 and 8.4 visits per night for males at supplemented and control nests, respectively), whereas prey deliveries by the females (and males) were recorded in the first week post-brooding (on average 1.7 and 3.8 visits per night for tending females at supplemented and control nests, respectively). From this, and from the fact that our monitoring method excluded visits following non-foraging movements in the nest vicinity, we conclude that nest visits without prey probably constituted only a small proportion of the total number of nest visits included in our data set. Moreover, this proportion should be smaller for males than for females, and smaller for control than for supplemented nests, making our tests for inter-sexual differences, and effects of food supplementation on prey deliveries, conservative.

In the post-fledging stage, prey deliveries to offspring were recorded by visual observation using portable receivers (Telomics, AZ, USA, and Televilt) and hand-held two-element Yagi antennas (Televilt). Prey deliveries were detected from signal strength of radio-transmitters, vocalisations of arriving parents, movements and vocalisations of offspring and visual observations. Deliveries were recorded at distances of 5–50 m from the young, and did not seem to disturb either the offspring or their parents. Each brood was localised by homing in on the radio-tagged fledgling. Prey deliveries were recorded from shortly before sunset until shortly after sunrise.

The occurrence and timing of desertion was determined from daytime and night-time radio-tracking of adults and offspring. 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 (about three times mean home range radius, own unpublished data). If we failed to pick up signals within this area, we assumed that the parent had deserted and left the area. The radio-transmitter of individual owls that were killed by predators was easily found, even though it was located on the ground (two fledged offspring in this study and two adults in a previous study; Eldegard and Sonerud (2009)). The range at which signals could be detected from the ground exceeded 10 km (own unpublished data), so the owls that we lost track of had moved even further (see Eldegard and Sonerud (2009) for more detailed descriptions of the field methods).

Brood size and fledging age

We kept count of brood size on the basis of frequent nest inspections, remains of dead nestlings and by X-raying prey remains from nests in order to reveal rings of dead nestlings. In the early brooding stage, many of the females were reluctant to leave the nest cavity when we inspected the nests. We did not force these females out, and therefore

we were unable to determine brood size until the oldest nestling was about 7 days old for many of the nests. At around the time of fledging, we visited the nests every day to determine fledging day of the first-fledged young. In the post-fledging stage, 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.

Data analyses

Sample size was reduced from 20 broods in the late brooding period to 16 broods 4 weeks after fledging, due to predation of nestlings in one supplemented and one control nest, and predation of the radio-tagged fledgling in one supplemented and one control brood. In addition, for one of the control broods, it was not possible to determine number of prey deliveries by the parents in the late post-fledging stage, because the brood mates were too widely dispersed. Data were analysed using SAS/STAT® 9.2 (SAS Institute, Inc., Cary, NC, USA) and SigmaStat 1.0 (Jandel Scientific GmbH, Ekrath, Germany) statistical software.

Provisioning by parents

The data on provisioning by parents were counts (number of prey deliveries per night). The data were not transformable to normality because of many zero values (many females did not deliver any food post-fledging). We used generalised linear mixed models (GLMMs) for analyses of the prey delivery data, following procedures recommended by Bolker et al. (2008). First, we created a full (most complex) model including the fixed effects ‘sex’, ‘treatment’, ‘brood age’ and the ‘sex × treatment’ and ‘sex × brood age’ interactions (Table 1). The two interaction terms were included because our purpose was to find out whether there was an inter-sexual difference in parental effort, and whether this inter-sexual difference changed when conditions (food, brood age) changed. ‘Brood identity’ was modelled as random effect because prey deliveries were measured repeatedly at the same broods. We initially fitted a model with log link function, Poisson distribution and Gauss-Hermite Quadrature (GHQ) technique for GLMM parameter estimation (Bolker et al. 2008). However, inspections of graphical diagnostics and the scaled Pearson statistic for the conditional distribution (1.58) suggested that there was moderate over-dispersion. Therefore, we adjusted the model by changing from a Poisson to a negative binomial distribution. All information criteria, inspections of graphical diagnostics and the scaled Pearson statistic (1.16) indicated that the negative binomial distribution provided a better fit. After fitting the full model, model selection was performed using the small sample size

Table 1 Results of model selection procedures to determine which factors influenced provisioning by Tengmalm’s owl parents

Model	Fixed effects included in model	Log (likelih)	Number of parameters	AICc	ΔAICc	AIC weight
A. Both parents (LN+EPF+LPF)						
1 ^a	S T S×T	-236.8	6	486.4	0.00	0.63
2	S T	-239.6	5	489.7	3.26	0.12
3	S T B S×T S×B	-234.1	10	490.6	4.19	0.078
4	S	-241.2	4	490.8	4.34	0.072
5	S T B S×T	-236.8	8	491.1	4.63	0.062
6	S T B S×B	-236.7	9	493.3	6.87	0.020
7	S T B	-239.5	7	494.2	7.80	0.013
B. Males (MN+LN+EPF+LPF)						
1	T	-173.9	3	354.1	0.00	0.81
2	B, T	-172.0	6	357.3	3.18	0.17
3	B, T, B×T	-170.2	9	361.4	7.24	0.022

Generalised mixed models with log link function, negative binomial distribution (A) or Poisson distribution (B), and Gaussian Hermite Quadrature approximation to the likelihood. Models are sorted by their degree of support from the data, which is indicated by the AIC weight. ‘Brood identity’ was modelled as random effect. Response variable was number of prey deliveries to offspring per night. Prey deliveries by both parents were monitored at three different brood ages. In addition, prey deliveries by male parents were monitored in the MN. Food supply was experimentally increased from hatching to fledging

AIC Akaike’s Information Criterion, S sex of parent, T treatment (supplemented or control), B brood age, LN late nestling, EPF early post-fledging, LPF late post-fledging, MN mid-nestling stage

^a Wald F tests for fixed effects and likelihood ratio tests for random effects for the model best supported by the data (Model A1) are reported in Table 2

corrected Akaike information criterion (AICc) as recommended by Anderson et al. (2001). Model selection using information criteria like AICc will identify the best model in a set of candidate models, even if all models are poor. Therefore, we also provide Wald F tests of fixed effects and likelihood ratio (LR) tests of random effects for the model best supported by the data (Tables 1 and 2). Because only males provided food in the mid-nestling stage, we also fitted a sex-specific GLMM for prey deliveries by males, with log link function, Poisson distribution (there was no over-dispersion) and GHQ approximation to the likelihood (Table 1).

As no experimental food was supplied after fledging, we also analysed the effects of food supplementation on provisioning by male and female parents using data from the late nestling stage only. We performed two analyses: one including all the nests and one including only nests that had not (yet) been deserted by the female (Fig. 2). We fitted full (most complex) models with ‘treatment’, ‘sex’ and the

Table 2 Results of analysis of factors influencing provisioning by Tengmalm's owl parents

Explanatory variables	df	Log (likel)	χ^2	F	p value
Fixed effects					
Sex	1.83		83.0	<0.0001	
Treatment	1.83		6.62	0.012	
Sex × treatment	1.83		5.56	0.021	
Random effect					
Brood identity ^a	1	-237.2	0.86	0.18	

Response variable was number of prey deliveries to offspring per night. Wald F tests of fixed effects and likelihood ratio tests of random effects for the model best supported by the data in Table 1 (Model A1). Food supply was experimentally increased from hatching to fledging

^aThe ‘brood identity’ effect amounted to 13.3% to of total variance. Generalised mixed models with log link function, negative binomial distribution and Gaussian Hermite Quadrature approximation to the likelihood

‘treatment × sex’ interaction as explanatory variables, and log link function, Poisson distribution and GHQ approximation to the likelihood. We report estimated least squares means and 95% confidence limits, and results of Wald F tests of the fixed effects.

Body measurements of parents and offspring

In order to estimate the effects of food supplementation on body measurements of parents and offspring, we fitted linear (mixed) models with identity link function, Gaussian distributions and restricted maximum likelihood estimation. It was not necessary to transform the response variables.

The effect of food supplementation on body mass of females was estimated by fitting a full (most complex) model with ‘treatment’, ‘brood age’, ‘wing length’ and the ‘treatment × brood age’ interaction as fixed effects. Each female was weighed twice, and therefore ‘female identity’ was modelled as random effect. Each male was weighed only once, and the effect of food supplementation on body mass of males was estimated by fitting a full model with ‘treatment’ and ‘wing length’ as fixed effects. We decided a priori to include ‘wing length’ as covariate in the statistical models in order to control for the effect of linear body size on body mass. Thus, we report estimated body mass for parents of supplemented and control nests, controlled for the effect of wing length (estimated least squares means and 95% confidence limits from the full models; Fig. 3).

Tengmalm's owl is sexually dimorphic for linear body measurements, and is regarded as Europe's most sexually dimorphic owl in mass (Hipkiss 2002). Therefore, we decided a priori to include ‘nestling sex’ as covariate when modelling effects of food supplementation on body meas-

urements of nestlings. The effect of food supplementation on body mass of nestlings was estimated by fitting a full (most complex) model with ‘treatment’, ‘nestling sex’, ‘brood age’ and the ‘treatment × brood age’ interaction as fixed effects. ‘Nestling identity’ and ‘nestling identity within brood identity’ were modelled as random effects, because body mass of individual nestlings was measured twice (in the mid- and late nestling stage). The effect of food supplementation on foot length was estimated in the same way. The effect of food supplementation on wing length of nestlings was estimated by fitting a full model with ‘treatment’, ‘nestling sex’ and the ‘treatment × nestling sex’ interaction as fixed effects, and ‘brood identity’ as random effect (wing length of each nestling was measured only once). We report estimated body size measurements of supplemented and control nestlings in the mid- and late nestlings stage, when the effect of ‘nestling sex’ was controlled for (estimated least squares means and 95% confidence limits from the full models; Fig. 4).

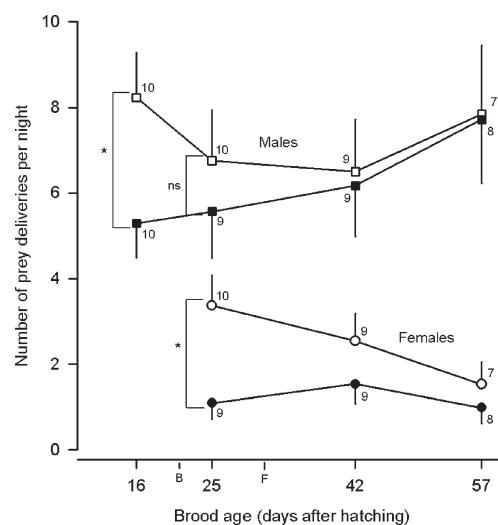


Fig. 1 Food provisioning by parents of supplemented and control Tengmalm's owl broods at different brood ages. Open squares control males, filled squares supplemented males, open circles control females, filled circles supplemented females. The figures close to the symbols show sample size. The symbols and error bars for males and females at brood ages 25, 42 and 57 days show estimated means and standard errors from model A3 in Table 1 (i.e. the full model). The symbols and error bars for males at brood age 16 show estimated least squares means and standard errors from model B3 in Table 1 (i.e. the full model). Pair-wise differences between supplemented and control broods at the level $p<0.05$ are indicated by *, whereas ns indicates that $p>0.05$. Prey deliveries to offspring were monitored from sunset to sunrise throughout four nights for each brood; in the female brooding stage, when only males delivered prey (day 16 after hatching of the first egg), in the late nestling stage (day 25) and in the early (day 42) and late (day 57) post-fledging stages. Food supply was experimentally increased from hatching to fledging. The letter B on the x-axis indicates the end of the female brooding period and the letter F indicates fledging age of the first-fledged offspring in each nest (average of all nests within the two treatment groups)

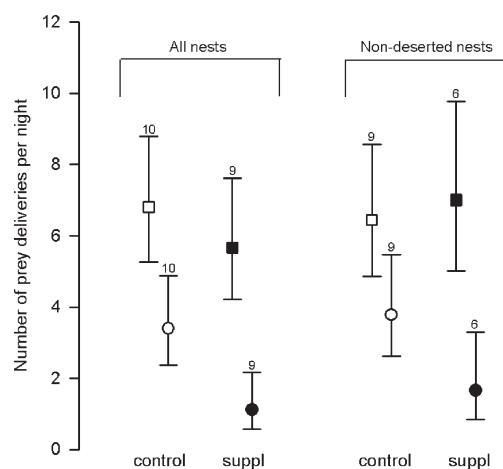


Fig. 2 Food provisioning by Tengmalm's owl parents in the late nestling stage; at all nests and at nests not (yet) deserted by the female. Open squares control males, open circles control females, filled squares supplemented males, filled circles supplemented females. Symbols and error bars represent estimated least squares means and 95% confidence limits. Sample size is shown as figures above the error bars. Food supply was experimentally increased from hatching to fledging

Results

Provisioning by parents

Both at supplemented and at control nests, males delivered a larger number of prey to the offspring than did the females in the late nestling stage, and this inter-sexual difference in provisioning was even larger in the post-fledging period (Fig. 1). Food supplementation increased the inter-sexual difference in provisioning (Figs. 1 and 2, 'sex \times treatment' interaction in Tables 1 and 2). In response to food supplementation, males reduced provisioning in the mid-nestling stage (when the females were brooding); the estimated reduction in mean number of prey deliveries to the nest was 36% (Fig. 1). In the late nestling stage, the estimated reduction in provisioning by males at supplemented nests was smaller (17%; Fig. 1). In contrast, females reduced number of prey deliveries by 68% in the late nestling stage (Fig. 1). There were no pronounced differences in provisioning between supplemented and control nests in the post-fledging stages (Fig. 1; note that experimental food supply was terminated at fledging).

Five out of nine females from supplemented broods deserted their offspring during the experimental period (i.e. during the nestling stage) as compared to only one out of ten females from control broods, but this difference in frequency of desertion between supplemented and control broods was not statistically significant (Fisher exact test; $p=0.057$; Fig. 2a in Eldegard and Sonerud (2009)). In the late nestling stage, food supplementation increased the inter-sexual difference in provisioning, both when all nests

were considered, and when only non-deserted nests were considered (Fig. 2, all nests; sex: $F_{1,17}=32.9$, $p<0.0001$, treatment: $F_{1,17}=10.3$, $p=0.0051$, sex \times treatment: $F_{1,17}=5.35$, $p=0.034$, non-deserted nests; sex: $F_{1,13}=22.8$, $p=0.0004$, treatment: $F_{1,13}=3.17$, $p=0.098$, sex \times treatment: $F_{1,13}=4.76$, $p=0.048$). By the end of the post-fledging period, the majority of females from both supplemented and control broods had deserted (five versus six out of nine females), and an analysis of inter-sexual differences among non-deserted broods could not be carried out because of small sample size. None of the males deserted, and all the males that were deserted by their partner continued to care for their offspring alone.

Body mass of parents

Food supplementation reduced mass loss in brooding females by 66%; from 27 to 9 g (Fig. 3). At the end of the brooding period (day 17 after hatching), estimated mean body mass of females was 12% higher at supplemented nests than at control nests (166 vs 146 g). The random effect 'female identity' constituted 57% of the overall variance in body mass of females (LR test: $\log(\text{likelihood})=-146.3$, $\chi^2=6.91$, $df=1$, $p=0.0043$). At around the same time (day 14 after hatching), estimated mean body mass of males was 5% higher at supplemented nests than at control nests, but this difference was not statistically significant (Fig. 3; 109 vs 103 g).

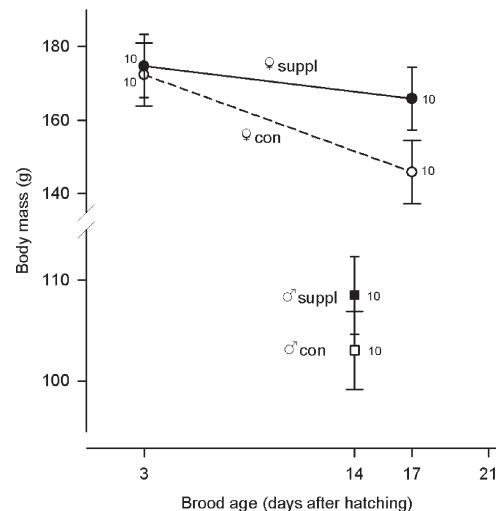


Fig. 3 The effects of food supplementation on body mass of female and male Tengmalm's owl parents at different brood ages, when the effect of wing length was controlled. Symbols and error bars represent estimated least squares means and 95% confidence limits, filled symbols and solid lines supplemented broods, open symbols and dashed lines control broods. Food supply was experimentally increased from hatching to fledging. On average, females of both supplemented and control brood terminated brooding on day 21. The figures close to each symbol show sample size

Body measurements, fledging age and survival of offspring

We found no effects of food supplementation on body size measurements of offspring when the effect of ‘nestling sex’ was controlled for (Fig. 4). For body mass, the random effects amounted to 32% (‘nestling identity’) and 16% (‘nestling identity within brood identity’) of overall variance (LR test: $\log(\text{likelihood})=-710.5$, $\chi^2=9.26$, $df=2$, $p=0.0036$). For foot length, the random effects amounted to 40% (‘nestling identity’) and 30% (‘nestling identity within brood identity’) of overall variance (LR test: $\log(\text{likelihood})=-444.0$, $\chi^2=20.3$, $df=2$, $p<0.0001$). We found no effect of food supplementation on survival of offspring during the nestling or post-fledging stage, or on fledging age of the first-fledged offspring (Table 3).

Discussion

Provisioning by parents

In the female brooding stage, males at supplemented nests reduced food provisioning. In the late nestling stage, both male and female parents at supplemented nests reduced food provisioning, but the reduction was more pronounced in females. Females generally contributed less to food provisioning than did males in both supplemented and

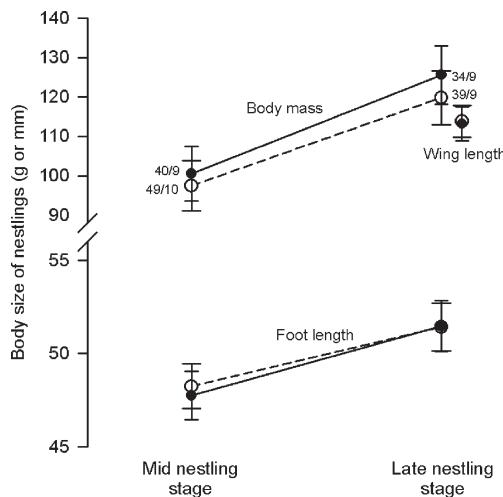


Fig. 4 The effects of food supplementation on body size of Tengmalm's owl nestlings, when the effects of nestling sex was controlled for. Filled circles and solid lines supplemented broods, open circles and dashed lines control broods. Symbols and error bars represent estimated least squares means and 95% confidence limits. Food supply was experimentally increased from hatching to fledging. The figures close to each symbol show sample size; number of nestlings/number of broods. Sample size is only shown for body mass measurements, but was the same for all body measurements at the same brood ages. Note that body mass and wing length in the late nestling stage was measured at the same brood age, but the symbols for wing length have been slightly displaced to the right

Table 3 Survival and fledging age of offspring from supplemented and control Tengmalm's owl broods

Trait	Treatment	Median	Lower qrt	Upper qrt	n	T	p value
Nestling survival ^a					84.0	0.93	
Control	0.60	0.48	0.90	9			
Supplement	0.71	0.60	0.80	9			
Post-fledging survival ^b					70.5	0.80	
Control	0.59	0.33	0.72	8			
Supplement	0.55	0.45	0.60	8			
Fledging age ^c					96.0	0.38	
Control	31.0	30.8	32.5	9			
Supplement	30.0	30.0	31.3	9			

Food supply was experimentally increased from hatching to fledging. Test statistics and *p* values from Mann–Whitney rank sum test

qrt quartile

^a Nestling survival: number of fledglings/number of eggs

^b Post-fledging survival: number of offspring alive in the late post-fledging stage/number of fledglings

^c Fledging age (days after hatching) for the first-fledged offspring in each brood

control broods, and food supplementation increased the difference between the sexes. A large proportion of the females even stopped feeding at an early stage. The difference in provisioning rates between supplemented and control broods was reduced post-fledging, when no experimental food was supplied, and cancelled out by the end of the post-fledging period. To our knowledge, no previous study has recorded effects of food supplementation on provisioning by males in the female brooding stage, or on provisioning rates in the post-fledging stage. For the late nestling stage, our results are in accordance with those of Dawson and Bortolotti (2002), who found that American kestrel (*Falco sparverius*) males responded to extra food by reducing provisioning, but to a much lesser extent than females. Similarly, Wiehn and Korpimäki (1997) found that female Eurasian kestrels (*Falco tinnunculus*) responded to food supplementation by decreasing food provisioning to nestlings, whereas food provisioning by males did not change. Furthermore, a reduction in parental effort in response to food supplementation has been found in other long-lived species (e.g. Wernham and Bryant 1998; Jodice et al. 2002). Longevity or breeding life span are important determinants of lifetime reproductive success in Tengmalm's owl (Korpimäki 1992), as well as in other birds of prey (Wallin 1988; Newton 1989; Brommer et al. 1998; Espie et al. 2000). By reducing parental effort, a parent may improve its chances of surviving to the next breeding season (Martin 1987; Dawson and Bortolotti 2002), or starting egg-laying earlier in the next breeding season (Brommer et al. 2004).

In the early and mid-nestling stage, when the female Tengmalm's owl is brooding constantly, only the male can reduce his provisioning effort. In contrast, in the post-brooding stage, the female is probably in a position to decide on her level of provisioning effort first, because she is better informed about brood needs (Eldegard and Sonerud 2009). According to the bi-parental care model of Johnston and Hinde (2006), the best-informed parent should be expected to respond more strongly to changes in brood needs. We have previously found that a majority of the Tengmalm's owl females desert before their offspring reach independence, and leave the male to raise them alone (Eldegard and Sonerud 2009). The probability of female offspring desertion increased with increasing food supply (Eldegard and Sonerud 2009). It has previously been documented that female Tengmalm's owls may re-mate and raise a second brood with another male within the same breeding season (Solheim 1983; Sonerud 1988a; Korpimäki 1989), and we suggest that an important motivation for deserting may be the possibility of starting a second brood with another male. If the female deserts or only makes a small contribution to the total food provisioning, the male cannot reduce his provisioning effort without seriously compromising the survival prospects of the current offspring. The observed increase in female offspring desertion and reduction in female provisioning effort in response to food supplementation may also explain why the difference in provisioning rates between supplemented and control males cancelled out by the end of the post-fledging stage (Fig. 1).

Females of control broods exhibited slightly higher provisioning rates than females of supplemented broods in the early post-fledging stage (Fig. 1; day 42). This may be related to the fact that females of control broods deserted later than females of supplemented broods (Eldegard and Sonerud 2009).

Body mass of parents

Mass loss during the brooding period was substantially lower for supplemented than for control females. Males at supplemented nests were 5%, though not significantly, heavier than males at control nests. Brommer et al. (2004) found a similar pattern in Ural owls (*Strix uralensis*), but when the experiment was repeated in the subsequent year, only marginal effects on female body mass and no effects on male body mass were found (Karell et al. 2009). Wiehn and Korpimäki (1997) found that kestrel females at supplemented nests were heavier than females at control nests, whereas food supplementation did not affect body mass of male kestrels. Korpimäki (1990) reported that mass loss in brooding female Tengmalm's owls was less pronounced in years when food was abundant than in years

when food was scarce. According to the model developed by Brodin et al. (2003), large fat reserves early in the nestling period are very important for successful breeding in female birds of prey. By allocating supplemental food to self-maintenance, female Tengmalm's owls may more quickly acquire the energy reserves needed for a new clutch, either in the same breeding season (desertion and sequential polyandry) or in future ones. Brooding females at supplemented nests also experienced mass loss, although not as pronounced as in control broods, and we cannot completely rule out the possibility that the mass loss was a preparation for hunting in the post-brooding period (Freed 1981; Norberg 1981). However, the female Tengmalm's owls contributed little to food provisioning and were likely to desert (probably with the intention of re-mating), and they should benefit from having as high body mass as possible.

It is often argued that male birds of prey should not accumulate body reserves that would increase flight costs (e.g. Korpimäki 1990). Hakkarainen and Korpimäki (1991, 1995) found that prey delivery rates of male Tengmalm's owls were negatively correlated with wing loading when voles were scarce, but positively so when voles were abundant. Being light may be beneficial when voles are scarce and the owls have to hunt smaller prey, such as shrews, and compensate for smaller prey size by increasing the number of foraging flights (Korpimäki 1988b). Accumulating body reserves may be less costly when voles are more abundant, as in our study. In addition to within-species trade-offs between hunting success and self-maintenance, between-species differences in foraging ecology and hunting techniques may also explain the varying outcomes of different studies. For example, localising prey from perches demands far less energy than wind hovering (Andersson 1981). Thus, the energy savings from reduced body reserves is likely to be of less importance to strict perch-hunters, such as Tengmalm's owls and Ural owls (Norberg 1970; Bye et al. 1992; own unpublished data), as compared to species that to a larger extent hunt on the wing, such as kestrels (Masman and Klaassen 1987).

Body measurements and survival of offspring

We found no effects of food supplementation on body measurements or survival of offspring. Many food supplementation studies have found that parents of supplemented nests raise heavier or larger fledglings than parents of control nests, or realise a higher fledging success (e.g. Ward and Kennedy 1996; Wiehn and Korpimäki 1997; González et al. 2006; Granbom and Smith 2006), whereas other studies have found no significant differences between supplemented and control broods (e.g. Dawson and Bortolotti 2002; Brommer et al. 2004). The results vary

not only among, but also within species; Ward and Kennedy (1996) and Hipkiss et al. (2002) found a significant effect of food supplementation on nestling mortality in only 1 out of 2 years. Hipkiss et al. (2002), who studied the same species as we did, ascribed the between-years differences to differences in natural food abundance. Within breeding seasons, Byholm and Kekkonen (2008) found that food supplementation reduced nestling mortality in low-quality goshawk (*Accipiter gentilis*) territories, but not in high-quality ones. In addition to between- and within-years differences in natural food supply, one should also consider the amount of food added when interpreting results of food supplementation studies. For example, Hipkiss et al. (2002) supplied substantially more experimental food to the Tengmalm's owl nests than we did in our study, and this may explain why they found a significant effect on body mass of nestlings, whereas we found no such effect.

It has long been acknowledged that food availability is an important factor regulating reproduction in wild birds (Martin 1987; Clutton-Brock 1988). When no statistically significant effects of food supplementation on growth or survival of offspring have been found, it has often been concluded that the natural food abundance was too high to give an effect (e.g. Hipkiss et al. 2002). Alternatively, it has been suggested that even though nestlings from supplemented and un-supplemented broods develop in outwardly similar ways, they might differ in their long-term fitness prospects (e.g. Mock et al. 2005). Hipkiss et al. (2002) found that nestling mortality was substantial among both supplemented and control broods, and concluded that the youngest nestlings died from siblicide despite plentiful natural food supply. Offspring mortality was substantial also in our study (c. 30% at around the time of fledging). However, our results suggest an alternative explanation for the lack of effects of food supplementation on growth and survival of offspring; namely a reduction in parental effort by parents of supplemented nests (see also Dawson and Bortolotti 2002). If we had provided food in excess, we might have found significant positive effects on the number or quality of offspring. However, in that case, we would not have known whether the parents decided to reduce provisioning rates and prioritise self-maintenance only after having exhausted the potential for improving survival and growth of nestlings. By carrying out only a moderate increase, we revealed that the parents prioritised investment in self-maintenance (i.e. future reproduction) rather than investment in the current offspring when food supply increased.

Parental care and varying natural food abundance

Between-years variation in food abundance may cause between-years variation in offspring survival values (e.g.

Brommer et al. 2000). According to Korpimäki and Lagerström (1988), the survival prospects of Tengmalm's owl offspring, and thus their probability of entering the breeding population in the next year, are relatively low in a year preceding a year of low prey abundance (as in our study). The level of nest defence in Tengmalm's owl and Ural owl *Strix uralensis* varies in accordance with vole abundance, and hence offspring survival values (Hakkarainen and Korpimäki 1994; Kontiainen et al. 2009). We acknowledge the value of repeating food supplementation experiments at different levels of natural food abundance (cf. Wiehn and Korpimäki 1997; Hipkiss et al. 2002; Karell et al. 2009). As we did not find any effect of food supplementation on size or survival of offspring, it would be of particular interest to repeat our study in a year of low population densities of natural prey. Yet, we found that the prevalence of female offspring desertion increased with increasing natural food abundance (Eldegard and Sonerud 2009). This indicates that the behavioural responses of Tengmalm's owl parents vary with the level of natural food abundance.

Parental care patterns in bi-parental birds are influenced by a number of factors (e.g. Hinde and Kilner 2007; Olson et al. 2008). Our study has provided novel insights into how changes in food supply may influence the outcome of within-family conflicts. We conclude that Tengmalm's owl parents used the increased food supply to reduce the costs of caring instead of improving conditions for their current brood, and that female parents responded more strongly than males. Our results are in line with the traditional view of sexual conflicts over parental care which place great importance on ecological factors in determining levels of care (e.g. Orians 1969; Emlen and Oring 1977).

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Ethical standards The experiments in this study comply with Norwegian law, the Directorate for Nature Management and the National Animal Research Authority in Norway granted permission to trap and radio-tag the owls, and the Directorate for Nature Management granted permission to trap small mammals.

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