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Original Article

Parental care in nesting hawks: breeding experience and food availability influence the outcome

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Parental food provisioning and sibling rivalry have inspired abundant investigations of evolutionary conflicts within families. Nevertheless, their joint effects have seldom been assessed in relation to parental and environmental state. We investigated state dependency of feeding behaviors through the complete nesting phase in a species whose young both partly beg for food and partly self-feed, the northern goshawk *Accipiter gentilis*. After hatching, when young relied on being fed beak-to-beak, siblings achieved equal amounts of food irrespective of hatching rank, body condition, and sex. However, mothers new to a territory fed their offspring less than experienced ones independently of food availability. This pattern persisted also after nestlings grew and initiated to self-feed and aggressively monopolize prey. Mothers never interfered with aggressions but stayed with their even feeding strategy paying little attention to begging activity. Although mothers' even feeding strategy is likely to equalize siblings' survival probabilities when food is abundant, the fact that nestlings in good condition monopolize prey in self-feeding situations will boost brood asymmetries when food decreases. Because new mothers feed their offspring less than experienced ones, aggressive sibling rivalry will be particularly crucial among mothers lacking previous local breeding experience. Albeit hitherto overlooked, feeding behaviors constitute important mechanisms explaining experience-related differences in reproductive performance of wild animals. *Key words:* begging behavior, experience-dependent fecundity, food availability, parent–offspring conflict, parental breeding experience, sibling competition. *[Behav Ecol 22:609–615 (2011)]*

INTRODUCTION

In species with advanced levels of parental care, such as birds and mammals, dependent young commonly beg for food from the care-giving parents (Mock and Parker 1997; Wright and Leonard 2002). Although both offspring and parents benefit from care in an evolutionary sense, begging behavior has greatly inspired investigations into evolutionary conflicts within families given its potential role in distorting the amount and duration of care (Kacelnik et al. 1995; Wright and Leonard 2002; Wells 2003; Rodríguez et al. 2008). Traditionally parent–offspring feeding interactions have either been tackled in the light of scramble competition theory (offspring control resource allocation) or in relation to theories of honest signaling of offspring need (parents control resource allocation) (Godfray 1995; Mock and Parker 1997; Royle et al. 2002). However, considering the great diversity and context dependence of different begging and provisioning strategies (Mock and Parker 1997; Davis et al. 1999; Wright and Leonard 2002; Smiseth, Ward, et al. 2007; Smiseth, Lennox, et al. 2007) and that honest-signaling and scramble competition models are not fully mutually exclusive (Parker et al. 2002; Royle et al. 2002), many issues in the debate about

the evolutionary causes and consequences of begging and subsequent parental food allocation patterns are far from settled.

For example, although offspring size and condition are known to be of critical importance for offspring survival and future fitness (Lindström 1999; Alonso-Alvarez et al. 2007), the relative importance of parent–offspring interactions and sibling rivalry in shaping and maintaining food access hierarchies between contemporary siblings have achieved little attention (Drummond 2002). This is because much of the research performed hitherto has concentrated either on parental care or sibling competition separately, while the 2 traits seldom have been studied together (Smiseth, Ward, et al. 2007; Smiseth, Lennox, et al. 2007, but see Mock and Parker 1997). Similarly, state dependency in parental provisioning rules in relation to offspring age and parents' previous breeding experience is not well understood (Royle et al. 2002). Thus, although birds commonly have functioned as model species in studies on begging behavior and conflicts of interest within families (Magrath 1990; Mock and Parker 1997; Wright and Leonard 2002; Royle et al. 2004), most research has been confined to species that actively feed their young throughout the nestling period, such as passerines and herons (Drummond 2002; Royle et al. 2004). Studies of within-family conflicts in species whose young both partly beg for food and partly self-feed are virtually absent, and when food allocation patterns of such species have been studied (Fargallo et al. 2003), parental provisioning and nestlings' self-feeding were not distinguished. Moreover, even if parental state such as age and experience commonly relates to reproductive performance in birds and mammals (e.g., Fowler 1995; Nussey et al. 2008), there exist—to the best of our knowledge—no

studies deducing whether parental breeding experience induce state dependency in parent–offspring interactions while simultaneously accounting for aggressive sibling rivalry. Consequently, because parental care may have repercussions for offspring survival, opening of new research investigating how parental and environmental state relates to parental care is needed. In particular among age-structured populations of long-lived species in which individual-level processes feed into population-level patterns (Sutherland 1996; Byholm et al. 2007; Byholm and Kekkonen 2008), such knowledge is valuable for judging the demographical and evolutionary significance of parent–offspring interactions in a wider context.

In relation to the idea that different food allocation rules might be context dependent, we here investigate parental provisioning, begging, and aggressive competition behaviors in nestling Finnish northern goshawks *Accipiter gentilis* (hereafter goshawk). Considering that the nestling stage in goshawks lasts for one and a half months (Kenward 2006) and that the nestlings during this time both self-feed and are fed by their mother, the goshawk is likely to prove an excellent species for getting insight into complex patterns and the evolution of conflicts of interests within families. Simultaneously accounting for confounding factors, particular effort was put to investigate how parent–offspring interactions and sibling rivalry were influenced by variation in 1) food availability and 2) breeding experience as well as 3) to the extent to which sibs in a brood utilize begging as a signal to reinforce/attenuate the effects of innate size hierarchies arising from hatching asynchrony. Because the goshawk constitutes a long-lived species with well-documented food and age effects on reproductive performance (Nielsen and Drachmann 2003; Rutz and Bijlsma 2006; Byholm and Kekkonen 2008), the efficiency of begging in relation to self-feeding for realized reproductive performance is discussed acknowledging that goshawk young regularly practice aggression based sibling rivalry.

MATERIALS AND METHODS

Study site, video equipment, and goshawk data

In Finland, goshawks hatch their eggs in late May (Tornberg et al. 2006) and at an age of 44–46 days the young leave the nest. Until then the attending female practically solely guards, broods, and feeds (from beak to beak) the young, whereas the attending male is responsible for providing his family, including the female, with prey (Kenward 2006). As part of a long-term population study (Byholm and Nikula 2007; Byholm et al. 2007), goshawk parents and young were videotaped at 15 nests in the surroundings of the small town of Närpes on the Finnish west coast (lat $62°00'$–$62°55'$N, long $21°05'$–$22°40'$E) during 2001–2004. At each location, a 12 V CCTV camera (Panasonic WV-CP232E) was set up adjacent to the nest tree providing a good view toward the nest. The camera was connected to a 230 V time-lapse video recorder (Panasonic AG-TL500E), which was placed in a waterproof box on the ground beneath the nest tree. Images were recorded on 180 min video tapes but in order to minimize tape use and disturbance, the duration of each video was prolonged to 96 h using time-lapse recording (corresponding to 0.66 frames per second). Because goshawks do not deliver prey to the nest during night (cf. Reif and Tornberg 2006) and in order to save power, both the camera and the video recorder were switched off during the night (ca. 11.00 PM–5.00 AM) using a switch timer (Flash Micromat). Information about date and time was included on each video with one second's accuracy from the tape recorder's internal clock. All equipment but the tape recorder operated on 12 V

electricity and were powered by a set of 3 12 V 165 Ah Oldham tractor batteries that were replaced and recharged at intervals. To run also the tape recorder using battery power, an inverter (Voltteri 122) was used. Videotapes were played-back and analyzed on a TV-screen with an editing VHS recorder (Panasonic NV-HS930) allowing manual frame-wise forwarding of the tape.

As part of the field protocol, all video nests were climbed at least 3 times during the nestling stage in order to monitor breeding performance (timing of breeding, number of eggs, and fledglings), to take morphological measurements of young, and to collect shed feathers left by the attending female. Nestling age, hatching rank as well as degree of hatching asynchrony (max. age difference [in days] between brood members) were either established directly from nest visits conducted at hatching and/or backdated from wing length (Kenward 2006). All young were sexed on the basis of morphology and/or DNA (Byholm et al. 2002). Residual mass (measured when video tapes were replaced), that is, the deviation between the observed and the expected mass for a given wing length as calculated from separate equations for each sex (see Byholm and Kekkonen 2008) was used as a measurement of nestling condition. Using 11 polymorphic microsatellite markers optimized for Finnish goshawks (Ylinen 2008), DNA extracted from feathers shed by attending females was used to establish female identity in the video nests for year t (the current year) and year $t − 1$. Whether the genotypes remained identical or not in the subset of territories from where feathers were available for consecutive years ($n = 12$), the filmed broods were categorized into 2 groups describing the stability of the pair bond (i.e., same or different female present in year t as in year $t − 1$, $n = 6$ and 6, respectively).

Video recordings and image analysis

In order to tell apart the young on the tapes, nestlings were marked with differently colored nontoxic spray paints (marks were freshened when video tapes were replaced). To induce natural variation in the video material, recordings were initiated at different times in different nests and lasted for 5–10 days (mean ± standard deviation [SD]: 6.9 ± 1.3 days) in all but one nest that was followed for two-thirds (28 days) of the nestling stage. Altogether the 15 broods were filmed during 131 days for 1725 h between 21 May and 19 July when the nestlings were 23.9 ± 10.9 days old (range: 2–44 days; Table 1). At each nest, the approximate body mass (with 50 g accuracy) of the 494 prey items that were caught on the film were estimated (by H.R.) by comparing the size of the prey with the size of the brooding female and/or the growing nestlings, size of branches of known size etc. Using this information, a nest-specific standardized weight measure (summed grams prey/second/film day) was calculated in order to get an estimate that expresses variation in the amount of food brought to the nest per time unit. This value was used as a measure of food availability.

The tapes were then checked once again (by I.S.) to make notes of nestling and parental activities quantified as the number of actions and as time budgets for each activity separately on a daily basis. Due to the pronounced size-dimorphism in goshawks (Kenward 2006), parental birds could be identified and sexed directly as judged from their size. The activities of the parental birds and the nestlings were then classified into 7 and 6 different categories, respectively (Table 2). However, for the purposes of this study, only behaviors directly or indirectly related to feeding (i.e., parental beak-to-beak feeding of young, nestlings' self-feeding, begging, and contests for food) were analyzed in detail.

Table 1

The coverage of video recordings in time blocks of 3 h (5-8 AM, etc.) expressed in minutes and as the proportion of the total recording time collapsed into 6-day averages in relation to nestling age

Nestling age	3-h time block						Grand total	Film days
	5–8 AM minutes (%)	8–11 AM minutes (%)	11 AM–2 PM minutes (%)	2–5 PM minutes (%)	5–8 PM minutes (%)	8–11 PM minutes (%)		
2–7	2039 (13)	2880 (18)	2987 (19)	3252 (20)	3420 (21)	1452 (9)	16 030	19
8–13	2022 (15)	2767 (20)	2928 (21)	2829 (22)	2549 (18)	692 (5)	13 787	18
14–19	2263 (13)	3240 (18)	3825 (21)	3720 (21)	3763 (21)	1156 (6)	17 967	22
20–25	1676 (13)	2520 (21)	2428 (20)	2498 (21)	2562 (21)	441 (4)	12 125	17
26–31	2597 (13)	3706 (19)	3600 (20)	4001 (21)	4140 (21)	1214 (6)	19 258	25
32–37	2098 (14)	2882 (20)	2967 (20)	2940 (20)	2747 (19)	1044 (7)	14 678	18
38–44[a]	1494 (15)	2095 (22)	1980 (21)	1980 (21)	1882 (19)	230 (2)	9671	12
Grand total	14 189 (14)	20 090 (20)	20 715 (20)	21 220 (20)	21 063 (20)	6229 (6)	103 516	131

Number of film days for each block during which recordings were performed is given. No recordings were done during night (see MATERIALS AND METHODS).

[a] seven-day block.

Statistical analyses

To get a general impression of how the time spent in different activities changed as young developed, time budgets (expressed as the proportion of the total time) for each behavior of both parents and young were constructed. To reduce the impact of extreme values, the original values were collapsed into 2-day averages in relation to nestling age (2–3 days, 4–5 days etc., altogether 22 categories). Using this material, on average originating from observations of 9.3 ± 3.9 (mean ± SD) nestlings in 3.9 ± 1.3 nests per category, the relationship between nestling age and the activities of interest was tested with Spearman correlation tests (data non-normally distributed) in order to identify the time window when the behaviors occurred/altered.

Because the nestlings in a brood share the same growth environment and because multiple observations were made on the same individuals, feeding behaviors were analyzed using generalized linear mixed models in which nestling identity nested within brood were specified as random factors (Crawley 2002). The probability that a parent will feed its young as well as that young will beg for food, self feed or compete for food was then modeled as a binomial response (behavior of interest occurring = 1, behavior of interest not occurring = 0) (Monk 2002) and fitted with a logistic link function toward a set of explanatory variables and their first order interactions (offspring sex, offspring age, offspring condition, hatching rank, hatching asynchrony, brood size, food availability, and previous local breeding experience). Unless stated otherwise, model selection was performed following a manual step procedure by excluding nonsignificant

explanatory variables until reaching the minimum adequate model (Pinheiro and Bates 2000). At this point, the significance on fixed effects was assessed with F-statistics. When relevant, the significance of random effects was judged from variance comparisons. Owing to imbalance in the dataset regarding the different explanatory variables (female breeding experience not known in all cases), the functional sample size was variously reduced from the original level in individual analyses. All modeling was implemented in S-Plus, version 6.1 (Insightful Corporation, Seattle, WA) using the pseudo quasilikelihood approach with the MASS library (Venables and Ripley 2002) first assuring that the standard deviations of the random effects were not too large (Bolker et al. 2009).

RESULTS

General time budget

The attending males were away from the nests for 99.9 ± 0.1% (mean ± SD) of the time and subsequently their behaviors were not analyzed in more depth. The attending females spent most of their time brooding and guarding the young in the nest until the young were about 2–3 weeks old (Figure 1). The females fed their young at a constant rate for the first 2 weeks after hatching ($r_s = -0.05$, $P = 0.91$, $n = 8$) but from here onwards beak-to-beak feeding rapidly decreased ($r_s = -0.95$, $P < 0.001$, $n = 14$), even though continuing through the whole nestling stage (Figure 1, Figure 2a). This decrease in beak-to-beak feeding coincided with the emergence and increase of self-feeding among the nestlings as they turned 14 days old ($r_s = 0.84$,

Table 2

Percentage ± SD (n) of the total amount of individual activities classified into logical categories performed by attending female goshawks and goshawk nestlings (female: $n = 4896$, nestlings: $n = 8554$) at 15 nests filmed during 2001-2004 in Suupohja, Western Finland when the nestlings were 2-44 days old

| Attending females	% ± SD (n)	Nestlings	% ± SD (n)
Away from nest	48.4 ± 21.1 (2096)	Away from nest	0.5 ± 0.9 (49)
Brooding	8.0 ± 14.2 (462)	Sleeping/resting/preening	61.3 ± 6.2 (5433)
Guarding/preening	16.7 ± 9.4 (735)	Begging	2.3 ± 1.8 (281)
Delivering prey	1.2 ± 1.2 (55)	Fed by attending female	25.3 ± 13.2 (1837)
Feeding young	9.7 ± 4.0 (524)	Self-feeding	8.3 ± 6.6 (748)
Self-feeding	2.6 ± 2.3 (129)	Aggressive competition	2.3 ± 3.3 (206)
Repairing nest	13.4 ± 8.3 (895)		
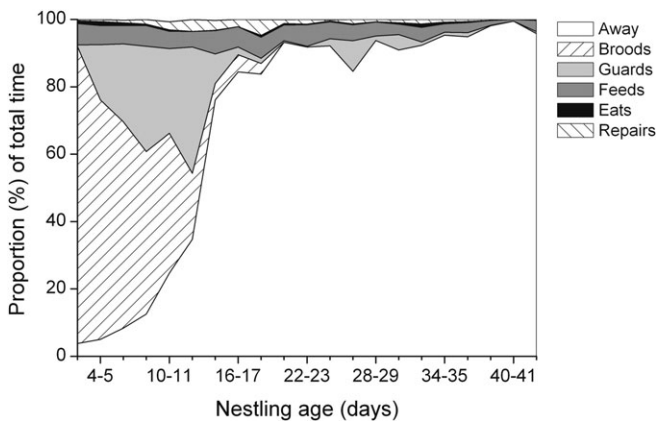
Figure 1
General time budget of female goshawks during the nestling stage in relation to nestling age (data collapsed into 2-day averages). For clarity, the behavioral activities "delivering prey" and "feeding young" are here combined into the category "feeds," whereas the grouping of all other activities follow the general categorization (see Table 2). Data from all broods inspected (video recordings lasting for 5–28 days/brood, see "MATERIALS AND METHODS" for further details) are merged.

$P < 0.001$, $n = 16$; Figure 2a). The overall gross time nestlings spent eating (parental beak-to-beak feeding and nestlings' self-feeding combined) did, however, not change as they aged ($r_s = -0.07$, $P = 0.77$, $n = 22$).

As they learned to eat by themselves, nestlings started to aggressively compete for access to food with their contemporary nest mates. These events typically involved rushes of all nestlings toward the prey as soon as it was delivered by the parents. To settle access to prey, nestlings then fiercely started hitting each other with their wings (talons and beaks more seldom used)—simultaneously loudly screaming—after which the winner spread its wings in order to hinder competing siblings from gaining access to the prey. Even though such sessions typically lasted only for 10–40 s, new fights never arose later on, and the winner was left in peace to eat until sated. If there was meat left of the prey at this point, the next sibling then took the prey in possession without any new disagreements arising (in all cases), neither with the winner nor possible other sibs. The time spent competing for prey access increased significantly until the young left the nest ($r_s = 0.84$, $P < 0.001$, $n = 13$; Figure 2b).

Begging (nestlings sit in a stooped down position in front of the female aiming and moving their head toward the beak of

the providing mother) increased significantly with nestlings' age until they initiated to eat by themselves ($r_s = 0.83$, $P = 0.005$, $n = 9$), after which begging decreased ($r_s = -0.53$, $P = 0.06$, $n = 13$; Figure 2b).

Food provisioning and self-feeding

In agreement with the time-budget result, the exploration of the total behavioral data (young 2–44 days old) showed that the attending females decreased their beak-to-beak feeding effort as nestlings aged ($F_{1,7861} = 518.0$, $P < 0.001$). The more prey that was brought to the nest, the more often did females actively feed their young beak-to-beak ($F_{1,7861} = 44.7$, $P < 0.001$), and females previously breeding on the focal territory beak-fed their nestlings more than did new ones ($F_{1,34} = 19.6$, $P < 0.001$, Figure 3a). Still food availability did not differ as compared between females with and without previous local breeding experience ($F_{1,10} = 0.5$, $P = 0.51$) as did not also the time novel and experienced females themselves spent eating from delivered prey ($F_{1,10} = 0.2$, $P = 0.64$). None of the significant variables interacted with any of the other explanatory variables and neither did any other variable or their first order interactions turn out significant (all $P > 0.07$). The random variance component describing variation in beak-to-beak feeding within broods ($\sigma^2 < 0.001$) explained less than 0.001% of the total random variance, but the variance component describing variation in beak-to-beak feeding between broods was much higher ($\sigma^2 = 0.10$, 95% confidence interval [CI] 0.04–0.27). Thus, although beak-to-beak feeding activity varies considerably between females, there are no consistent differences in the distribution of food within individual nests (Figure 3b).

Because goshawk nestlings did not start self-feeding until they turned approximately 2 weeks old (see general time budget), self-feeding was only analyzed with a subset of the total data where all nestlings were ≥14 days old. Analyses of this dataset revealed that nestlings in good body condition self-fed significantly more often than did nestlings in low body condition (Table 3a). Furthermore, nestlings self-fed less often in large broods than in small and self-feeding decreased as territorial food availability increased (Table 3a). During the same time (i.e., young ≥14 days old), the beak-to-beak feeding of the attending female continued to follow the overall pattern: Female feeding effort decreased with nestling age and decreasing food availability, and experienced females fed their young more than females new to the territory (Table 3b). As for the self-feeding result, none of the significant variables interacted with any of the other explanatory variables.

Figure 2
The average proportion (measured as percentage) of the total time (a) nestlings are fed beak-to-beak by the attending female (white stacks) and feed by themselves (gray stacks) and (b) nestlings beg (white stacks) and aggressive competition for food (gray stacks) in relation to nestling age in 15 goshawk broods (collapsed into 2-day averages). Data from all broods inspected (video recordings lasting for 5-28 days/brood, see "MATERIALS AND METHODS" for further details) are merged.
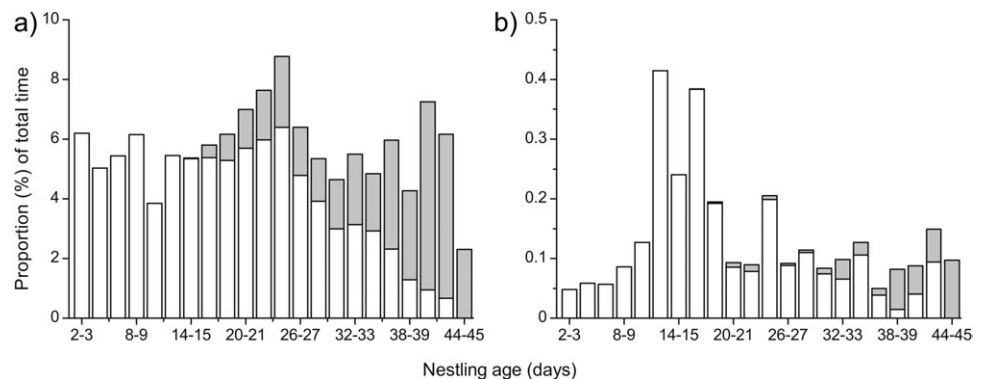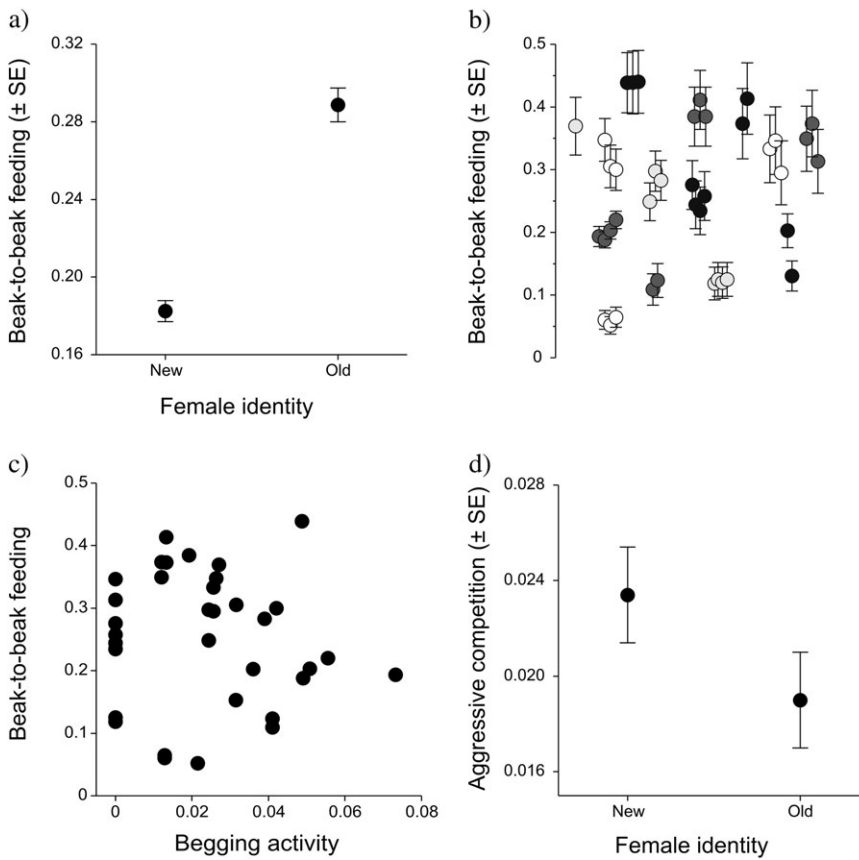
Figure 3
(a) Occurrence of beak-to-beak feeding in broods of females new to the territory (new) and females with previous local breeding experience (old), (b) variation in inter- and intra-brood beak-to-beak feeding activity of attending goshawk females (with broods containing 1-4 nestlings; siblings are aggregated together with different broods separated by different shade of gray), (c) relationship between begging activity and beak-to-beak feeding, and (d) occurrence of aggressive competitions for food in broods of novel and experienced females.

Begging and aggressive competition for food

Nestlings' begging decreased as more food was brought to the nest (Table 3c), and nestlings begged more often when there were no prey items in the nest than when prey were present (probability of begging: 0.06 ± 0.005 vs. 0.02 ± 0.002; $F_{1,8160} = 79.3$, $P < 0.001$). Furthermore, nestlings begged more in large broods than in small, and begging varied with age (Table 3c), with begging being most intense when nestlings were around 2 weeks of age and began to feed by themselves (Figure 2b). None of the other explanatory variables (see MATERIALS AND METHODS) nor their first order interactions were related to begging probability. Nestlings that begged were not fed more often by their mother than their non-begging brood mates ($F_{1,8160} = 0.02$, $P = 0.89$), Figure 3c. Because the random variance as compared between broods was high ($\sigma^2 = 3.1$, 95% CI 1.3–7.4) in comparison with the within-brood variance ($\sigma^2 = 0.03$, 95% CI 0.01–0.21), evidence for variation in intrabrood begging activity was small while begging activity differed substantially between broods.

As nestlings never aggressively competed for food during their first 2 weeks of life (see general time budget), aggressive based sibling rivalry was only analyzed with a subset of the data when nestlings were older than 14 days. Whereas none of the interactions among the explanatory variables turned out significant and the probability that a fight would initiate differed neither between sexes nor was related to hatching rank, food availability or nestling body condition (all $P > 0.14$), nestlings fought more often if the attending female was new to the focal territory than if the female had previous local breeding experience ($F_{1,26} = 5.6$, $P = 0.03$; Figure 3d). In line with the time-budget pattern, aggressions increased as nestlings aged ($F_{1,6579} = 17.5$, $P < 0.001$). Finally, aggressions decreased significantly with increasing brood size ($F_{2,6579} = 13.5$, $P <$

0.001) and increasing hatching asynchrony ($F_{1,6579} = 7.3$, $P = 0.007$). Interestingly enough, in the total of 1264 cases of beak-to-beak feeding, nestlings did not even once attempt to aggressively monopolize the prey when the attending female actively fed the young beak-to-beak.

DISCUSSION

Our main findings can be summarized in 3 steps. Firstly, both females with previous local breeding experience and females new to a territory responded toward increasing food availability by increasing their beak-to-beak feeding effort, but new territory holders always fed their young less often than experienced ones irrespective of food availability. In opposite to previous findings in the osprey (Poole 1985), this was not due to new breeders eating more of delivered prey than old ones. Secondly, even though chicks' begging effort varied in relation to multiple factors, all mothers always fed their young in a strictly even manner. Consequently, goshawk nestlings do not have the possibility to alter the innate size hierarchy arising from hatching asynchrony by varying their begging activity. Thirdly, because females new to a territory fed their offspring less than did females with previous local breeding experience, this inflicted the situation where aggressive competition among young old enough to feed actively by themselves ($\geq$14 days old) occurred more often in broods of new females than of experienced ones. As a consequence of these courses of events inherent within-brood size asymmetries resulting from hatching asynchrony—often of paramount importance for subsequent offspring survival (Laaksonen 2004)—are likely to be reinforced onward from the point in time when goshawk young initiate to feed actively by themselves. This interpretation is strongly supported by our previous finding that body condition does not differ significantly

Table 3

Minimum adequate models of 3 binomial generalized linear mixed models (logistic link function, brood and nestling identity as random factors) with explanatory variables adding significantly to (a) nestlings' self-feeding, (b) attending female's beak-to-beak provisioning, and (c) begging among goshawk nestlings (a and b: nestlings ≥14 days old; c: nestlings ≥2 days old)

Explanatory variable	Estimate	95% CI	df	F	P
(a)					
Brood size	−0.31[a]	−0.49, −0.13	2	11.8	<0.001
	−0.19[b]	−0.28, −0.10			
Condition	0.01	0.001, 0.001	1	6.5	0.01
Food availability	−17.9	−30.0, −5.75	1	8.3	0.004
(b)					
Offspring age	−0.06	−0.05, −0.04	1	76.6	<0.001
Female experience	0.29	0.14, 0.35	1	17.4	<0.001
Food availability	27.85	19.1, 35.0	1	38.4	<0.001
(c)					
Brood size	1.37[a]	−0.96, 3.69	3	10.9	<0.001
	−0.06[b]	−0.86, 0.73			
	0.22[c]	−0.21, 0.67			
Offspring age	−0.13	−0.14, −0.11	1	148.4	<0.001
Food availability	−21.9	−41.9, −0.78	1	4.1	0.04

For a list of all explanatory variables included in the initial full models, see MATERIALS AND METHODS. df = degrees of freedom.
[a] 2 young, [b] 3 young, [c] 4 young.

between brood members before they turn 2 weeks old (Byholm and Kekkonen 2008). Because attending mothers do not respond to nestlings' begging effort, aggressive competition constitutes the ultimate mechanism generating size hierarchies within goshawk broods, not begging or innate size asymmetries per se. Although this option has been paid little attention to and emphasis has been on patterns generated by hatching asynchrony as such (e.g., Stoleson and Beissinger 1995), it seems unlikely that it would not be the case in other species as well. This possibility should be addressed more thoroughly in future empirical and theoretical studies of conflicts of interests within families.

A question that inevitably arises from our findings is why attending goshawk females in contrast to many other species studied (Kilner and Johnstone 1997) do not seem to respond to the begging displays of their young? Even though mothers' ignorance at first glance might appear maladaptive, relevant theoretical approaches have shown that a random distribution of food among multiple brood members in fact is likely to be an optimal strategy for maximizing the number of nestlings when food is sufficient (Davis et al. 1999; Rodríguez et al. 2008). Although this part of theory not only successfully explains why goshawks feed their offspring in a strictly even manner when young are small and their demand for food is restricted (Rutz 2003), it also explains why mothers beak-to-beak feed their young more when food is abundant than when food is limited also when young are older than 2 weeks and in principle are capable of actively feeding by themselves. By actively feeding the young in the nest mothers then not only control the distribution of food but also limit the number of aggressive interactions that otherwise would boost innate size hierarchies within the brood (Byholm and Kekkonen 2008). Consequently, when the overall food demand of the brood can be met, the even feeding strategy applied by goshawk mothers is exactly what to expect given that the female by being present in the nest can control the amount of competitive interactions between brood members. Also the finding that attending goshawks leave their young self-feeding when food is limited (see self-feeding results) is in line with theory (Rodríguez et al. 2008), stating that skewed allocation

is likely to be the best strategy for maximizing reproductive performance in terms of number of young when food is limited (improves the survival probability of at least the fittest offspring). To sum up: The food distribution strategy employed in goshawk families is clearly state dependent, shifting from mothers to young with decreasing food availability (and as young age).

Although this interpretation would explain why mothers' insensitivity toward begging could be an evolutionarily stable strategy, it does not explain why goshawk young practice costly begging behavior (Maynard Smith 1991; Johnstone and Godfray 2002) given its limited signal value. Because several of our findings suggest that begging honestly signals hunger (e.g., nestlings beg more when there is no food in the nest than when prey are present), it cannot be ruled out that a common begging effort might be beneficial for the average brood member presuming that an elevated begging level induces mothers to fetch prey for their young even if the exact individual benefits would be impossible to predict. However, given that the parent toward whom the begging displays are directed, that is, the female, bears a minor role in hunting for her brood prior to fledging (Kenward 2006), it is unclear how this would work in practice. This is because as in raptors in general (Newton 1979), it is the goshawk male parent that is responsible for providing his family with prey. One possibility is that females communicate offspring need to the male (e.g., through vocalizations) when he delivers the prey to his family. Clearly, however, the current setup cannot provide any definite answer to these questions but merely serves to point out the existence of a complex situation calling for more detailed future investigations.

Unrelated to this complex of issues, the finding that females new on a territory fed their young less than females with previous local breeding experience is an issue that deserves some more attention. Whether females that were observed breeding for the first time at a specific territory were real first-time breeders or represented individuals that had performed breeding dispersal (i.e., had previous breeding experience in another territory) was not possible to infer with 100% accuracy but in one case when the mother could be aged 1-year old from plumage characteristics (Kenward 2006). In this case, the mother was thus definitely a first-time breeder. Because breeding dispersal events were responsible for only 21% of all females turnovers (n = 65) in 37 territories studied during 1999–2006 (Ylinen 2008), it is likely that most other females classified as new breeders had no previous breeding experience irrespective of their age. Following this chain of logic—albeit we cannot separate the effects of age per se and breeding experience with full certainty—the difference in the participation of direct beak-to-beak feeding as observed between new and old territory holders would mainly be a breeding experience effect (Limmer and Becker 2009). As already stated in the beginning of the discussion, this difference is likely to boost inherent size asymmetries between brood members, especially when food availability is limited. Because such asymmetries have consequences not only for offspring size and body condition (see Figure 3b in Byholm and Kekkonen 2008) but also for offspring survival and life histories (Stoleson and Beissinger 1995; Lindström 1999; Laaksonen 2004; Alonso-Alvarez et al. 2007), parental commitment to beak-to-beak feeding is likely to be an important, although hitherto overlooked, mechanism causing experience-related differences in reproductive performance among bird species that mix parental provisioning and offspring self-feeding strategies (e.g., Fowler 1995; Newton and Rothery 1997; Rutz et al. 2006).

We have here demonstrated that parental involvement in active beak-to-beak feeding (parental care) in goshawks strongly

depends on parental experience and food availability. Given that goshawks practice resource-based aggressive brood reduction (e.g., Boal and Bacorn 1994; Byholm P, personal observations), this state dependency together with parents' negligence toward begging and lack of interference with nestlings' competitive actions is likely to have repercussions for patterns of offspring mortality and size asymmetries within and between broods. Although hitherto paid limited attention, we suspect that parental and environmental state affect feeding strategies and subsequent offspring fitness also in other species, especially when young are actively fed by their parents along with that they simultaneously self-feed and aggressively competes for food.

REFERENCES

Alonso-Alvarez C, Bertrand S, Sorci G. 2007. Sex-specific transgenerational effects of early developmental conditions in a passerine. Biol J Linn Soc. 91:469–474.

Boal C, Bacorn J. 1994. Siblicide and cannibalism at northern goshawk nests. Auk. 111:748–750.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, Whithe J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol. 24:127–135.

Byholm P, Kekkonen M. 2008. Food regulates differently in different habitats: experimental evidence in the goshawk. Ecology. 89:1696–1702.

Byholm P, Nikula A. 2007. Nesting failure in Finnish Northern Goshawks *Accipiter gentilis*: incidence and cause. Ibis. 149:597–604.

Byholm P, Nikula A, Taivalmäki J-P, Kentta J. 2007. Interactions between habitat heterogeneity and food affect reproductive output in a top predator. J Anim Ecol. 76:392–401.

Byholm P, Ranta E, Kaitala V, Lindén H, Saurola P, Wikman M. 2002. Resource availability and goshawk offspring sex ratio variation: a large-scale ecological phenomenon. J Anim Ecol. 71:994–1001.

Crawley MJ. 2002. Statistical computing: an introduction to data analysis using S-Plus. Chichester (UK): John Wiley.

Davis JN, Todd PM, Bullock S. 1999. Environment quality predicts parental provisioning decisions. Proc R Soc B Biol Sci. 266:1791–1797.

Drummond H. 2002. Begging versus aggression in avian broodmate competition. In: Wright J, Leonard M, editors. The evolution of begging. Competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer. p. 337–360.

Fargallo JA, Laaksonen T, Korpimäki E, Pöyri V, Griffith SC, Valkama J. 2003. Size-mediated dominance and begging behaviour in Eurasian kestrel broods. Evol Ecol Res. 5:549–558.

Fowler GS. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. Am Zool. 35:318–328.

Godfray HCJ. 1995. Evolutionary theory of parent-offspring conflict. Nature. 376:133–138.

Johnstone RA, Godfray HCJ. 2002. Models of begging as a signal of need. In: Wright J, Leonard M, editors. The evolution of begging. Competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer. p. 1–20.

Kacelnik A, Cotton PA, Stirling L, Wright J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc R Soc B Biol sci. 259:259–263.

Kenward R. 2006. The Goshawk. London: T & A D Poyser.

Kilner R, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours signals of need? Trends Ecol Evol. 12:11–15.

Laaksonen T. 2004. Hatching asynchrony as a bet-hedging strategy—an offspring diversity hypothesis. Oikos. 104:616–620.

Limmer B, Becker PH. 2009. Improvement in chick provisioning with parental experience in a seabird. Anim Behav. 77:1095–1101.

Lindström J. 1999. Early development and fitness in birds and mammals. Trends Ecol Evol. 14:343–348.

Magrath RD. 1990. Hatching asynchrony in altricial birds. Biol Rev. 65:587–622.

Maynard Smith J. 1991. Honest signalling: the Philip Sidney game. Anim Behav. 42:1034–1035.

Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press.

Monk DS. 2002. Logistic regression and the analysis of begging and parental provisioning. In: Wright J, Leonard M, editors. The evolution of begging. Competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer. p. 451–472.

Newton I. 1979. Population ecology of raptors. Berkhamsted (UK): T & A D Poyser.

Newton I, Rothery P. 1997. Senescence and reproductive value in sparrowhawks. Ecology. 78:1000–1008.

Nielsen JT, Drachmann J. 2003. Age-dependent reproductive performance in Northern Goshawks. *Accipiter gentilis*. Ibis. 145:1–8.

Nussey DH, Coulson T, Festa-Bianchet M, Gaillard J-M. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Funct Ecol. 22:393–406.

Parker GA, Royle NJ, Hartley IR. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecol Lett. 5:206–215.

Pinheiro JC, Bates DM. 2000. Mixed-effects models in S and S-Plus. New York: Springer-Verlag.

Poole A. 1985. Courtship feeding and osprey reproduction. Auk. 102:479–492.

Reif V, Tornberg R. 2006. Using time-lapse digital video recording for a nesting study of birds of prey. Eur J Wildl Res. 52:251–258.

Rodríguez C, Johst K, Bustamante J. 2008. Parental versus offspring control of food division within the brood: the role of hatching asynchrony. Oikos. 117:719–728.

Royle NJ, Hartley IR, Parker GA. 2002. Begging for control: when are offspring solicitation behaviours honest? Trends Ecol Evol. 17:434–440.

Royle NJ, Hartley IR, Parker GA. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. Popul Ecol. 46:231–241.

Rutz C. 2003. Assessing the breeding season diet of Goshawks *Accipiter gentilis*: biases of plucking analysis quantified by means of continuous radio-monitoring. J Zool. 259:209–217.

Rutz C, Bijlsma RB. 2006. Food limitation in a generalist predator. Proc R Soc B Biol Sci. 273:2069–2076.

Rutz C, Whittingham MJ, Newton I. 2006. Age-dependent diet choice in an avian top predator. Proc R Soc B Biol Sci. 273:579–5896.

Smiseth PT, Lennox L, Moore AJ. 2007. Interaction between parental care and sibling competition: parents enhance offspring growth and exacerbate sibling competition. Evolution. 61:2331–2339.

Smiseth PT, Ward RJS, Moore AJ. 2007. Parents influence asymmetric sibling competition: experimental evidence with partially dependent young. Ecology. 88:3174–3182.

Stoleson SH, Beissinger SR. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? Curr Ornithol. 12:191–270.

Sutherland WJ. 1996. From individual behaviour to population ecology. Oxford: Oxford University Press.

Tornberg R, Korpimäki E, Byholm P. 2006. Ecology of the Northern Goshawk in Fennoscandia. Stud Avian Biol. 31:141–157.

Venables WN, Ripley BD. 2002. Modern applied statistics with S. New York: Springer-Verlag.

Wells JCK. 2003. Parent-offspring conflict theory, signalling of need, and weight gain in early life. Q Rev Biol. 78:169–202.

Wright J, Leonard ML, editors. 2002. The evolution of begging. Competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer.

Ylinen E. 2008. Feathers as a source of DNA and information: individual identification and territory fidelity of Northern Goshawks *Accipiter gentilis* [MSc Thesis]. Joensuu (Finland): University of Joensuu.