# THE FUNCTION OF FOOD STORES IN BIRD NESTS: OBSERVATIONS AND EXPERIMENTS IN THE BARN OWL *TYTO ALBA*

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Several hypotheses have been proposed to explain why food is found uneaten in or near nests of raptors, owls and shrikes. The ‘insurance’ hypothesis states that parents store food to buffer offspring against temporary food shortages generally due to adverse weather. Under the ‘large prey’ hypothesis, the offspring’s inaptitude in dismembering large items might explain the presence of uneaten items. In the present paper, I review these hypotheses and propose a novel hypothesis called ‘feeding time’. It postulates that parents accumulate food items in their nest to allow offspring to eat at any time. Using Barn Owl *Tyto alba* nests, I examined predictions of these mutually non-exclusive hypotheses. Parents did not change prey delivery rate when prey remains accumulated in the nest, only 1.5 prey remains were wasted per nest during the entire rearing period, and fledging success was not greater in years when parents stored more prey items in their nest. Without being consistent with the insurance hypothesis, this observation did, however, not refute it either. In accord with the large prey hypothesis, nestlings ate small prey items before large ones. A test of the feeding time hypothesis showed that nestlings provided with food *ad libitum* at night, continued to spread their meals over 24 h. Hence, the large prey and feeding time hypotheses can both explain the presence of uneaten prey remains in Barn Owl nests.

Keywords: *Tyto alba* – digestion - food shortage - food store –prey remain - prey size

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## INTRODUCTION

Food caching in the breeding season occurs in owls, raptors and shrikes (Kalländer & Smith 1990). Two hypotheses tried to explain why food is found uneaten in or near nests. The ‘large prey’ hypothesis (Korpimäki 1987) postulates that nestlings have difficulties in eating large prey items, hence swallow the smallest items first and take time to dismember large prey once the benefits of eating them outweigh handling and processing costs. This may explain why large items are eaten several hours after parents brought them. Both in the Barn and Tengmalm’s owls *Aegolius funereus*, food stores were shown to consist of the largest prey species (Baudvin 1983; Korpimäki 1987). The large prey hypothesis, however, does not account for the presence of small items. Under the ‘insurance’ hypothesis, parents store food as a buffer against temporary food shortages commonly resulting from adverse weather (Baudvin 1980; Korpimäki 1987), especially if the cost of killing more prey than required is low (McNamara *et al.* 1990). Therefore, this hypothesis predicts that parents store food when foraging conditions are good, allowing them to reduce foraging effort when the cost of collecting food increases, as shown in shrikes (Carlson 1985; Hernandez 1995).

In the strictly nocturnal Barn Owl parents forage only at night, whereas offspring spread the consumption of meals over 24 h; in addition, parental provisioning is not evenly distributed through the night, whereas offspring more evenly distribute food intake (Roulin 2001). In such a situation, parents may build food stores allowing offspring to feed at a time when they are hungry and when parents cannot forage, or not adequately. Under this ‘feeding time’ hypothesis, I propose that a function of food stores is to allow offspring to eat at a time when parents are not able to forage. The feeding time hypothesis therefore states that when nestlings face digestive constraints, food stores allow chicks to spread meals evenly over 24 h. In the Barn Owl, digestion time is 2.25 h (Guérin 1928), time required to produce a pellet 6.5 h (Smith & Richmond 1972), and both the sight of a vole and the predictability of an imminent meal induce pellet ejection (Bunn *et al.* 1982).

To determine whether the mutually non-exclusive hypotheses insurance, large prey, and feeding time can explain why prey items are frequently found uneaten in nests, I examined some of their predictions in the Barn Owl. The insurance hypothesis predicts that if the function of food stores is to buffer offspring against temporary food shortages (Korpimäki 1987) or to allow parents to reduce foraging effort (Carlson 1985), parental provisioning rate should be on average lower the night following than before the discovery of larger food stores. If parents store food just in case food will become short, as suggested by the insurance hypotheses (McNamara *et al.* 1990), some prey remains may be wasted. Wastage may occur if offspring cannot afford to eat the extra food which then rapidly perishes. Finally, this hypothesis predicts that reproductive success is higher in years when parents store more food, since chicks are less likely to die during periods of food shortages. The large prey hypothesis predicts that large prey items may constitute a bigger meal than nestling’s appetite can accommodate (MacDonald 1976), and hence nestlings should consume small items before large ones. As a consequence, large prey species should be over-represented in food stores. The feeding time hypothesis predicts that offspring distribute meals over 24 h even if food was supplied *ad libitum* at night. The feeding time hypothesis differs from the insurance hypothesis in that parents can predict that every day offspring are willing to eat at a time when parents cannot bring food to the nest.

## METHODS

### The study species

The Barn Owl mainly feeds upon small mammals (Roulin *in press*). It is a medium-sized bird with breeding males weighing on average 295 ± 1.6g (range 241-380g; $n$ = 230) and breeding females 367 ± 1.5g (range 263-478g; $n$ = 283; *pers. observ.*). On the European continent, clutches are laid from the end of February to mid-September (Schönfeld & Girbig 1975). Females brood their chicks until the youngest nestling is 12 to 16 d old (Taylor 1994). After that, parents are usually no more in the nest during daylight hours (*pers. observ.*). Nestlings take their first flight when about two months old, and return to the nest till independence at an age of about 95 d (Roulin 1999). This species is particularly fit to examine the function of food stores in nests, since uneaten prey items are frequently found lying next to nestlings. When nestlings were less than 20 d of age, Baudvin (1980) found on average 4.7 prey items in 58% of the nests. Over 24 h, a single 36 d old nestling consumed on average 3.4 voles (Roulin 2001), and under laboratory conditions mean daily food intake was 67 g between 20 and 60 d of age (Durant & Handrich 1998). In summer, when ambient temperatures are high, prey remains rapidly rot, often in less than a day (*pers. observ.*). The chick’s behaviour to sit on prey items accelerates the process of prey degradation; observations in 275 nests with prey remains (mean brood size 4.5 chicks) showed that this behaviour is frequent with at least one prey monopolised by chicks in 31% of the nests (277 of 572 stored items were monopolised; *pers. observ.*). In this context, 'prey remains' are defined as undried prey items next to or under nestlings during daylight hours (also used synonymously for food store and food storage).

**Frequency of prey remains**

From 1990 to 2003, I studied a Barn Owl population in Switzerland (46°49'N, 06°56'E). On a plain covering 190 km$^2$ located at an altitude of 430 to 520 m, 110 nestboxes (dimensions: 1 x 0.6 x 0.5m) were mounted on the external wall of barns. Wing length (i.e. length of the flattened wing from the bird's wrist to the tip of the longest primary) of the biggest nestling was measured to the nearest mm to estimate its age in days. The relationship between wing length and age was determined by repeatedly measuring 187 nestlings of known age (*n* = 1300 measures; Fig. 1). Wing length is a good estimator of age because this trait is weakly correlated with body condition (Durant & Handrich 1998; Roulin 1998). Frequency of prey remains was determined in 644 broods totalling 3800 diurnal visits. On these occasions, prey remains were identified and counted. Between 1996 and 2003, 3164 intact prey remains were weighed. If parents store more prey items when food is abundant, I expect a positive correlation between number of breeding pairs and mean annual number of prey remains per nest. This prediction is based on the premise that Barn Owl population size is larger in vole-rich years (review in Roulin 2002).

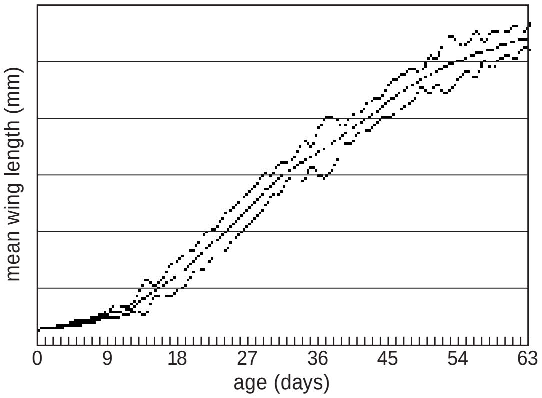

**Fig. 1.** Relationship between age and mean nestling wing length (± SD) in 187 nestlings of known hatching date (day 0). All nestlings fledged successfully. This figure is based on 1300 measures (5-35 measurements day$^{-1}$).

**The insurance hypothesis**

Parental provisioning rate was measured in 18 nests (one in 1997, one in 1998 and 16 in 2001) the nights before and after I found at least one prey remain. The oldest chicks were 23 to 43 d (mean 31 d). An infrared camera was installed in nest boxes without any apparent signs of distress to either adults or nestlings. Number of prey items delivered at night was recorded during eight hours from sunset to dawn, denoted as 'parental provisioning rate'. 'Change in parental provisioning rate' was defined as the difference in number of prey items brought in the night after and before at least one prey remain had been discovered. From 1990 to 2003, I counted the number of prey remains that were wasted (rotten and dried items) during the rearing period in 617 nests. An item was considered to be rotten when it was clear that owlets would not eat them (partially rotten prey are sometimes consumed). To investigate whether food stores have a positive effect on reproductive success, I correlated mean annual clutch size, brood size at fledging and fledging success (i.e. number of fledglings/number of hatchlings) with mean annual number of prey remains per nest.

**The large prey hypothesis**

To examine whether large prey species were over-represented among prey remains, I determined the proportion of each prey species in the diet after determination of skulls found in pellets regurgitated by nestlings (Chaline *et al.* 1976; Raczynski & Ruprecht 1974). This was done in 34 nests in 1999, 41 nests in 2001, 69 nests in 2002 and 44 nests in 2003 where the chicks were 23 to 53 d of age (mean 36 d). This allowed me to compare the mean biomass of prey eaten (i.e. those found in pellets) and of prey remains, using body mass values of each prey species calculated from the masses of intact prey remains (Table 1). This

**Table 1.**Frequency of prey species found as remains in the nest and mass of intact prey remains.

| Species | 1990-2003 Number of intact or partially eaten prey remains | 1996-2003 Mass of intact prey remains |  |  |
|---|---|---|---|---|
|  |  | Mean ± SD | Range | Number of individuals |
| *Microtus arvalis* | 3067 (41.5%) | 29.1 ± 7.7 | (4-62) | 1481 |
| *Microtus agrestis* | 4 (0.05%) | 38.8 ± 1.1 | (38-40) | 5 |
| *Clethrionomys glareolus* | 28 (0.4%) | 26.2 ± 5.4 | (17-33) | 17 |
| *Arvicola terrestris* | 2046 (27.7%) | 49.2 ± 15.5 | (10-120) | 725 |
| *Apodemus spp.* | 2043 (27.7%) | 33.5 ± 10.3 | (9-79) | 884 |
| *Mus musculus* | 9 (0.1%) | 22.0 ± 4.2 | (16-28) | 8 |
| *Rattus rattus* | 2 (0.03%) |  |  |  |
| *Muscardinus avellanarius* | 5 (0.1%) | 15.5 ± 4.9 | (12-19) | 2 |
| *Glis glis* | 1 (0.01%) |  |  |  |
| *Crocidura russula* | 54 (0.7%) | 11.5 ± 3.0 | (6-16) | 20 |
| *Sorex araneus* | 37 (0.5%) | 8.9 ± 1.6 | (6-11) | 11 |
| *Talpa europaea* | 13 (0.2%) | 44.9 ± 8.9 | (33-58) | 9 |
| Bat | 1 (0.01%) |  |  |  |
| Birds | 15 (0.2%) | 23 ± 0 | (23) | 2 |
| *Tyto alba* | 12 (0.2%) |  |  |  |
| Frogs | 4 (0.05%) |  |  |  |
| Unidentified prey items | 43 (0.6%) |  |  |  |
|  | 7384 (100%) | 34.8 ± 13.6 | (4-120) | 3164 |

method is probably slightly biased since body mass is calculated using a sub-set of the eaten items, i.e. the largest ones. To test the hypothesis that nestlings consume small items before large ones, I performed an experiment in 13 nests in 2001 where the oldest chicks were 30 to 56 d (mean 43 d) and where the female was not in the nest during daylight hours. At 21.30 h, I added two dead Common Rats *Rattus norvegicus*, a large one (mean mass 105 g; range 96-115 g) and a small one (24 g; range 15-36 g). The next morning at 09.15 h, I recorded which rat was still in the nest. Disappearance of a rat is used as evidence that it had been eaten, because on a subsequent visit I relocated the skull in a pellet. Since pellets are usually produced during the day (*pers. observ.*) and parents were not at the nest at that time, the rats were probably devoured by the nestlings.

### The feeding time hypothesis

To estimate how frequently prey remains were eaten during daylight hours, in 31 nests (11 in 1997, 1 in 1998, 1 in 2000, 18 in 2001) I counted prey remains at 10.00 h and 20.45 h. Mean brood size was 4.4 (range 2-8) and the oldest nestling 38 d old (range 25-53 d). Since these observations were not made at random, I performed an experiment using 11 nests in 2001 (mean brood size 4.5; mean age 37 d, range 33-40 d). In each nest, seven dead laboratory mice, weighing 24 g each, were added at 21.30 h. The next morning at 09:00h, on average four prey remains were found (3.3 voles and 0.7 laboratory mice), indicating that more food was available at night than chicks could eat. On this occasion, two extra dead laboratory mice were added to test whether nestlings eat prey remains during daytime. At 18:30h (range 16:00-19:30 h; first parental visit not before 22:15 h), it was recorded whether prey remains were missing or not. As a means of determining the exact time at which nestlings consume food, three nestlings from three broods were selected in 2000. At

17:00h, each chick was put alone in a plastic box (diameter = 0.6 m; height = 0.8 m), 10 m away from its nest. At 22:00h, six dead laboratory mice were added (25 g) and the birds were filmed during 24 h with an infra-red camera. Experiments had shown that nestlings are as likely to eat laboratory mice as voles (Roulin 2001).

### Statistical procedure

All statistical analyses were two-tailed and *P*-values smaller than 0.05 were considered significant. Means are quoted ± 1 standard deviation.

## RESULTS

The proportion of nests with at least one prey remain decreased progressively from 80% at hatching to approximately 15% at fledging (Fig. 2). I found on average three to four items in the first three weeks after hatching; from four weeks onwards the number of prey remains per nest was on average less than one (Fig. 3a). Figure 3b presents mean number of prey remains per nest per nestling in relation to age. Mean number of prey remains per nest in the first two weeks after hatching was higher in years when breeding pairs were more numerous ($r_S = 0.69$, $n = 14$ years, $P = 0.006$; Fig. 4), suggesting that birds can store food mainly when prey are abundant. The maximum number of intact or partially eaten prey remains found between 1990 and 2003 was 33 (605 g) in a brood of four nestlings. Most intact prey remains weighed 31 to 49 g (range: 4–120 g; Table 1, Fig. 5).

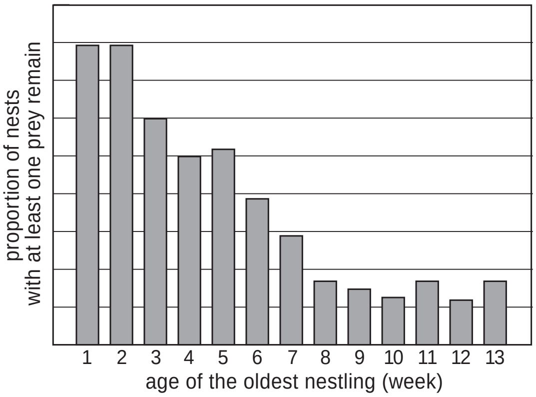

**Fig. 2.** Relationship between the proportion of nests with at least one prey remain and age (in weeks) of the oldest nestling. This figure is based on 3800 diurnal visits of 644 nests. Each nest appears only once per week.

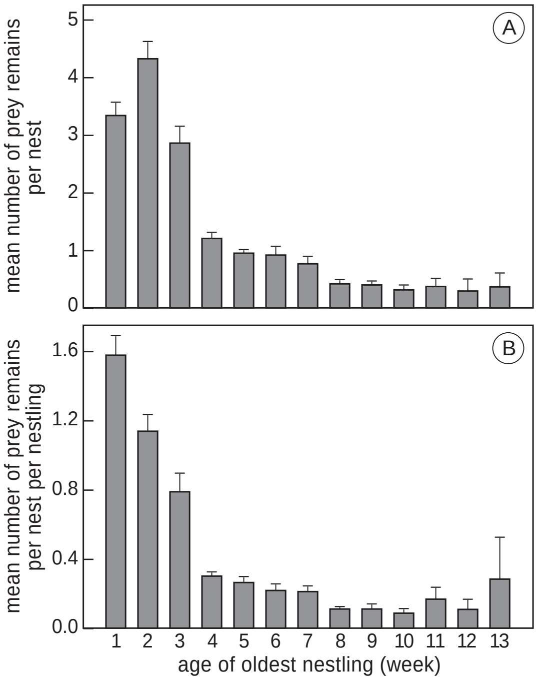

**Fig. 3.** Relationship between (A) the age (week age classes) of the oldest nestling and number of prey remains per nest and (B) number of prey remains per nest per nestling (mean ± SE). Figure based on 3800 diurnal visits of 644 nests. When a nest was visited more than once a week, the mean number of prey remains was calculated so that each nest appears only once per week.

### The insurance hypothesis

If parents store food to allow for variable weather conditions, or because hunting cost is low, parental provisioning rate should decrease to a larger extent the night after more prey remains were stored. This relationship was not significant (Spearman correlation between change in provisioning rate and number vs. mass of prey remains:

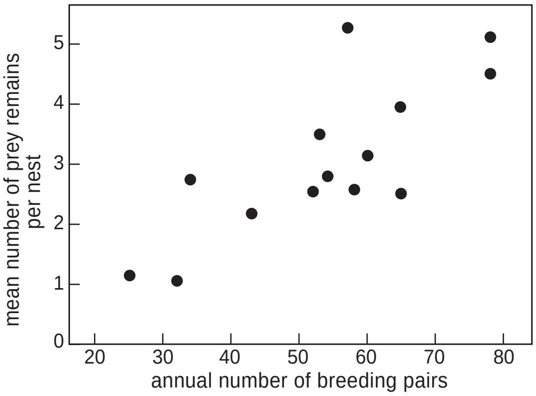

**Fig. 4.** Relationship between mean number of prey remains per nest found in the first two weeks after hatching and annual number of breeding pairs. The data were collected between 1990 and 2003.

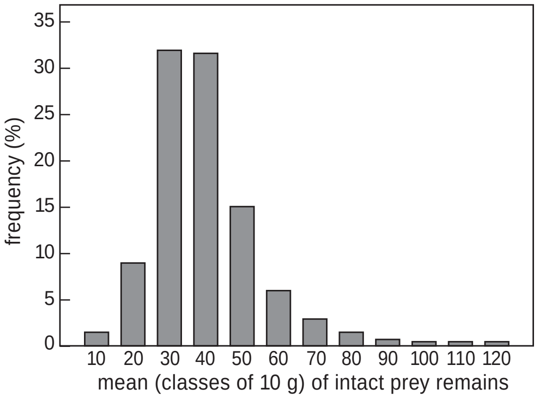

**Fig. 5.** Frequency mass distribution of 3164 intact prey remains, in classes of 10 g. For instance, the class ‘50’ refers to prey items weighing 41 to 50 g.

$r_S$ = -0.31, $n$ = 18, $P$ = 0.09 vs. $r_S$ = -0.24, $n$ = 18, $P$ = 0.17). Moreover, only 1.25 prey remains (0.52 rotten, 0.73 dried) were wasted per nest. The prediction that reproductive success is higher in years when parents can store more food items was not supported. Correlations between mean annual number of prey remains per nest and mean clutch size ($r_S$ = 0.49, $n$ = 14, $P$ = 0.07), brood size at fledging ($r_S$ = 0.48, $n$ = 14, $P$ = 0.08) and fledging success ($r_S$ = -0.27, $n$ = 14, $P$ = 0.34) were not significant.

### The large prey hypothesis

In 188 nests, mean mass of prey remains was 36.6 ± 5.6 g and of prey species found in pellets 32.5 ± 2.2 g (paired *t*-test: $t$ = 11.15, df = 187, $P < 0.001$). When I simultaneously offered a large and a small rat in the evening in 13 nests, the large rat had not been eaten in seven nests the next morning, whereas the small rat had disappeared in all nests (binomial test comparing seven and zero: $P$ = 0.016).

### The feeding time hypothesis

In 31 nests with prey remains (3.36 ± 2.41 items at 10.00 h), nestlings consumed 2.14 ± 1.63 items (64%) before 20.45 h. In eleven nests where chicks had been experimentally fed *ad libitum* at night, the next morning nestlings ate at least one food item in ten of the nests from 09.00 to 18.30 h (binomial test: $P$ = 0.012; per nest on average 3.5 items consumed). The exact time when nestlings consumed food was recorded in three nestlings: (1) a mouse was eaten at 22.08, another one at 00.56, 04.00, 09.07, 13.14 and 15.15 h; (2) 22.33, 02.10, 08.49 and 17.46 h; (3) 22.27, 22.30, 01.55 and 11.02 h.

## DISCUSSION

The hypothesis that Barn Owls store food to counter temporary food shortages did not receive strong support, since parental provisioning rate did not change the night after I found food stores. Even if prey remains may sometimes buffer chicks against food shortages, the absence of a relationship between size of food stores and change in feeding rate suggests that other hypotheses may also explain the presence of uneaten prey in Barn Owl nests. When prey abounds, and foraging costs are low, parents may capture more prey than chicks can eat. Parent should, however, adjust the size of food stores to the chick’s needs and the speed with which food goes to waste (in summer, within a day; *pers. observ.*) before chicks have the chance to consume it (Gendron & Reichman 1995). My data show that less than two prey remains were wasted per nest during the rearing period, indicating that parents do not kill more prey than required each day. Interestingly, parent Barn Owls provision their brood mainly in the first part of the night (Ritter & Görner 1975; Michelat & Giraudoux 1992, Roulin 2001), probably not because foraging cost is higher in the second part but because they satisfy their own needs at that time (Handrich *et al.* 1990; Taylor 1994; *pers. observ.*; see below). Data collected over 14 years showed that parents store more food when the number of breeding pairs is greater. This suggests that parents can store food mainly when small mammals are abundant, since Barn Owl population size is larger in vole-rich years (review in Roulin 2002). Because short periods of adverse weather during the rearing period are as likely to occur in years with a low or high number of breeding pairs, I predicted a positive correlation between mean annual fledging success and size of food stores. However, the correlation was negative, indicating that in the Barn Owl a major function of food storage may not be to buffer offspring against temporary food shortages.

### A proximate reason why prey remains are found in Barn Owl nests: the large prey hypothesis

Nestling Barn Owls preferred the small rat and took longer to consume the large one. The size difference between large and small rats laid within the natural range (Fig. 5). Results would probably have been similar if the size difference had been smaller, given that large prey species were over-represented among prey remains in natural situations (Baudvin 1983; Korpimäki 1987; present study)**.** The large prey hypothesis is therefore relevant in explaining why prey remains are frequently found in the nests of owls and raptors in which prey species are relatively large compared to nestling body size. For instance, Golden Eagles *Aquila chrysaetos* bring to their nest large items such as Marmots *Marmota marmota* (2800-4300 g) that chicks (3000-4000 g) can probably not eat rapidly (Cramp & Simmons 1983). In the Pygmy Owl *Glaucidium passerinum*, nestlings weigh 50-70 g and parents deliver prey items that weigh on average 25 g (max: 60 g; Kellomäki 1977). Large items may therefore constitute several meals, explaining the presence of uneaten prey items.

### An adaptive function of prey remains: the feeding time hypothesis

The basic idea of the feeding time hypothesis is that due to digestive constraints, nestlings have to spread meals evenly over 24 hours. Since parents can provide food only during about 12 h each day, food stores allow chicks to eat at a time when hunting has ceased. In the Barn Owl, this situation is even more extreme because parents bring 50% of the prey items in the first 2.5 h of the night (Roulin 2001), whereas owlets consume food day and night. Two mutually non-exclusive explanations may account for this observation. Firstly, parents may be more efficient at hunting when their stomach is empty, implying that they should delay eating to the second part of the night. This is plausible because males provision most food and have a lower body mass than females. This indicates that a low body mass is a prerequisite to ensure a high foraging success. In line with this idea, adults eat mainly in the second part of the night (Handrich *et al.* 1990; Taylor 1994; *pers. observ.*). Secondly, hunting success may decrease progressively from sunset to sunrise. Unfortunately, no data are yet available on time-dependent foraging success, and hence I cannot discuss this possibility.

Barn Owl nestlings consume on average 3.4 voles in 24 h (Roulin 2001), corresponding to 67 g (Durant & Handrich 1998). Since daily food requirement is satisfied with few meals, digestive constraints may prevent nestlings to take their daily food requirement during the relatively short time period when parents deliver food (see also the model of Bednekoff & Houston 1994 for a similar idea). Before taking another meal, nestlings may have to wait until previous items have been digested and/or a pellet regurgitated. In the Barn Owl, the minimum time required for digestion is 2.25 h (Guérin 1928) and to produce a pellet 6.5 h (Smith & Richmond 1972). Fur, feathers and bones of their prey are not fully digested and consequently regurgitated as a pellet. In captivity, nestlings expel on average 1.89 pellets per 24 h (Handrich *et al.* 1993), exceptionally four (Bunn *et al.* 1982). Given these constraints, parents have two possibilities to satisfy the chick's need: either hunt when chicks beg for food (i.e. hungry and able to consume an item) or allocate a fixed amount of energy in foraging (Drent & Daan 1980), and store food for chicks for them to decide when to eat. The present study and previous ones suggest that parents store food in their nest irrespective of chick's begging. Indeed, parents did not adjust feeding rate in brood size manipulation experiments (Roulin *et al.* 1999) nor during experimental manipulation of food supply available to chicks (Roulin *et al.* 2000).

## CONCLUSION

Parent Barn Owls frequently store food in their nest. The fact that many prey remains are eaten during daylight hours suggests that a primary function of food stores is to allow offspring to spread meals over 24 h. In the Barn Owl, the feeding time hypothesis is not only applicable to the latter stages of the nestling period when chicks are able to tear prey items apart themselves or to swallow whole prey. Indeed, mothers feed their hatchlings during day and night (*pers. observ.*), and hence the feeding-time hypothesis may explain why prey remains are more abundant when chicks are younger, since at that age they cannot eat their daily food requirement very quickly as in older chicks. This hypothesis may also be applicable to raptors, with prey remains allowing chicks to spread their meals during daytime. The feeding time hypothesis does not exclude that prey remains may sometimes buffer nestlings against temporary food shortages or allow parents to adjust hunting effort. However, I found little evidence for this hypothesis even though researchers tend to privilege it (e.g. Baudvin 1980; Korpimäki 1987).

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## REFERENCES

Baudvin H. 1980. Les surplus de proies au site de nid chez la chouette effraie (Tyto alba). Nos Oiseaux 35: 232-238.
Baudvin H. 1983. Le régime alimentaire de la chouette effraie (Tyto alba). Le Jean le Blanc 22: 1-108.
Bednekoff P.A. & A.I. Houston 1994. Avian daily foraging patterns: effects of digestive constraints and variability. Evol. Ecol. 8: 36-52.
Bunn D.S., A.B. Warburton & R.D.S. Wilson 1982. The barn owl. Poyser, London.
Carlson A. 1985. Central place food caching: a field experiment with red-backed shrikes (Lanius collurio L.). Behav. Ecol. Sociobiol. 16: 317-322.
Chaline J., H. Baudvin, D. Jammot & M.-C. Saint-Girons 1974. Les proies des rapaces (petits mammifères et leur environnement). Doin, Paris.
Cramp S. & K.E.L. Simmons 1983. The birds of the Western Paleartic, 2. Oxford Univ. Press, Oxford.
Drent R.H. & S. Daan 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.
Durant J.M. & Y. Handrich 1998. Growth and food requirement flexibility in captive chicks of the European barn owl (Tyto alba). J. Zool. (Lond.) 245: 137-145.
Gendron R.P. & O.J. Reichman 1995. Food perishability and inventory management: a comparison of three caching strategies. Am. Nat. 145: 948-968.
Guérin G. 1928. Régime et croissance de l'effraye commune en Vendée. Paul Lechevalier, Paris.
Handrich Y., D. Bersuder, J.P. Gendner, C. Plumeré & Y. Le Maho 1990. Système automatique de pesée adapté à la chouette effraie: perspectives. Alauda 58: 50-51.
Handrich Y., L. Nicolas & Y. Le Maho 1993. Winter starvation in captive common barn-owls: bioenergetics during refeeding. Auk 110: 470-480.
Hernandez A. 1995. Temporal-spatial patterns of food caching in two sympatric shrike species. Condor 97: 1002-1010.
Källander H. & H.G. Smith 1990. Food storing in birds. An evolutionary perspective. Curr. Ornithol. 7: 147-207.
Kellomäki E. 1977. Food of the pygmy owl Glaucidium passerinum in the breeding season. Ornis Fennica 54: 1-29.
Korpimäki E. 1987. Prey caching of breeding Tengmalm's owls Aegolius funereus as a buffer against temporary food shortage. Ibis 129: 499-510.

MacDonald D.W. 1976. Food caching by red foxes and some other carnivores. J. Tierpsychol. 42: 170-185.

McNamara J.M., A.I. Houston & J.R. Krebs 1990. Why hoard? The economics of food storing in tits, Parus spp. Behav. Ecol. 1: 12-23.

Michelat D. & P. Giraudoux 1992. Activité nocturne et stratégie de recherche de nourriture de la chouette effraie Tyto alba à partir du site de nidification. Alauda 60: 3-8.

Raczynski J. & A.L. Ruprecht 1974. The effect of digestion on the osteological composition of owl pellets. Acta Ornithol. 14: 25-37.

Ritter F. & M. Görner 1975. Untersuchungen zur Aktivität und Ernährung der Schleiereule (Tyto alba) in Thüringen. Falke 24: 344-348.

Roulin A. 1998. Importance de la nichée et croissance pondérale chez les jeunes chouettes effraies Tyto alba. Alauda 66: 273-278.

Roulin A. 1999. Natural and experimental nest-switching in barn owl Tyto alba fledglings. Ardea 87: 237-245.

Roulin A. 2001. Food supply differentially affects sibling negotiation and competition in the barn owl (Tyto alba). Behav. Ecol. Sociobiol. 49: 514-519.

Roulin A. 2002. Barn owl. BWP Update 4: 115-138.

Roulin A. In press. Covariation between plumage colour polymorphism and diet in the barn owl Tyto alba. Ibis.

Roulin A., A.-L. Ducrest & C. Dijkstra 1999. Effects of brood size manipulations on parents and offspring in the barn owl Tyto alba. Ardea 87: 91-100.

Roulin A., M. Kölliker & H. Richner 2000. Barn owl (Tyto alba) siblings vocally negotiate resources. Proc. R. Soc. Lond. B 267: 459-463.

Schönfeld M. & G. Girbig 1975. Beiträge zur Brutbiologie der Schleiereule (Tyto alba) unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte. Hercynia 12: 257-319.

Smith C.R. & M.E. Richmond 1972. Factors influencing pellet egestion and gastric pH in the barn owl. Wilson Bull. 84: 179-186.

Taylor I.R. 1994. Barn owls. Predator-prey relationships and conservation. Cambridge Univ. Press, Cambridge.

## SAMENVATTING

In nesten van roofvogels en uilen worden in de jongenfase geregeld intacte prooien aangetroffen. Hiervoor zijn verschillende verklaringen bedacht, waaronder de ‘grote prooi’ hypothese, de verzekeringshypothese en varianten hierop. Nestjongen hebben, vooral als ze nog klein zijn, moeite om grote prooien te verscheuren en prefereren daarom kleine, makkelijk in te slikken prooien. De grote prooien blijven zodoende langer in het nest liggen. Deze ‘grote prooi’ hypothese verklaart echter niet waarom ook kleine prooien onaangetast in de nestkom kunnen liggen. De verzekeringshypothese gaat ervan uit dat ouders hamsteren als buffer voor slechte tijden. Het hamsteren zou vooral plaatsvinden wanneer de foerageeromstandigheden tijdelijk gunstig zijn (en de prooien dus makkelijk kunnen worden verschalkt zonder grote kosten voor de vogel).

In de onderhavige studie wordt aan de hand van onderzoek aan Kerkuilen Tyto alba in Zwitserland een derde verklaring voorgesteld, namelijk de ‘eettijd’ hypothese. Kerkuilen zijn namelijk strikte nachtjagers. De helft van de prooiaanbreng op het nest vindt bovendien in de eerste 2,5 uren van de nacht plaats (jaagsucces beter met laag gewicht vanwege lege maag, en/of afnemend jachtsucces met vorderende nacht?). De ouders eten vooral in tweede helft van de nacht. Gemiddeld verorbert een kuiken van de Kerkuil 3,4 muizen (67 gram) per 24 uur. Dat lukt het kuiken niet in één maaltijd. De ouders kunnen de voedselbehoefte van de jongen bevredigen door te gaan jagen wanneer de jongen bedelen, dan wel door een vaste hoeveelheid energie in jacht te stoppen en een voedselvoorraad aan te leggen, opdat de jongen zelf kunnen bepalen wanneer ze willen eten. Het onderhavige onderzoek en eerdere studies lijken aan te tonen dat de volwassen uilen voor het laatste kiezen: ouders passen hun prooiaanvoer niet aan wanneer het jongental in het nest wordt gemanipuleerd, noch wanneer het voedselaanbod wordt gemanipuleerd.

Om na te gaan hoe frequent prooien overdag worden gegeten, werd om 10:00u en om 20:45u in 31 nesten een prooitelling gedaan. Daarnaast werd de ‘eettijd’ hypothese getoetst door om 21:30u bij elf nesten elk zeven dode muizen toe te voegen. De volgende ochtend, om 9:00u, bleken in die nesten gemiddeld nog vier prooien aanwezig te zijn. Vervolgens werden daar twee prooien aan toegevoegd om te zien of er overdag werd gegeten. Indien de verzekeringshypothese van toepassing zou zijn, valt te verwachten dat er minder prooien worden aangebracht in de nacht volgend op een nacht waarin juist veel prooien werden aangevoerd. Dat bleek niet het geval. Evenmin werd een verband gevonden tussen het gemiddelde aantal prooiresten per nest en legselgrootte, aantal jongen ten tijde van het uitvliegen en uitvliegsucces. Dit alles pleit niet onmiddellijk voor de verzekeringshypothese als verklaring voor de gevonden extra prooien (wat niet wegneemt dat tijdelijk gunstige jaagomstandigheden tot extra prooiaanvoer kunnen leiden). De ‘grote prooi’ hypothese werd getest door tegelijk een grote en een kleine rat aan te bieden. In alle gevallen was de kleine rat de dag daarop verdwenen, terwijl de grote rat niet was aangevreten. Die laatste is kennelijk moeilijker te verscheuren en vertegenwoordigt meer dan één maaltijd. In overeenstemming met de ‘eettijd’ hypothese bleken de uilskuikens hun maaltijden over de dag te spreiden; aan de hand van videobeelden kon dat ook daadwerkelijk worden geregistreerd. Het grotere aantal prooien in nesten met kleine kuikens heeft te maken met het feit dat deze kuikens sneller 'vol' zitten dan oudere kuikens. Overigens sluit de 'eettijd' hypothese niet uit dat ook de andere hypotheses op enigerlei moment geldig kunnen zijn. (RGB)

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