Prey Delivery Rates as Estimates of Prey Consumption by Eurasian Kestrel Falco tinnunculus Nestlings

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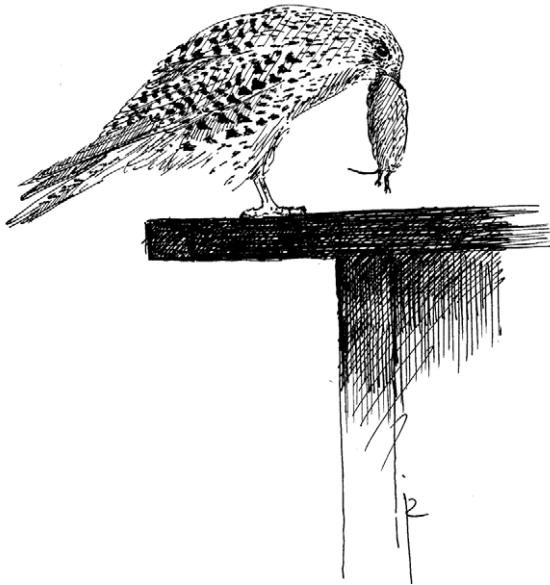
In altricial birds the type of prey selected by parents for their nestlings may affect the allocation of time and energy spent on hunting, preparing prey and feeding the nestlings, which in turn may affect the rate of provisioning. Raptors take relatively large prey items, which facilitates the quantification of rates of prey items and prey mass delivered to nestlings. Estimates of rates of prey delivery in raptors are nevertheless few and have been based on direct observations from a hide in combination with analyses of prey remnants and regurgitated pellets. To obtain better estimates we video monitored prey deliveries at 55 nests of Eurasian Kestrels *Falco tinnunculus*. Of the 2282 prey items recorded, voles were most abundant by number, followed by birds, shrews and lizards, while insects and frogs were rare. An average brood of 4.3 nestlings was estimated to consume 18.3 g/h, hence a nestling consumed on average 4.2 g/h. This is equivalent to 67.8 g/d, given an average daily activity period of 16.1 h. The estimated delivery rate of prey items required to feed an average brood in our study was 91 per h if the kestrels had provided only insects, and 3.4, 1.9, 0.83 and 0.52 if they had provided only lizards, shrews, voles or birds, respectively. This corresponds to one prey delivery per 40 s if feeding solely on insects and one per 18, 32, 75 and 120 min if feeding solely on lizards, shrews, voles or birds, respectively. We argue that kestrels in the boreal forest would be unable to raise an average brood solely on insects or lizards, unlikely to do so solely on shrews, but able to do so solely on voles in a vole peak year.

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In altricial birds the type of prey selected by parents for their nestlings affects the allocation of time and energy spent on food collection, preparation and feeding (e.g. Slagsvold & Sonerud 2007, Slagsvold & Wiebe 2007, Steen *et al.* 2010). Parents are assumed to maximize the total delivery to the brood, given the time constraints set by self-feeding and hunting (Ydenberg 2007), and to capture prey that most optimally covers the daily energy and nutritional needs of the nestlings (Fagerström *et al.* 1983). Because the nestlings' probability of survival depends on parental investment, parents must trade off the costs and benefits of their investment to maximize their reproductive fitness. Hence, parents must trade off between offspring quality and quantity (Morris 1985). Raptors take relatively large prey for their size, and need to allocate a significant amount of time to prepare the prey and feed the nestlings (Newton 1986, Slagsvold & Sonerud 2007, Steen *et al.* 2010). This makes raptors suitable model organisms for a study on food provisioning.

A well studied avian raptor taking a wide spectrum of prey types is the Eurasian Kestrel *Falco tinnunculus*, hereafter referred to as the kestrel; an open country raptor which feeds mainly on ground dwelling animals

like voles (Cricetidae), shrews (Soricidae) and lizards, and also on birds and insects (Village 1990). The kestrel shows both a functional and a numeric response to voles (Korpimäki & Norrdahl 1991). During years with low vole abundance kestrels feed on a wider variety of prey including more birds and insects (Fargallo *et al.* 2003) and usually have a reduced brood size (Wiebe *et al.* 1998), which increases the probability of fulfilling the energy demand of the nestlings.

Estimates of prey delivery rate in raptors in general, and in the kestrel in particular, are few and have been based on direct observations from a hide in combination with analyses of prey remnants and regurgitated pellets (e.g. Masman *et al.* 1989, Holthuijzen 1990, Olsen *et al.* 1998, Geng *et al.* 2009). In this study we provide more accurate estimates of the rate of prey delivery in the kestrel by using data from video monitoring of prey deliveries in the nestling period. We use these estimates to quantify the rate of prey consumption (i.e. prey mass per hour) by the nestlings and to predict the rate of prey items necessary to raise a kestrel brood on each type of prey separately.

METHODS

We used video to monitor prey deliveries at 55 kestrel nests in the boreal zone in Hedmark county, southeastern Norway (61°07'–61°32' N; 11°56'–12°48' E) during June–July in 2003 and 2005–09. The average brood size at the time of filming was 4.3 ± 0.2 (mean ± SE, *n* = 55). The study area covers c. 1200 km^2 and is dominated by intensively managed coniferous forest with a high proportion of clear-cuts interspersed with bogs, and with only negligible patches of farmland.

Video monitoring

The 55 nests monitored were in 47 different nestboxes. Six nestboxes were filmed for two years and one for three years. Of the nestboxes filmed for two years, three were filmed in subsequent years, one was filmed three years apart and two were filmed five years apart. The nestbox filmed for three years was first filmed two years apart and then three years apart. The kestrel is a migrant in our study area, as it is also in western Finland (63°N), where only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen & Korpimäki 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village 1990). Applying these high turnover rates on our frequency of reuse of boxes for filming suggests that maximally one individual of each sex would have been filmed during two seasons. Thus, we assume that very few, if any, adult kestrels were involved in more than one of our 55 monitoring sessions. Therefore, we treated breeding pairs as the statistical unit. Even with different individuals nesting, however, reuse of the same boxes for filming in separate years may not be regarded as independent replicates. On the other hand, in our study area there is high inter-annual variation in the abundance of shrews and voles (Steen 2010), making the quality of each territory highly variable from year to year.

In 2003 each nest was filmed on two separate days, in 2005 and 2006 each nest was filmed for two subsequent days and in 2007–09 each nest was filmed for three subsequent days (Table 1). In 2003 and 2005, prey deliveries were monitored with digital camcorders, either mounted on top of the box (2003) or placed on the ground functioning only as a recorder, and

Table 1. Year of filming of kestrel nests, number of nests filmed, mean monitoring time (days), brood age (i.e. the age of the last hatched nestling; mean ± SE, range) and brood size (mean ± SE, range). Brood size varied significantly among years (ANOVA, $F_{5,49}$ = 5.27, P <0.001).

Year	Nests	Days	Monitoring (h)	Age	Brood size
2003-A	9[a]	1	10.7	12.3 ± 0.7 (8–15)	5.0 ± 0.3 (4–7)
2003-B	9[a]	1	10.7	25.9 ± 0.6 (23–28)	5.0 ± 0.3 (4–7)
2005	10	2	10.0	12.6 ± 0.8 (8–16)	3.1 ± 0.5 (1–5)
2006	6	2	11.5	13.3 ± 0.6 (12–15)	4.5 ± 0.3 (3–5)
2007	10	3	61.5[b]	10.2 ± 0.6 (8–12)	5.0 ± 0.3 (3–6)
2008	11	3	61.5[b]	10.9 ± 0.4 (9–13)	5.0 ± 0.3 (3–6)
2009	9	3	61.5[b]	11.3 ± 0.4 (10–14)	3.4 ± 0.4 (2–5)

[a]Same nests in period A and B.
[b]Each brood was continuously monitored (subtracting the period of 3.5 h without prey deliveries for each night).

connected to a camera lens in the box with a 50-m modified video cable (2005). For the kestrel nests in 2006, the camcorder was substituted by a time lapse video cassette recorder or a hard disk drive recorder as recording equipment. In 2007–08, mini digital recorders (mini DVR) were used as recording equipment, as described by Steen (2009). This method was further improved in 2009; instead of replacing the original nestbox with a nestbox with the camera inside we used a special-made camera stand, which was placed into the original nestbox while an observer watched a monitor on the ground to ensure the correct camera view. Different set-ups between years were a consequence of technical improvements and all set-ups were equally capable of recognizing prey items delivered at the nests.

We identified each prey item delivered by the kestrels to type, i.e. whether it was a Common Lizard *Zootoca vivipara*, shrew *Sorex* sp., *Myodes* vole (Bank Vole *Myodes glareolus* or Grey-sided Vole *Myodes rufocanus*), *Microtus* vole (Field Vole *Microtus agrestis* or Root Vole *Microtus oeconomus*), Wood Lemming *Myopus schisticolor*, bird, frog *Rana* sp., insect or remains from Mountain Hare *Lepus timidus*.

In some cases, a parent arrived at the nest with a prey without providing it to the nestlings and instead flew off with the prey (*n* = 42). Such cases were not counted as prey delivered to the nestlings.

Prey mass estimation

We estimated the body mass of each prey item recorded in 2003 and 2005 (see below). These estimates were used to calculate a mean body mass for each prey type and were then used for the whole data set. If kestrels select for prey-size when hunting small mammals, as shown by Masman *et al.* (1986), our estimates are more reliable than mean values obtained from the literature. The body mass of each lizard and small mammal item was estimated by comparing the size of the prey item displayed on a grid on the video frame with sizes of prey items of known body mass, as explained in detail by Steen (2010). For birds a mean value for each prey species was obtained from data in the literature most pertinent to the breeding season in Fennoscandia (see Steen 2010). The body mass of insects was obtained from Itämes & Korpimäki (1987). All insects recorded were assigned a body mass of 0.2 g because all were of similar size. The mass of unidentified bird remains was set to 15% of the mean avian body mass. Too few frogs and wood lemmings were delivered to estimate a consistent mean, and these were consequently estimated from specimens trapped in the study area during the

kestrels´ nestling period in 2007–09 (G.A. Sonerud, unpubl. data). The mass of the few juvenile mountain hare remains were set to 15% of the mean body mass of juvenile mountain hares (Bray *et al.* 2002). The body mass of unidentified voles was set to the mean body mass of an average *Myodes* vole, *Microtus* vole and Wood Lemming. Correspondingly, the body mass of unidentified small mammals was set to the mean mass of an average shrew, *Myodes* vole, *Microtus* vole and Wood Lemming. The body mass of unidentified prey was set to the mean body mass of all identified prey. The mass of unidentified prey remains was set to 15% of the mean unidentified prey mass. In a few cases only the rear part of the prey item was delivered. In these cases we set the mass to 75% of the estimated body mass of the given prey type. Estimated prey body masses of the different prey types (Table 2) were used for the whole data set (2003, 2005 and 2006–09).

Table 2. Estimated body mass (mean ± SE), mass-specific gross energy content (GE), and metabolizable energy (MEC) of prey types delivered at the kestrel nests. GE and MEC were obtained from Karasov (1990) and Studier & Sevick (1992) for insects, from Tryjanowski & Hromada (2005) and Voituron *et al.* (2002) for lizards and from Masman *et al.* (1986) for shrews, voles and birds.

Prey type	Body mass (g)	GE (kJ/g)	MEC
Insect	0.2[a]	24.5	0.77
Common Lizard	5.3 ± 0.3 (*n* = 54)[b]	22.1	0.75
Frog	22.6 ± 4.0 (*n* = 7)[c]	-	-
Shrew	9.5 ± 0.3 (*n* = 64)[b]	21.6	0.65
Myodes voles sp.	16.7 ± 1.5 (*n* = 28)[b]	-	-
Microtus voles sp.	22.9 ± 1.8 (*n* = 21)[b]	21.5	0.70
Wood Lemming	25.2 ± 0.9 (*n* = 100)[c]	-	-
Vole unidentified	21.8[d]	-	-
Mammal unidentified	16.6[d]	-	-
Mountain Hare part	60.0[a]	-	-
Bird	34.7 ± 2.5 (*n* = 118)[e]	22.3	0.75
Bird remains unidentified	5.2[d]	-	-
Prey unidentified	17.2[d]	-	-
Prey remains unidentified	2.6[d]	-	-

[a]All items delivered given the same value as estimated from data in the literature (see text).
[b]Each item delivered estimated separately from relative size on the video frame (see text).
[c]All items delivered given the same value as estimated from specimen snap-trapped during the kestrels' nestling period in 2007–09.
[d]Average estimated mass of recorded prey (see text).
[e]Each item estimated separately from data in the literature (see text)

Statistics

The rate of prey mass (g/h) delivered at each kestrel nest ($n = 55$) was calculated by dividing the estimated mass of prey items delivered at the nest by the duration of the video monitoring period at the nest. We assume that the rate of prey mass delivered reflected consumption rate, because the few cases when the parent landed on the nestbox with a prey without providing it to the nestlings and instead flew off with the prey (see above), were not counted as prey consumed by nestlings. We also assume that the mass-specific energy content and also the assimilation quotient (i.e. assimilated portion of the energy consumed) are similar for the different prey types (Table 2).

To estimate the number of items of a prey type (i.e. insect, lizard, shrew, vole or bird) required to be delivered per hour to feed an average kestrel brood we divided the estimated prey consumption rate (g/h) of that prey type by the estimated mass of an item of that prey type. Prey-specific consumption rates were estimated from the parameter estimates of the best fitting model and the average brood size.

Statistical analyses were performed with the R software package, version 2.11.1 (R Development Core Team 2010), using analysis of variance and a linear mixed effect model in the lme package (Pinheiro & Bates 2000). We used a linear mixed-effect model with prey mass delivery rate (g/h) as the response variable and brood size and average nestling age as the explanatory variables. We believe that nestling age would have a minor effect because the variation of this variable in our data set was low, but we included it to control for a possible effect. We also tested whether a non-linear relationship between prey mass delivery rate and brood size gave a better fit than a linear model by adding a quadratic term in the equation. The response variable and the explanatory variables were $\log_{10}$-transformed to obtain normality of the residuals of the selected model. Year was included as a random factor to control for possible variation in delivery rate associated with inter-annual changes in environmental conditions.

One could argue that any effect of brood size on prey delivery rate would be an artefact of kestrels having smaller broods when voles are rare and constitute a smaller proportion of the diet (Korpimäki 1986, Korpimäki & Wiehn 1998, Wiebe *et al.* 1998). Hence, prey mass delivery rate may not only be affected by brood size itself, but also by the associated proportion of voles in the diet. We therefore included the proportion of delivered mass made up of voles as a covariate. Because this proportion was zero in five cases, we added a minimum value (i.e. lowest proportion value for this variable) to all before $\log_{10}$ transforming. We used the most parsimonious model and an explanatory variable was included only when the value of AIC_c (corrected Akaike Information Criterion) improved with ≤ 2.0 (Burnham 2002). We used AIC_c because it provides better model selection than AIC for moderate sample sizes (Hurvich & Tsai 1991). From our best fitted model we used the parameter estimates to calculate the regression line between rate of prey mass delivered and brood size, from which we used the slope to estimate the effect of brood size on the rate of prey mass delivered. If the rate of prey mass delivered increases slower than the increase in brood size, i.e. if the slope is significantly smaller than one, each nestling in larger broods will obtain less food compared to smaller broods. Finally, we used the parameter estimates to calculate prey mass consumption by the nestlings in an average brood. To control for contributions of the random effect, the estimated values and the associated 95% confidence intervals were calculated using the function 'intervals' in R (R Development Core Team 2010).

RESULTS

The kestrels delivered a total of 2282 prey items during the 2337 h of video monitoring at the 55 nests. In total, the kestrels were estimated to deliver 43283 g of prey, and voles were the most common prey type delivered (Table 3).

The rate of prey mass delivered was significantly affected by brood size ($F_{1,48} = 24.38$, $P < 0.001$, $n = 55$, $AIC_c = -71.1$). Adding the proportion of prey mass made up by voles gave a poorer fit ($AIC_c = -68.5$), as did adding nestling age ($AIC_c = -70.9$) or the quadratic term of brood size ($AIC_c = -70.5$). For an average brood size (4.3), the parents were estimated to deliver 18.1 g/h when we applied the parameter estimates from the best fitting lme model. As a result, given the average brood size in our study, each nestling was estimated to consume on average 4.2 g/h.

The earliest and latest recorded prey deliveries during the day at any of our kestrel nests occurred at 2:49 am and 11:39 pm, respectively. The maximum daily activity period was thus 20 hours 50 minutes. At the nests monitored continuously for 24 hours per day, data from 88 nights and 96 mornings showed that the earliest prey delivery was on average at 5:34 am (± 12.6 min) and the latest at 9:40 pm (± 7.2 min). Hence, the daily activity period was on average 16 hours 6 minutes. Given a maximum daily activity period

of 20.84 h, the daily delivery rate per nestling was 87.8 g/d when applying the parameter estimates of the best lme model. Correspondingly, given an average daily activity period of 16.10 h, the daily delivery rate per nestling was 67.8 g/d.

The slope of the log-log plot of prey mass delivery rate as a function of brood size (Fig. 1) was significantly less than one: $y = 0.98 + 0.44 \times x$ (95% CI = 0.26 –0.62). Hence, each nestling obtained less food
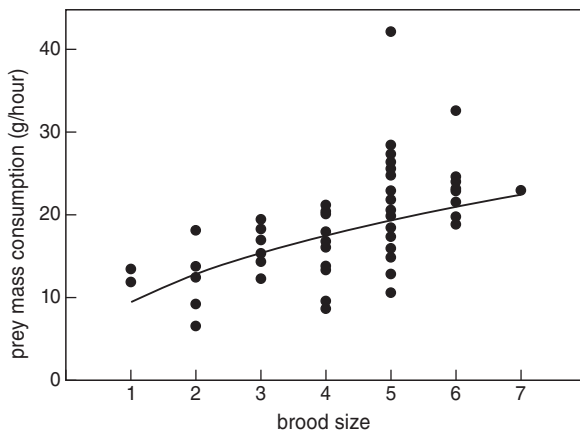

Figure 1. Prey mass delivery rate (g/h) for kestrel nests plotted against brood size. The regression line is calculated from back-transformed values (10^y) from the parameter estimates of the lme model ($y = 0.98 + 0.44 \times x$, $F_{1,48} = 24.4$, $P < 0.001$, $n = 55$ nests, random effect = 6 years).

Table 3. Relative frequency of different prey types delivered at kestrel nests ($n = 55$) given as percentage of the number of prey items ($n = 2282$) and of total prey mass (43,283 g).

Prey type	Number of prey (%)	Prey mass (%)
Frogs	0.4	0.4
Insects	2.9	0.03
Lizards	9.4	2.6
Shrews	12.4	6.3
Voles	60.0[a]	65.1[b]
Birds	13.7	24.7
Small mammal unidentified	0.5	0.5
Prey unidentified	0.04	0.04
Bird remains unidentified	0.1	0.04
Hare remains	0.1	0.4
Prey remains unidentified	0.4	0.5

[a]Voles constituted of 32.0% *Myodes* voles, 53.2% *Microtus* voles, 4.0% Wood Lemming, and 10.8% unidentified voles by number.
[b]Vole mass constituted of 25.3% *Myodes* voles, 59.1% *Microtus* voles, 4.6% Wood Lemmings, and 11.0% unidentified voles by mass.

with increasing brood size. For instance, a brood of two nestlings was estimated to consume a total of 12.9 g/h, compared to 22.5 g/h for a brood of seven. Thus, each nestling obtained 6.4 and 3.2 g/h in a brood of two and seven, respectively.

The estimated number of prey items required per hour to feed an average kestrel brood in our study (4.3 nestlings) was 90.55 when the diet was based solely on insects, and 3.42, 1.89, 0.83 and 0.52 when based solely on lizards, shrews, voles and birds, respectively. This corresponds to one prey delivery per 40 s if the diet was based solely on insects and one delivery per 18, 32, 75 and 120 min if based solely on lizards, shrews, voles and birds, respectively.

DISCUSSION

Of the 2282 prey items recorded delivered by the kestrels to their nests during our six years of study, voles were by far the most abundant prey both by number and mass, followed by birds, shrews and lizards, respectively. Insects and frogs were rarely taken as prey by the kestrels. The dominance of voles among prey taken by kestrels during the breeding period agrees with earlier findings (Village 1990, Korpimäki 1986). The mass-specific energy content of insects, frogs, lizards, shrews, voles and birds appeared to be quite similar and this seemed to also be the case for the assimilated proportion of the energy content of the prey consumed (see references above). Hence, we assumed that the delivery rate of prey mass adequately reflected consumption rate.

With an average daily activity period of 16.1 h, each nestling was estimated to consume 67.8 g/d. In comparison, Masman *et al.* (1989) found that nestlings hand-raised in the laboratory had an average food intake of 66.8 g/d (seven nestlings 6–7 d old), compared to 62.6 g/d for nestlings in the field in an average brood of 5.5 nestlings (the average brood size was not given by Masman *et al.* (1989), and we therefore estimated it from the information given in their paper). Geng *et al.* (2009) estimated the prey consumption rate of a kestrel nestling in the field to be 48.2 g/d in an average brood of 4.8 nestlings. Our estimates were only 8% higher than the field estimates from Masman *et al.* (1989), but 29% higher than the estimates from Geng *et al.* (2009). The daily activity periods of kestrels did not vary much between the different studies (16.1 h in ours vs. c. 17 h in that of Masman *et al.* (1989) and c. 15 h in that of Geng *et al.* (2009)). Hence, the discrepancy in daily consumption rate may be caused by

other factors, for instance that our broods were on average smaller. In broods experimentally reduced by two nestlings, each nestling was found to consume 81 g/d, compared to 61 g/d in control broods (Dijkstra *et al.* 1990). To compare our estimate with that of Masman *et al.* (1989) and that of Geng *et al.* (2009) we set the activity period to 17 h and brood size to 5.5, and the activity period to 15 h and brood size to 4.8, respectively. This gave estimates of 62.4 and 59.4 g/d per nestling, respectively, which is very similar to the estimates of Masman *et al.* (1989), but still markedly higher than the estimate of Geng *et al.* (2009). The difference may be due to our study area being situated further north and thus in a colder climate than their study areas. A nestling´s food demand may be higher when the energy spent on thermoregulation is higher (Gil-Delgado *et al.* 1995). The discrepancy may also have been caused by methodological differences. For records of prey deliveries, close-up video monitoring may be more accurate than observations from a hide and pellet analyses (Lewis *et al.* 2004). Masman *et al.* (1989) used direct observations close behind the nestbox, and Geng *et al.* (2009) mainly used pellets from the nestbox, although some data were obtained by direct observations from a hide.

We found that although prey mass delivery rate increased with brood size, each nestling obtained less food in larger broods. Hence, rearing a larger brood implied a cost for the individual nestling, although less energy may have been needed for thermoregulation in large than in small broods. However, because brood size may be confounded with prey availability (Korpimäki 1986, Korpimäki & Wiehn 1998, Wiebe *et al.* 1998), i.e. parents may be able to provide more prey and thus be able to raise a larger brood in years with high prey abundance, we are unable to conclude whether the increase in delivery rate with brood size was due to brood size itself or due to higher vole abundance. Including the proportion of voles in the total prey mass delivered in the model did not give a better fit, suggesting an effect of brood size on delivery rate. However, to separate the effects of brood size and prey abundance a brood-size manipulation experiment is needed. As shown in a field experiment on kestrels, parents delivered more prey mass to enlarged broods, showing that to some extent they were able to compensate for larger broods by increasing hunting effort and prey delivery (Dijkstra *et al.* 1990). However, as in our study, each nestling consumed less food in large than in small (experimentally reduced) broods (Dijkstra *et al.* 1990). Less food obtained by each nestling in larger broods may cause lower nestling condition, as found in

kestrels when brood size was manipulated (Dijkstra *et al.* 1990, Korpimäki & Rita 1996), which in turn may lead to lower survival (Korpimäki & Rita 1996). On the other hand, smaller broods (e.g. 1–3 nestlings) may receive more food than is optimal for the parents´ total reproductive output. Data on juvenile survival and recruitment from our study area would be essential in revealing whether individual kestrel parents have an optimal brood size, and how this brood size might change with variation in the abundance of the various prey types.

During the first half of the nestling period, when the kestrel male usually provides most of the prey and the female feeds the nestlings (Village 1990), the male may be less able than the female to judge nestling hunger (cf. Eldegard & Sonerud 2009, 2010). In some instances we observed prey provided by the male to be removed by the female just after she had finished a feeding session, indicating that the female is more able to sense when the nestlings are satiated. Later in the season, when the female may also hunt, and as the nestlings become able to feed unassisted, the male more often delivers the prey directly to the nestlings (Village 1990; G.A. Sonerud *et al.*, unpubl. data). In this period, the male may judge the nestlings' hunger better and adjust his parental effort accordingly. In our study the largest brood size monitored was seven, which is similar to that found in other studies (Village 1990). We estimate that each nestling in a brood of seven would obtain 3.2 g/h (i.e. 51.2 g/d for a 16.1 h day), which may be the lower threshold to sustain growth for the kestrel. In line with this, Kirkwood (1981) found the lowest consumption rate in hand-reared individual nestlings to be 59 g/d. When less prey is available, parents may distribute the food selectively among the nestlings, favouring senior nestlings that may have higher reproductive value than juniors (Morris 1987).

The estimated delivery rate of insects required to feed an average kestrel brood in our study was one every 40 s, which is a rate unlikely to be achieved in the boreal forest. The corresponding estimate for lizards was one item every 18 min. Lizards probably occur too infrequently in our study area, due to the relatively cold climate (Pilorge 1987, Uller & Olsson 2003), to be the sole prey of the kestrels. In fact, lizards seem to be preyed upon by the kestrels in our area whenever available, determined by solar height and ambient temperature (Steen *et al.* 2011). If the kestrels were to feed exclusively on shrews or voles, they would have to deliver one prey item at the nest every 32 min or 75 min, respectively. The rate for voles seems realistic to

attain when voles are abundant. However, for a diet to be based exclusively on shrews, shrews would have to be twice as abundant as voles in a vole peak year, which never occurs in Fennoscandian boreal forests (e.g. Sonerud 1988).

In conclusion, in our Norwegian population of kestrels, the food demand of an average brood of 4.3 nestlings was about one vole per hour. This delivery rate would be realistic to achieve for a kestrel pair in peak vole years. In such years, the kestrels may respond by laying more eggs, although even in such favourable years, the optimal brood size may be restricted by the reduction in prey mass received by individual nestlings.

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SAMENVATTING

Bij nestblijvers is de grootte van de prooisoort van grote invloed op de tijd en energie die ouders besteden aan het voedsel zoeken, het voedsel voor de jongen in hapklare brokken te verdelen en het daadwerkelijk voeren van de jongen, en dus ook op de frequentie waarmee het voedsel naar de jongen wordt gebracht. Roofvogels voeren relatief grote prooien aan hun jongen. Dit maakt het mogelijk om de prooien te herkennen en te kwantificeren. Toch zijn kwantitatieve gegevens over prooi-aanvoer bij roofvogels schaars en meestal gebaseerd op directe zichtwaarnemingen in combinatie met een analyse van gevonden prooiresten en braakballen. Om zo betrouwbaar mogelijke informatie over het voedsel te verkrijgen, hebben we 55 nesten van Torenvalken *Falco tinnunculus* geobserveerd met behulp van videoapparatuur. Van de 2282 waargenomen prooien bestond het merendeel uit woelmuizen, gevolgd door vogels, spitsmuizen en hagedissen. Insecten en kikkers waren weinig voorkomende prooien. We schatten dat een gemiddeld broedsel van 4,3 jongen 18,3 g voedsel/uur consumeert (4,2 g/uur/jong). Dit komt overeen met 67,8 g/d/jong bij een gemiddelde actieve periode van de ouders van 16,1 uur. De geschatte aanvoerfrequentie die nodig is om een gemiddeld broedsel van voldoende voedsel op een menu van één prooitype te voorzien, is 91 prooien/uur voor insecten, 3,4 prooien/uur voor hagedissen, 1,9 prooien/uur voor spitsmuizen, 0,83 prooien/uur voor woelmuizen en 0,52 prooien/uur voor vogels. Dit komt overeen met 1 prooi per 40 seconden voor insecten, 1 prooi per 18 minuten voor hagedissen, 1 prooi per 32 minuten voor spitsmuizen, 1 prooi per 75 minuten voor woelmuizen en 1 prooi per 120 minuten voor vogels. We concluderen dat Torenvalken in boreale bossen geen broedsel groot kunnen brengen als ze alleen insecten of hagedissen zouden aanvoeren. Waarschijnlijk is dat ook niet het geval op een menu van alleen spitsmuizen, maar in een piekjaar van woelmuizen wel op een menu van alleen woelmuizen.   (PW)