

# Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*)

Ronny Steen · Geir A. Sonerud · Tore Slagsvold

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**Abstract** In altricial birds, parents are assumed to optimize the total food delivery to the brood given the time constraints set by self-feeding and food collecting. Older nestlings may require more food than younger ones, and nestlings may need more energy when their growth rate is higher. By video monitoring prey deliveries in ten nests of the Eurasian Kestrel (*Falco tinnunculus*), we examined whether parents adjusted feeding effort in relation to nestling age. Based on published data on the growth and energy intake of Kestrel nestlings, we predicted parental prey mass delivery to peak at a nestling age of 15–17 days. The prediction was supported. The decrease in provisioning rate during the later nestling stages was best explained by nestling age. However, we cannot be conclusive as to whether this was caused by a decrease in nestling food demand, or by a seasonal decrease in the availability of voles, the dominant prey. The change in provisioning was mostly an effect of a change in the number of prey items delivered. However, prey size also tended to decrease with increasing nestling age. This is opposite to what has been

found in most non-raptorial altricial birds, and may have been caused by the ability of Kestrel parents to dismember large prey and thus overcome the gape size-restricted swallowing capacity of small nestlings, together with a need to provide smaller prey to older nestlings when they start to feed unassisted.

**Keywords** Eurasian Kestrel · *Falco tinnunculus* · Feeding effort · Nestling age · Prey delivery rate · Prey mass

## Zusammenfassung

**Turmfalkeneltern (*Falco tinnunculus*) passen den Fütterungsaufwand an das Alter ihrer Nestlinge an.**

Bei Nesthockern ist die Futtermittellieferung durch die Eltern entscheidend für Wachstum und Entwicklung der Jungvögel. Man nimmt an, dass die Eltern versuchen, ihrer Brut die in Anbetracht der zeitlichen Beschränkungen, denen sie durch die eigene Nahrungsbeschaffung und die Futtersuche unterliegen, größtmögliche Nahrungsmenge zu beschaffen. Ältere Nestlinge können mehr Nahrung benötigen als jüngere bzw. der Energiebedarf der Nestlinge kann in Phasen stärkeren Wachstums höher sein. Durch Videoaufzeichnung der übergebenen Beutestücke in zehn Turmfalkennestern wurde untersucht, ob die Eltern den Fütterungsaufwand in Abhängigkeit vom Nestlingsalter regulieren. Auf der Grundlage von publizierten Daten zu Wachstum und Energieaufnahme von Turmfalkennestlingen stellten wir die Vermutung auf, dass die Beutelieferungen durch die Eltern bei einem Nestlingsalter von 15–17 Tagen ein Maximum erreichen. Diese Annahme bestätigte sich. Die Abnahme der Versorgungsrate in den späteren Nestlingsstadien ließ sich besser durch das

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R. Steen (✉) · G. A. Sonerud  
Department of Ecology and Natural Resource Management,  
Norwegian University of Life Sciences, P. O. Box 5003,  
1432 Ås, Norway  
e-mail: ronny.steen@umb.no

T. Slagsvold  
Department of Biology, Centre for Ecological and Evolutionary  
Synthesis (CEES), University of Oslo, P.O. Box 1066 Blindern,  
0316 Oslo, Norway

Nestlingsalter als durch die Jahreszeit erklären. Allerdings kann man nicht sicher sagen, ob dies durch eine Abnahme im Nahrungsbedarf der Nestlinge bedingt wurde, oder mit einem jahreszeitlichen Abfall in der Verfügbarkeit von Wühlmäusen, der Hauptbeute, zusammenhing. Die Änderung der Versorgungsmenge wurde hauptsächlich durch eine Änderung in der Anzahl der gelieferten Beutestücke bedingt. Allerdings nahm die Beutegröße mit steigendem Nestlingsalter tendenziell ab. Dies steht im Widerspruch zu den Befunden bei den meisten Nesthockern, die nicht zu den Beutegreifern gehören, und könnte auf die Fähigkeit letzterer zurückzuführen sein, große Beutetiere zu zerlegen und somit das Problem der durch die Rachengröße bedingten begrenzten Schluckkapazität kleiner Nestlinge zu umgehen, in Verbindung mit dem Bedarf an kleineren Beutetieren für ältere Nestlinge, wenn diese selbständig zu fressen beginnen.

## Introduction

In altricial birds, parental food provisioning is essential for successful growth and development of the offspring, and parents are assumed to maximize the total food delivery to the brood given the time constraints set by self-feeding and food collecting (Ydenberg 2007). Life history theory predicts that parents should optimize provisioning with regards to their growing offsprings' need and to costs in terms of their own survival and potential future reproductive success (Trivers 1974). However, growth rate is not constant, and nestlings may need more energy when growth rate is higher (Barba et al. 2009). Parental food provisioning increases in general with nestling age, especially during the phase when the nestlings' growth rate is at its peak. When the nestlings approach their final body mass, the provisioning rate tends to level off (e.g., Collopy 1984; Grundel 1987; Blondel et al. 1991; Barba et al. 2009). Prey size may also increase with nestling age because the swallowing capacity of the nestlings improves as they grow (Slagsvold and Wiebe 2007).

The European Kestrel (*Falco tinnunculus*), hereafter called the Kestrel, is an excellent study species for an investigation of the relationship between parental provisioning and nestling age. The Kestrel lives in open landscapes and feeds mainly on ground-dwelling animals like voles (Cricetidae), shrews (Soricidae), and lizards, and also on birds and insects (Village 1990). Kestrels respond both numerically and functionally to vole abundance: they raise more offspring and feed on a narrower variety of prey, including fewer birds and shrews, during years with high vole abundance (Korpimäki and Norrdahl 1991; Fargallo et al. 2003). Kestrel parents appear to adjust the rate of

food provisioning to the current needs of the young (Daan et al. 1989). We studied this relationship in more detail by video-monitoring Kestrel nests to obtain more precise measurements of prey mass delivered by the parents than have been obtained from traditional analyses based on pellet samples or direct observation from a hide (Lewis et al. 2004). In this study, we asked whether parent Kestrels adjust their food provisioning in relation to the current food demands of the young. The Kestrel parents may have evolved a fixed level of parental effort during breeding (fixed feeding hypothesis; Ricklefs 1987; Mauck and Grubb 1995; Navarro and González-Solis 2007; Erikstad et al. 2009), not responding to the actual current nestling food demands but rather to the mean expected food demand at the actual nestling age (Erikstad et al. 2009). Alternatively, parental effort may be flexible (flexible investment hypothesis; e.g., Johnsen et al. 1994; Reid 1987), depending on the current nestling energy needs, and thus involving complex parent–offspring interactions (Erikstad et al. 2009). To separate between these hypotheses would require an experimental procedure, so we refrained from investigating them further.

Parental decisions on food provisioning do not only concern total mass of prey delivered but also type and size of prey. In the early nestling period, the female Kestrel is permanently present at the nest, receiving prey items from the male and feeding them to the young, while later the nestlings start to feed unassisted and the female is able to hunt (Village 1990). We would expect males to provide larger prey as long as the nestlings depend on the female, because larger prey items are more efficient to feed when the female dismembers the prey for the nestlings (Steen 2010). As nestlings become able to feed unassisted, we would expect smaller prey items, like insects, lizards, and shrews, to be delivered more often, because the nestlings are best able to feed unassisted on such small prey items (Steen 2010). Providing larger prey early in the nestling period, and smaller prey later, is the opposite to what is found in most passerine birds, where prey size increases with nestling age because the swallowing capacity of the nestlings improves as they grow (Slagsvold and Wiebe 2007). In Kestrels, as in other raptors, parents are able to dismember large prey, and are therefore relieved from the prey size constraint set by the limited swallowing capacity of young nestlings. However, when the nestlings start to feed unassisted, the constraint set by their dismembering skills and ingestion ability would apply (cf. Steen et al. 2010). A further reason to deliver smaller prey when nestlings are older may be to avoid that dominant offspring monopolizing prey items (Mock and Parker 1997; Fargallo et al. 2003).

Hence, we predicted that prey size would decline with nestling age. Note that this is opposite to the prediction

based on the hypothesis that male and female raptors have different feeding niches (e.g., Selander 1966; Snyder and Wiley 1976; Newton 1979; Andersson and Norberg 1981; Temeles 1985), namely that the mean prey size delivered to the young would increase after the larger female starts hunting. Our detailed video-filming enabled us to study whether the Kestrels adjusted type and size of prey in relation to nestling age. Such knowledge may contribute to a general understanding of the feeding biology of raptors and also give insights into foraging constraints, parent-offspring conflict, and sibling competition (Mock and Parker 1997; Slagsvold and Wiebe 2007; Steen et al. 2010, 2011a, b).

**Methods**

**The peak food demand**

For laboratory-raised Kestrel nestlings, Masman et al. (1989) found that food intake increased from day 11 to day 18 after hatching, and then decreased over the remaining 12 days of the nestling period. A non-linear relationship would be expected, because above a certain age the nestlings would grow at a gradually slower rate (e.g., Grundel 1987; Blondel et al. 1991; Barba et al. 2009).

To predict the age at which the growth pattern changes from accelerating to decelerating, we analyzed data on body mass of Kestrel nestlings from Village (1990, fig. 54). From the growth curve, we calculated the

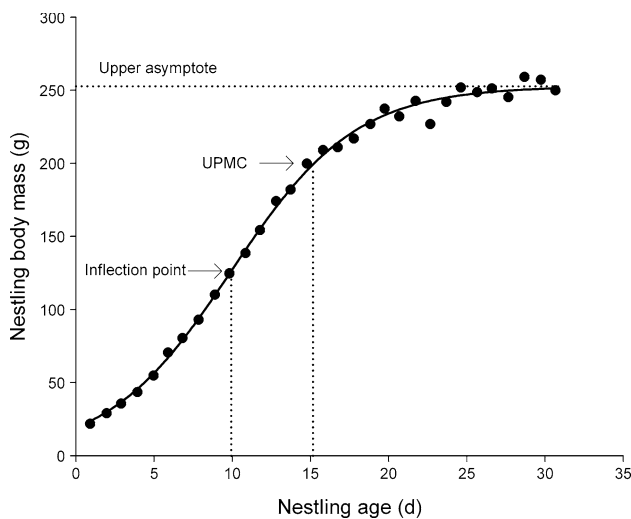
inflection point and the point of upper maximum curvature (UPMC; Fig. 1). The inflection point denotes the time when the growth is at the maximum (i.e. for a sigmoid curve, the time when growth is half complete). We used a non-linear regression in the Sigma-Plot version 9.01 graphic package (SPSS) to obtain a sigmoid (i.e. three-parameter nonlinear regression) growth curve by means of the equation.

$$f(x) = \frac{a}{1 + e^{-\frac{(x-x_0)}{b}}} \tag{1}$$

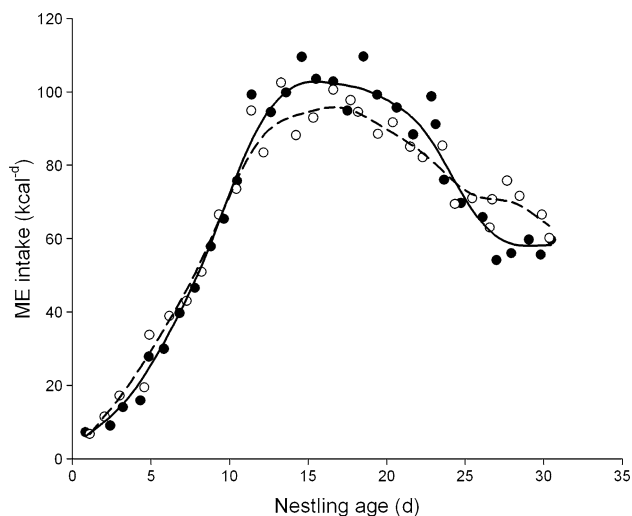
where  $f(x)$  denotes the nestling body mass (g),  $a$  denotes the upper asymptote,  $x$  denotes nestling age (d),  $x_0$  denotes the nestling age when  $f(x)$  is 50 % of the maximum, and  $b$  denotes the slope at  $x_0$ . We used the second derivative to find the inflection point of the curve ( $f(x)'' = 0$ ), where the growth rate peaks, and the third derivative to find the upper point of maximum curvature ( $f(x)''' = 0$ ), where the growth levels off (Banks 1994).

We did not expect a peak in nestling energetic demands at the calculated inflection point, however, because the nestlings at this age are still growing fast, and because larger nestlings that have passed the peak of growth and are growing slower may still need more food than smaller nestlings that are at the peak of growth. Therefore, we needed to adjust for changes in nestling body mass during growth. More precisely, we needed to locate the point where the growth rate no longer continues to rapidly rise (UPMC) and instead follows either a stable state or a slow rise (cf. Stirling and Zakyntinaki 2008), i.e. the point of maximum deceleration (Banks 1994). Using the data on nestling growth in Village (1990), and following Banks (1994), we found that the UPMC is reached when the nestlings are 15 days old. We assumed that the growth curve provided by Village (1990) is representative for the Kestrels in our population, because other studies of nestling growth in wild Kestrels in Europe have yielded similar results (Village 1990 and references therein).

Nestlings need to allocate energy not only for growth in general but also for growth of muscles and feathers (Kirkwood 1981), which develop after the nestlings have attained their overall maximum mass (Kirkwood 1981). Hence, the body mass of the nestlings may in itself be an insufficient index for the total energy demand. To calculate the ME intake of the nestlings, we extracted the mean values from the figure presented in Kirkwood (1981, fig. 9.15) on the metabolisable energy (ME) intake of Kestrel nestlings. To visualize the peak, we generated a smoothed curve by use of smooth data option in Sigma-Plot version 9.01 graphic package (SPSS). The peak occurred when the nestlings were 15–17 days old (Fig. 2). We predicted that the daily rate of prey mass delivered to the Kestrel nestlings would peak when the nestling age was



**Fig. 1** The growth curve of Eurasian Kestrel (*Falco tinnunculus*) nestlings, extracted from Village (1990), with the inflection point ( $f(x)'' = 0$ ) and the point of upper maximum curvature (UPMC;  $f(x)''' = 0$ ), i.e. maximum deceleration shown; sensu Banks 1994) were calculated as  $f(x) = 252.63/(1 + e^{-((x-9.94)/3.97)})$ ,  $R^2 = 0.99$ ,  $**p < 0.001$ ,  $n = 30$



**Fig. 2** The metabolisable energy (ME) intake of Eurasian Kestrel nestlings, extracted from Kirkwood (1981). To visualize the peak two smoothed curves were generated; nestlings on a diet of mice (*filled circles, solid line*) and nestlings on a mixed diet of mice and 1-day-old chickens (*open circles, dashed line*)

close to the point of UPMC, but with a small time lag due to the peak in ME intake (Kirkwood 1981).

#### Video monitoring

The estimates of the daily rate of prey mass consumption by a nestling were based upon video monitoring of adult Kestrels delivering prey at ten nests in the boreal zone in Hedmark county in south-eastern Norway (61°N, 12°E) during June–July 2007. The nests had a mean nearest neighbour distance of  $3.3 \pm 0.3$  km (range 2.3–5.8), and were in nest boxes situated  $637 \pm 15$  m a.s.l. (range 558–694). The study area is dominated by large bogs and intensively managed coniferous forest with a high proportion of clear-cuts and with only negligible patches of farmland.

One week or more after hatching, the original nest box was replaced with a nest box designed for filming. A CCD camera was placed in the top back corner of the nest box and pointed towards the entrance of the nest box. The camera was mounted with a wide angle lens to cover a broad view inside the nest box, connected with a video cable to a mini-digital video recorder (mini DVR) which stored data on SD cards. For details of the monitoring setup, see Steen (2009). The number of days after hatching of the last chick (hereafter termed nestling age) was on average  $10.2 \pm 0.6$  days (range 8–12) when filming started, and  $26.7 \pm 0.5$  days (range 24–29) when it ended. Average brood size was  $5.0 \pm 0.3$  (range 3–6). No nestlings died during filming. Average monitoring time per nest was  $16.4 \pm 0.6$  days (range 14–19). The monitoring of separate nests overlapped in time, but did not start on the

same day; filming started on day 1 in one nest (nestling age 12 days), on day 2 in one nest (nestling age 12 days), on day 3 in one nest (nestling age 12 days), on day 4 in three nests (nestling age 8, 9 and 9 days), on day 4 in three nests (nestling age 12, 8, and 8 days), and finally on day 6 in one nest (nestling age 12 days). The variable termed season was taken as the number of days elapsed from day 1, i.e. the start of filming in the first nest.

From the video recordings, we identified each prey item delivered by the parents to main type, i.e. whether it was an insect, a lizard, a shrew, a vole, a bird, or a fragment of a bird or of an unidentified prey item (see Electronic Supplemental Material). To estimate the mass of each of the prey types, we used the estimates of prey body mass data provided by Steen et al. (2011a, b), which were based on estimates of the body mass of single prey items delivered to 19 Kestrel nests in our study area in 2003 and 2005. In the case of the Kestrel being prey size selective when hunting small mammals, as shown by Masman et al. (1986), our mass estimates of prey delivered to the nest are more reliable than mean mass values per prey type obtained solely from the literature.

#### Prey mass delivered

We estimated the daily rate of prey mass delivered to each nest during the nestling phase. The measurements started on the first complete day of monitoring after the onset of filming (i.e. immediately after midnight) and ended on the last complete day of monitoring before conclusion of filming (i.e. immediately before midnight). From a total of 164 monitoring days, we subtracted eight incomplete monitoring days. Examples of monitoring days we regarded as incomplete were when the 1st day of monitoring started in the afternoon, this half-day was not counted, and when the last day of monitoring ended in the afternoon. Hence, we include only complete days of monitoring. In addition, due to technical failure during monitoring, 2 days of recording were subtracted for two nests and 1 day for a third nest. Thus, the measurement covered 151 complete monitoring days. The total prey mass (g) delivered per nestling at each nest for each day (G) was calculated by means of the equation.

$$G = \frac{1}{b} \sum_{i=1}^n k_i \quad (2)$$

where  $i = 1, \dots, n$  denotes prey item  $i$  delivered during the day,  $k_i$  denotes estimated body mass (g) of prey item  $i$ , and  $b$  denotes brood size. We calculated a value of G for each of the 151 complete days of monitoring.

We assumed that the rate of prey mass delivered adequately reflected consumption rate, because the mass-

specific energy contents of lizards, shrews, voles, and birds are similar, as is also the assimilated proportion of the energy content of the prey consumed (Masman et al. 1986; Karasov 1990; Tryjanowski and Hromada 2005).

### Statistics

Statistical analyses were performed with the software R, version 2.11.1 (R Development Core Team 2010). We used a linear mixed effect model (lme) in the nlme package (Pinheiro and Bates 2000) and tested whether there was a change in the daily rate of prey mass delivered per nestling as a function of nestling age (i.e. days after hatching of the last chick). Daily rate of prey mass delivered per nestling (G) was used as the response variable, and nestling age and brood size as explanatory variables.

Any change in the daily rate of prey mass delivered per nestling as a function of nestling age may not only be an effect of parents adjusting their prey item delivery rate but may also be an effect of parents providing smaller or larger prey items. To test for this, we first used the number of prey items delivered per day per nestling as the response variable and nestling age as the explanatory variable. Secondly, we used the daily average body mass of prey items delivered as the response variable and nestling age and brood size as the explanatory variables.

In addition, we tested for any seasonal effect (e.g., seasonal change in prey availability), rather than nestling age, by using the number of days elapsed from the first filming day as an explanatory variable, termed season. Nestling age and season are highly associated and therefore most likely confounding factors. The variables age and season were therefore run separately in the models. For all the models, we tested whether a linear (i.e.  $f(x) = \beta_0 + \beta x$ ) or a non-linear (i.e.  $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$  or  $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$ ) relationship gave the best fit, and selected the model with the lowest AIC-value (Burnham and Anderson 1998). We kept to the model when the differences in AIC were larger than 2.0 between this and other models (Burnham 2002). Brood size was considered to be a co-factor and only included if AIC improved with 2.0 or more. Breeding pair was treated as a random factor to control for a possible variation caused by individual differences.

The values of the two response variables daily rate of prey mass delivered per nestling, and number of prey items delivered per day per nestling, were  $\log_{10}$  transformed to obtain approximately normal distributions. To control for contribution of random effects, the values of the intercept, the slope and the associated 95 % confidence intervals were calculated from the lme parameter estimates, using the function “intervals” in R (R Development Core Team 2010). Mean and standard error are presented as mean  $\pm$  SE.

## Results

### Rate of prey mass delivered

Parent Kestrels delivered 3,595 prey items during the monitoring period. Of these, lizards constituted 2.7 %, shrews 9.8 %, voles 60.2 %, unidentified small mammals (shrews or voles) 19.4 %, and birds 4.0 %, whereas 3.9 % were unidentified prey items, and 0.3 % were fragments of a prey. No insects were recorded. The daily rate of prey mass delivered was highly associated with nestling age, and a non-linear relationship gave the best fit (Tables 1a and 2; Fig. 3). Removing  $\beta_2 x^2$ , adding  $\beta_3 x^3$ , or adding brood size as a co-factor, gave a poorer fit (Table 1a). In the non-linear models nestling age gave a much better fit than season ( $\Delta\text{AIC} = 71.4$ ). In addition, the linear effect of season gave better fit than the non-linear one ( $\Delta\text{AIC} = 15.0$ ). The daily rate of prey mass delivered decreased significantly with season (Table 3a; Fig. 3b).

The nestling age at which the peak in daily rate of prey mass delivered per nestling occurred (the maximum of the positive “U-shaped” curve in Fig. 2) was found by setting the second derivative of the function given in Fig. 3 to zero. This gave the value 16.7 days, which was close to the time when the growth “settled down” (UPMC), i.e. 15.2 days (Figs. 1 and 4), and even closer to the peak in ME intake, i.e. 15–17 days (Fig. 2). From the function given in Fig. 3, the maximum rate of prey mass delivered per nestling was predicted to be  $100.5 \text{ g}^{-\text{day}}$  when the nestlings were 16.7 days old,  $71.7 \text{ g}^{-\text{day}}$  when they were 9 days old, and  $48.4 \text{ g}^{-\text{day}}$  when they were 28 days old (Fig. 3). The predicted ME intake based on data reported by Kirkwood (1981) closely matched the curved based on our data (Fig. 5).

### Rate of prey items delivered

The daily rate of prey items delivered per nestling was highly associated with nestling age, and a non-linear relationship gave the best fit (Tables 1b and 2b; Fig. 6a). Removing  $\beta_2 x^2$ , adding  $\beta_3 x^3$ , or adding brood size as a co-factor, gave a poorer fit (Table 1b). The non-linear model with nestling age resulted in better fit than the non-linear model with season ( $\Delta\text{AIC} = 57.8$ ). In addition, the linear effect of season gave better fit than the non-linear one ( $\Delta\text{AIC} = 16.1$ ). There was a trend for the daily rate of prey items delivered to decrease with season (Table 3b; Fig. 6b).

The daily rate of lizards delivered per nestling was not significantly affected by nestling age or season, however a linear regression gave the best fit (Tables 1d, 2d and 3d; Fig. 7a, b). Adding  $\beta_2 x^2$ ,  $\beta_3 x^3$  or brood size as a co-factor



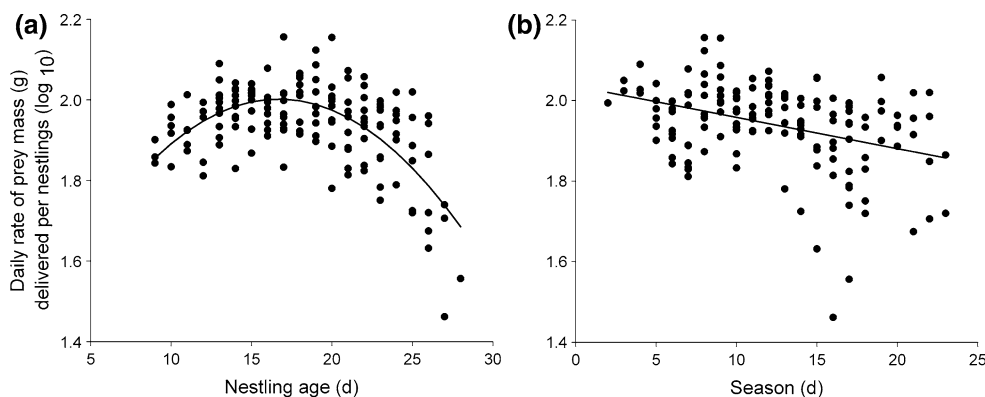
**Table 1** Model selection with a) the daily rate of prey mass delivered per nestling Eurasian Kestrel (*Falco tinnunculus*), b) the daily rate of prey items delivered per nestling, c) the daily average body mass of prey delivered, d) daily rate of lizards, e) shrews, f) voles, and g) birds delivered per nestling as response variable, and nestling age and brood size as explanatory variables, where  $x_1$  denotes nestling age,  $x_2$  denotes brood size and  $x_3$  denotes season (days elapsed after start of filming in the first nest)

| Test   | Model  | AIC  | $\Delta$ AIC |       |
|--|--|--|--------------|-------|
| a) Rate of mass  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | -316.85  | 0            |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | -309.12  | 7.73         |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | -303.53  | 13.33        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3$                                 | -260.88  | 55.97        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1$                                 | -259.81  | 57.04        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 | -245.84  | 71.01        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ | -226.17  | 90.68        |       |
|  | b) Rate of items   | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | -305.23      | 0     |
|  |  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | -297.01      | 8.23  |
|  |  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | -286.91      | 18.32 |
| $f(x) = \beta_0 + \beta_1 x_3$                                 |  | -263.62  | 41.61        |       |
| $f(x) = \beta_0 + \beta_1 x_1$                                 |  | -263.57  | 41.66        |       |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 |  | -247.48  | 57.75        |       |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ |  | -227.67  | 77.56        |       |
| c) Mass of items   |  | $f(x) = \beta_0 + \beta_1 x_3$                                 | 612.52       | 0     |
|  |  | $f(x) = \beta_0 + \beta_1 x_1$                                 | 615.75       | 3.23  |
|  |  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 | 621.71       | 9.19  |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | 623.71   | 11.19        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | 625.49   | 12.97        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | 632.30   | 19.78        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ | 635.74   | 23.22        |       |
|  | d) Rate of lizards   | $f(x) = \beta_0 + \beta_1 x_1$                                 | 19.65        | 0     |
| $f(x) = \beta_0 + \beta_1 x_3$                                 |  | 19.84  | 0.19         |       |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 |  | 25.85  | 6.2          |       |
| $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 |  | 30.59  | 10.95        |       |
| $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   |  | 37.43  | 17.79        |       |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ |  | 43.93  | 24.28        |       |
| $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ |  | 47.88  | 28.23        |       |
| e) Rate of shrews  |  | $f(x) = \beta_0 + \beta_1 x_1$                                 | 82.40        | 0     |
|  |  | $f(x) = \beta_0 + \beta_1 x_3$                                 | 84.33        | 1.93  |
|  |  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 | 96.01        | 13.61 |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | 96.34  | 13.95        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | 101.66   | 19.26        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ | 112.89   | 30.49        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | 113.27   | 30.88        |       |
|  | f) Rate of voles   | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | -142.32      | 0     |
|  |  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | -136.53      | 5.79  |
|  |  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | -127.20      | 11.05 |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 |  | -121.45  | 20.87        |       |
| $f(x) = \beta_0 + \beta_1 x_3$                                 |  | -120.63  | 21.69        |       |
| $f(x) = \beta_0 + \beta_1 x_1$                                 |  | -116.15  | 26.17        |       |
| $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ |  | -108.41  | 33.91        |       |
| g) Rate of birds   |  | $f(x) = \beta_0 + \beta_1 x_3$                                 | 31.59        | 0     |
|  | $f(x) = \beta_0 + \beta_1 x_1$                                 | 31.90  | 0.31         |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$                 | 42.44  | 10.85        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2$                 | 43.23  | 11.64        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2$   | 49.27  | 17.68        |       |
|  | $f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_1^3$ | 57.98  | 26.39        |       |
|  | $f(x) = \beta_0 + \beta_1 x_3 + \beta_2 x_3^2 + \beta_3 x_3^3$ | 60.78  | 29.19        |       |

$\Delta$ AIC = the difference in AIC-value between the best fitted model and a model resulting from adding or removing a variable. Therefore, the best model had  $\Delta$ AIC = 0.00

**Table 2** Parameter estimates of the best-fitted model for the effect of nestling age on a) the daily rate of prey mass delivered per nestling, b) the number of prey items delivered per day per nestling, c) the daily average body mass of prey items delivered, and d) the number of lizards, e) shrews, f) voles, and g) birds delivered per day per nestling, by Eurasian Kestrels ( $n = 151$  days, 10 breeding pairs)

|                    | Value  | SE     | df  | t value | p value |
|--------------------|--------|--------|-----|---------|---------|
| a) Rate of mass    |        |        |     |         |         |
| Intercept          | 1.313  | 0.083  | 139 | 15.77   | <0.001  |
| Age                | 0.083  | 0.093  | 139 | 8.88    | <0.001  |
| Age <sup>2</sup>   | -0.002 | 0.0003 | 139 | -9.78   | <0.001  |
| b) Rate of items   |        |        |     |         |         |
| Intercept          | 0.017  | 0.087  | 139 | 0.19    | 0.8484  |
| Age                | 0.079  | 0.010  | 139 | 8.13    | <0.001  |
| Age <sup>2</sup>   | -0.002 | 0.0003 | 139 | -8.45   | <0.001  |
| c) Mass of items   |        |        |     |         |         |
| Intercept          | 23.163 | 0.633  | 140 | 36.60   | <0.001  |
| Age                | -0.224 | 0.030  | 140 | -7.52   | <0.001  |
| d) Rate of lizards |        |        |     |         |         |
| Intercept          | -0.654 | 0.081  | 140 | -8.028  | <0.001  |
| Age                | 0.002  | 0.004  | 140 | 0.593   | 0.5542  |
| e) Rate of shrews  |        |        |     |         |         |
| Intercept          | -0.807 | 0.116  | 140 | -6.972  | <0.001  |
| Age                | 0.025  | 0.005  | 140 | 5.177   | <0.001  |
| f) Rate of voles   |        |        |     |         |         |
| Intercept          | 0.005  | 0.150  | 139 | 0.036   | 0.9712  |
| Age                | 0.084  | 0.0165 | 139 | 5.110   | <0.001  |
| Age <sup>2</sup>   | -0.003 | 0.0004 | 139 | -6.944  | <0.001  |
| g) Rate of birds   |        |        |     |         |         |
| Intercept          | -0.474 | 0.086  | 140 | -5.546  | <0.001  |
| Age                | -0.003 | 0.004  | 140 | -0.711  | 0.4782  |



**Fig. 3** The daily rate of prey mass delivered per nestling by Eurasian Kestrels in relation to **a** nestling age and **b** season (days elapsed after start of filming in the first nest). The regression is calculated from the parameter estimates of the best fitted lme model; **a**  $f(x) = 1.31$

(CI = 1.15–1.48) + 0.08 (CI = 0.06–0.10)  $x$  - 0.002 (CI = -0.003–(-) 0.002)  $x^2$  and **b**  $f(x) = 2.04$  (CI = 1.99–2.08) - 0.008 (CI = -0.01–(-) 0.005)  $x$

gave a poorer fit. Nestling age gave approximately the same fit as season ( $\Delta AIC = 0.19$ ).

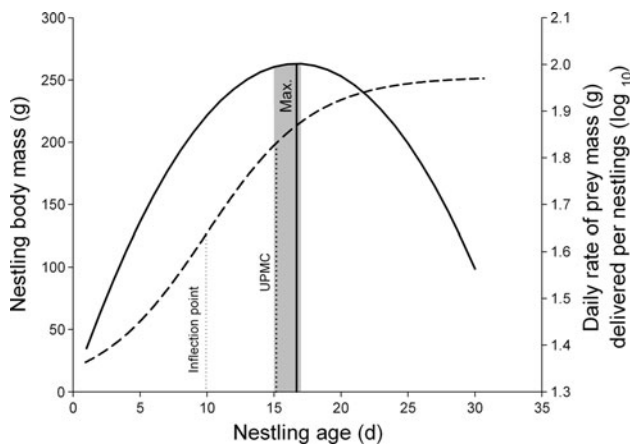
The daily rate of shrews delivered per nestling increased significantly with nestling age, and a linear regression gave the best fit (Tables 1e and 2e; Fig. 7c). Adding  $\beta_2x^2$ ,  $\beta_3x^3$  or brood size as a co-factor gave a poorer fit. However, because using season instead of nestling age as an explanatory variable in the model resulted in almost the same fit

as nestling age ( $\Delta AIC = 1.9$ ), we cannot be conclusive as to whether the increase in daily rate of shrews delivered per nestling was caused by nestling age or by a seasonal change in prey availability (Table 3e; Fig. 7d).

The daily rate of voles delivered per nestling was highly associated with nestling age, and a non-linear relationship gave the best fit (Tables 1d and 2d; Fig. 7e). Removing  $\beta_2x^2$ , adding  $\beta_3x^3$  or adding brood size as a co-factor gave a

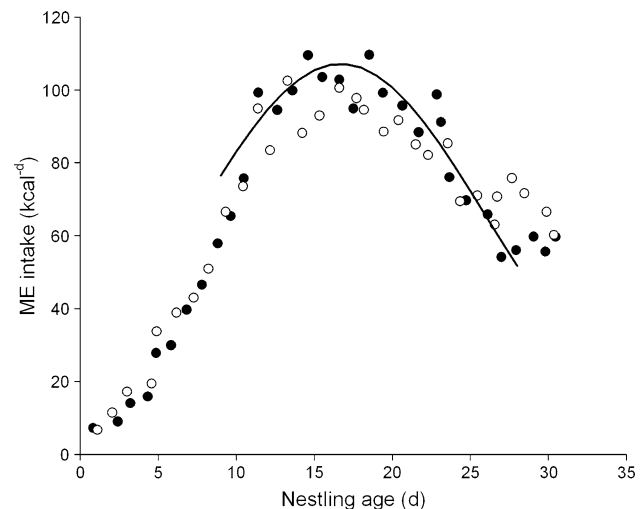
**Table 3** Parameter estimates of the best-fitted model for the effect of season (days elapsed after start of filming in the first nest) on a) the daily rate of prey mass delivered per nestling, b) the number of prey items delivered per day per nestling, c) the daily average body mass of prey items delivered, and d) the number of lizards, e) shrews, f) voles and g) birds delivered per day per nestling, by Eurasian Kestrels ( $n = 151$  days, 10 breeding pairs)

|                    | Value  | SE    | df  | <i>t</i> value | <i>p</i> value |
|--------------------|--------|-------|-----|----------------|----------------|
| a) Rate of mass    |        |       |     |                |                |
| Intercept          | 2.036  | 0.024 | 140 | 84.58          | <0.001         |
| Season             | -0.008 | 0.002 | 140 | -4.97          | <0.001         |
| b) Rate of items   |        |       |     |                |                |
| Intercept          | 0.694  | 0.025 | 140 | 28.08          | <0.001         |
| Season             | -0.002 | 0.002 | 140 | -1.57          | 0.1185         |
| c) Mass of items   |        |       |     |                |                |
| Intercept          | 21.785 | 0.443 | 140 | 49.15          | <0.001         |
| Season             | -0.226 | 0.030 | 140 | -7.71          | <0.001         |
| d) Rate of lizards |        |       |     |                |                |
| Intercept          | -0.631 | 0.058 | 140 | -10.850        | <0.001         |
| Season             | 0.002  | 0.004 | 140 | 0.456          | 0.649          |
| e) Rate of shrews  |        |       |     |                |                |
| Intercept          | -0.636 | 0.010 | 140 | -6.382         | <0.001         |
| Season             | 0.025  | 0.005 | 140 | 4.982          | <0.001         |
| f) Rate of voles   |        |       |     |                |                |
| Intercept          | 0.793  | 0.042 | 140 | 18.711         | <0.001         |
| Season             | -0.003 | 0.002 | 140 | -11.839        | <0.001         |
| g) Rate of birds   |        |       |     |                |                |
| Intercept          | -0.483 | 0.061 | 140 | -5.546         | <0.001         |
| Season             | -0.003 | 0.004 | 140 | -0.711         | 0.4782         |



**Fig. 4** The growth curve for Eurasian Kestrels nestlings (*dashed line*) obtained from Village (1990), with the inflection point and UPMC shown, in comparison with the curve for the daily rate of prey mass delivered per nestling obtained in the present study (*solid line*), with the point of maximum rate of prey mass delivered shown. The *shaded area* visualizes the approximate peak in metabolizable energy (ME) intake, taken from Kirkwood (1981)

poorer fit. The non-linear model with nestling age gave a much better fit than the non-linear model with season ( $\Delta\text{AIC} = 21.7$ ). In addition, the non-linear effect of season did not give a better fit than the linear one ( $\Delta\text{AIC} = 0.82$ ). The daily rate of voles delivered decreased significantly with season (Table 3d; Fig. 7f). From the function shown in Fig. 7e, the maximum daily rate of voles delivered per

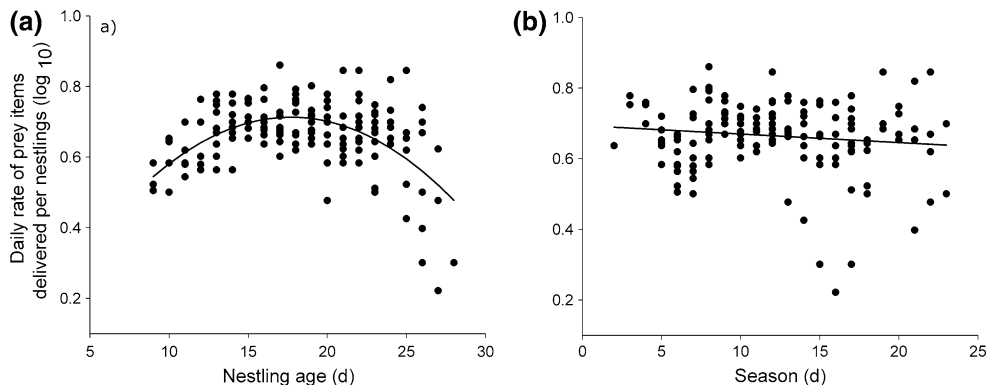


**Fig. 5** The metabolizable energy (ME) intake ( $\text{Kcal}^{-\text{day}}$ ) for Eurasian Kestrel nestlings, taken from Kirkwood (1981), based on nestlings on a diet of mice (*filled circles*) and nestlings on a mixed diet of mice and 1-day-old chickens (*open circles*), and the estimated ME curve ( $\text{Kcal}^{-\text{day}}$ ) for our data (*solid line*), given a conversion factor of  $1.067 \text{ kcal}^{-\text{g}}$  (Kirkwood 1981)

nestling was predicted to be 3.6 when the nestlings were 13.5 days old, compared to 3.1 when they were 9 days old, and 0.7 when they were 28 days old.

The daily rate of birds delivered per nestling was not significantly affected by nestling age or season, although a





**Fig. 6** The number of prey items delivered per nestling per day by Eurasian Kestrels in relation to **a** nestling age and **b** season (days elapsed after start of filming in the first nest). The regression is calculated from the parameter estimates of the best fitted lme model:

**a**  $f(x) = 0.017$  (CI =  $-0.15$ – $0.19$ ) +  $0.08$  (CI =  $0.06$ – $0.10$ )  $x - 0.002$  (CI =  $-0.003$ – $(-)$   $0.002$ )  $x^2$  and **b**  $f(x) = 0.69$  (CI =  $0.65$ – $0.74$ )  $-0.002$  (CI =  $-0.05$ – $0.001$ )  $x$

linear regression gave the best fit (Tables 1g, 2g and 3g; Fig. 7g, h). Adding  $\beta_2x^2$ ,  $\beta_3x^3$  or brood size as a co-factor gave a poorer fit. Nestling age gave approximately the same fit as season ( $\Delta AIC = 0.31$ ).

Size of items delivered

The daily average body mass of single prey items delivered decreased significantly with nestling age, and a linear regression gave the best fit (Tables 1c and 2c; Fig. 8a). Adding  $\beta_2x^2$ ,  $\beta_3x^3$  or brood size as a co-factor gave a poorer fit (Table 1c). However, because the linear effect of nestling age gave slightly poorer fit than a linear effect of season ( $\Delta AIC = 3.2$ ), the decrease in average body mass of single prey items was slightly less likely to be caused by nestling age than by a seasonal change in prey availability (Tables 2c and 3c; Fig. 8a, b.)

Thus, the adjustment of the daily rate of prey mass delivered per nestling to the age of the nestlings was due to parents changing both their prey item delivery rate and the prey size; the latter by providing smaller prey items as nestlings grew older.

Discussion

Fit between predicted and observed peak in delivery rate

Of the 3,595 recorded prey items delivered at the Kestrel nests, voles were most abundant by number, which fits with earlier findings for the Eurasian Kestrel in northern Europe (Korpimäki 1986; Village 1990; Korpimäki and Norrdahl 1991). The daily rate of prey mass delivered per nestling was highly associated with nestling age, which gave a

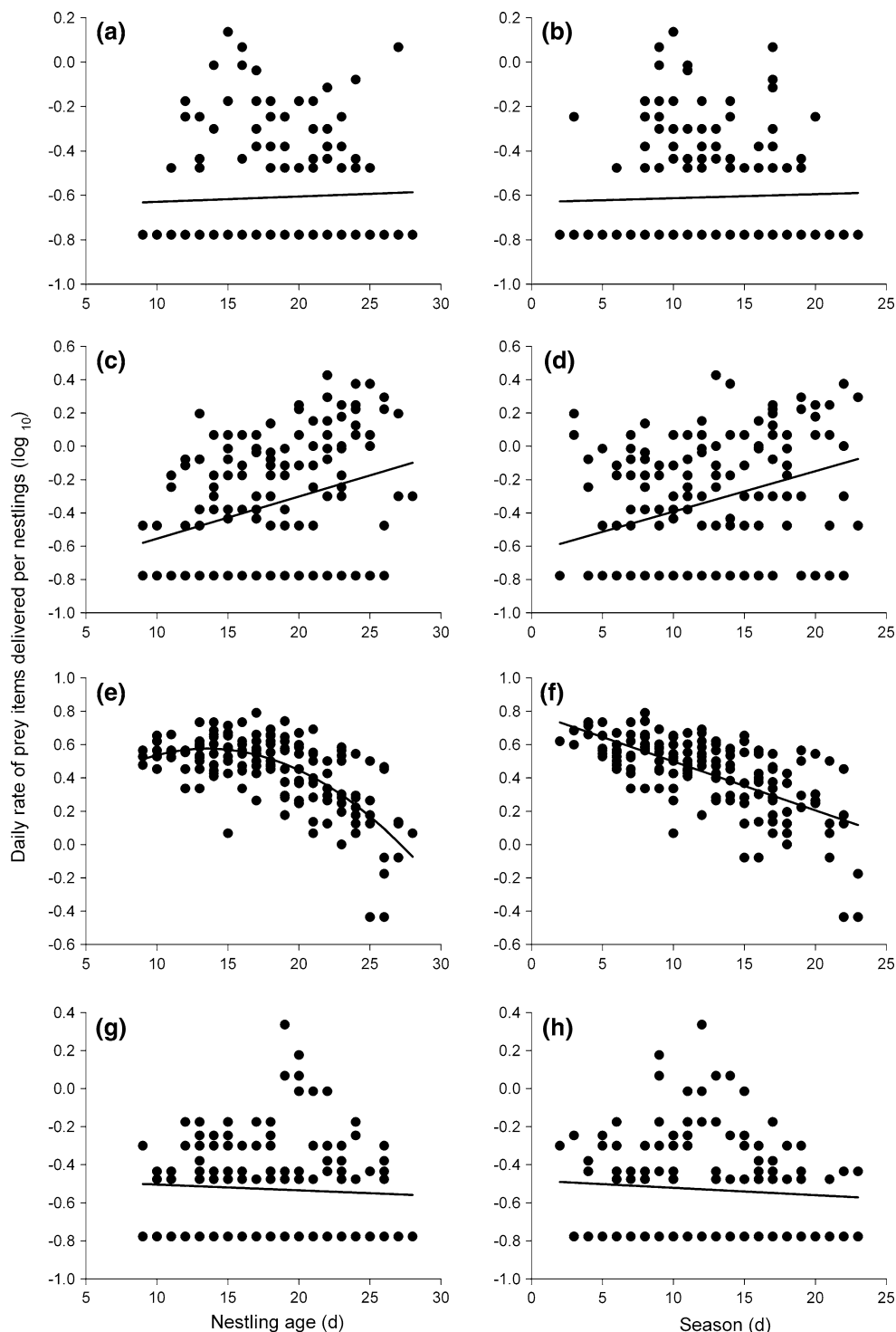
much better fit than season. The curve exhibited a typical positive “U-shape” and peaked when the nestlings were 17 days old. The timing of the peak daily rate of prey mass delivery was very close to the predicted time when growth settled down (UPMC; nestling age 15 days) and even closer to the predicted time of the peak in ME intake (nestling age 15–17 days). This indicates that the parent Kestrels adjusted their feeding effort to the demand of the nestlings (cf. Reid 1987; Ricklefs 1987; Mauck and Grubb 1995; Weimerskirch et al. 1995; Navarro and González-Solis 2007; Erikstad et al. 2009). A similar pattern has been found for passerine birds (Grundel 1987; Blondel et al. 1991; Barba et al. 2009).

There was a slight difference (1.5 days) between the estimates of predicted age (15.2 days) and observed age (16.7 days) for the peak in prey mass delivery rate. This may have been caused by a peak in food demand actually occurring slightly later than the time when growth levelled off, e.g., due to continued growth of muscles and to rapid growth of feathers (Kirkwood 1981). Also, increased activity of the nestlings as they grow older, including unassisted feeding and sibling competition, may have an effect (Village 1990). Hence, the body mass of the nestlings may in itself be an insufficient index for the energy demand (Kirkwood 1981).

Brood size did not contribute to the model, probably because the variation in brood size among the ten breeding pairs sampled was low.

In our study, the maximum daily rate of prey mass delivered per nestling was  $100.5 \text{ g}^{-\text{day}}$  and was achieved when the nestlings were 16.7 days old, compared to  $71.7 \text{ g}^{-\text{day}}$  when they were 9 days old and  $48.4 \text{ g}^{-\text{day}}$  when they were 28 days old. Kirkwood (1981) recorded a maximum daily consumption of  $100 \text{ kcal}^{-\text{day}}$  for hand-raised individual Kestrel nestlings at the age between 10 and

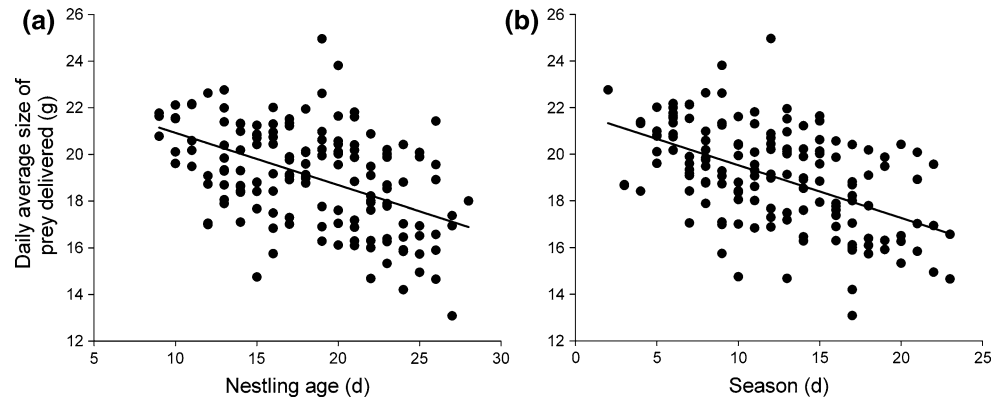
**Fig. 7** The number of prey items delivered per nestling per day by Eurasian Kestrels in relation to nestling age and season (days elapsed after start of filming in the first nest) for each prey type separately; **a–b** lizards, **c–d** shrews, **e–f** voles, and **g–h** birds. The regression is calculated from the parameter estimates of the best fitted lme model; Because the data set contained zero values a constant was added to each data set (lowest value recorded; 0.1667) before transforming. **a**  $f(x) = -0.653$  (CI =  $-0.81-0.49$ ) + 0.002 (CI =  $-0.005-0.010$ )  $x$ , **b**  $f(x) = -0.631$  (CI =  $-0.75-(-)0.52$ ) + 0.002 (CI =  $-0.006-0.10$ )  $x$ , **c**  $f(x) = -0.807$  (CI =  $-1.04-(-)0.58$ ) + 0.03 (CI =  $0.02-0.04$ )  $x$ , **d**  $f(x) = -0.636$  (CI =  $-0.83-(-)0.44$ ) + 0.02 (CI =  $0.01-0.3$ )  $x$ , **e**  $f(x) = 1.296$  (CI =  $1.20-1.39$ ) + 0.004 (CI =  $-0.006-0.014$ )  $x - 0.0003$  (CI =  $-0.0005-0.00003$ )  $x^2$ , **f**  $f(x) = 0.79$  (CI =  $0.71-0.87$ ) - 0.029 (CI =  $-0.03 - (-)0.02$ )  $x$ , **g**  $f(x) = -0.474$  (CI =  $-0.64-(-)0.31$ ) - 0.003 (CI =  $-0.01-0.05$ )  $x$  and **h**  $f(x) = -0.483$  (CI =  $-0.30-(-)0.36$ ) - 0.004 (CI =  $-0.01-0.004$ )  $x$



20 days, equivalent to  $94 \text{ g}^{-\text{day}}$  because the conversion is  $1.067 \text{ kcal}^{-\text{g}}$  (Kirkwood 1981). The daily consumption per nestling then fell to  $50-60 \text{ kcal}^{-\text{day}}$  (i.e.  $47-56 \text{ g}^{-\text{day}}$ ) at the age when fledging normally occurs (28–32 days). Thus, the maximum value recorded by Kirkwood (1981) was  $6.5 \text{ g}^{-\text{day}}$  (6 %) lower than ours for nestlings 10–20 days

old, which fits well. Masman et al. (1989) found a corresponding value of  $66.8 \text{ g}^{-\text{day}}$  for hand-raised nestlings in the laboratory. Masman et al. (1989) conducted their experimental feeding when nestlings were 6–7 days old, which means that an estimate being  $4.9 \text{ g}^{-\text{day}}$  (5 %) lower than ours for 9-day-old nestlings fits well.

**Fig. 8** The daily average body mass of prey items delivered by Eurasian Kestrels in relation to **a** nestling age and **b** season. The regression is calculated from the parameter estimates of the best fitted lme model; **a**  $f(x) = 23.16$  (CI = 21.91–24.41)  $- 0.22$  (CI =  $-0.28$ – $(-0.17)$ )  $x$  and **b**  $f(x) = 21.79$  (CI = 20.91–22.66)  $- 0.23$  (CI =  $-0.28$ – $(-0.17)$ )  $x$



### Components of delivery rates and dynamics of feeding strategies

At the nestling age when the rate of prey mass delivered peaks, the female often participates in hunting (Village 1990; Fargallo et al. 2003), enabling the parents to deliver more prey per day, and thus better matching the nestlings' food demands. By the time the nestlings were 23 days old, the parents had settled their delivery rate down and provided a similar daily mass as when the nestlings were 12 days old. The adjustment of the daily rate of prey mass delivered was mostly affected by parents adjusting their daily rate of prey items delivered, but also affected by providing smaller prey items as the nestlings grew older.

We found that the change in average prey size was equally well explained by time of season as by nestling age. It is difficult to disentangle whether the change in average prey size is a result of changes in the availability of different prey types (in particular voles and shrews) or the result of a preference for smaller prey items that allow unassisted feeding by the offspring. As long as the male provides all prey alone, he may be more likely to deliver larger items (in particular voles) at a lower rate to maintain the amount of delivered mass required. Larger items are also more efficient to ingest than smaller ones as long as the female dismember the prey and feeds the nestlings (Steen 2010). However, when Kestrels provide larger prey items, like voles and birds, the female needs to dismember the prey and cannot contribute to the provisioning (cf. Slagsvold and Sonerud 2007). When the nestlings are about 2 weeks old, the female starts foraging (Village 1990; Fargallo et al. 2003), and the parents may then together achieve a higher delivery rate. They are thus more likely to meet the nestlings' food demand even with smaller prey items, which the nestlings are able to ingest unassisted. The onset of switching strategies may not only depend on the nestlings' ability to feed unassisted on small prey items, as parents may choose to continue bringing large prey items at a low frequency, given that the benefit of female efficiently

dismembering the prey are greater than the costs of female being confined to the nest. Once the increasing offspring demand cannot be met anymore in this way, parents may switch to the strategy where both parents provision with small prey items at a higher rate.

When the nestlings become older and their food demand declines, the parents become even more likely to meet this demand by delivering small prey. As a consequence, we would expect Kestrels to deliver smaller prey items as the nestlings grow older. This may also help to avoid that dominant offspring monopolizing prey items (Mock and Parker 1997; Fargallo et al. 2003). Further, when the nestlings become 3 weeks old, they are quite agile, and the nest cavity becomes more crowded due to the size of the nestlings (personal observation). This may cause difficulties for the female to spend time partitioning large prey inside the nest cavity.

Although the availability of different prey types may affect the change in the delivery rates of these prey types, the daily rate of voles delivered per nestling was highly associated with nestling age, which gave a much better fit than time of the season, exhibiting a "U-shaped" inverted curve, where the delivery rate of voles increased until the nestlings were about 14 days old. This indicates that the parents adjusted their feeding effort to the age of the nestlings (cf. Reid 1987; Ricklefs 1987; Mauck and Grubb 1995; Weimerskirch et al. 1995; Navarro and González-Solis 2007; Erikstad et al. 2009). However, the observed decrease in vole delivery rate during the late nestling phase may have been a consequence of a decrease in vole availability, e.g., due to increase in the height and density of the vegetation cover that protects the voles against raptors (cf. Arroyo et al. 2009). This has been suggested as the explanation for a similar seasonal change in the vole–shrew ratio in the diet of nesting Eurasian Kestrels and Tengmalm's Owls (*Aegolius funereus*) in Finland (Korpimäki 1985, 1986). In addition, the observed decrease in vole delivery rate may have been a consequence of food depletion, as shown for Lesser Kestrels (*Falco naumanni*)

breeding in colonies and feeding mostly on insects (Bonal and Aparicio 2008).

The daily delivery rates of lizards and birds were not affected by nestling age or by season. The daily rate of shrews delivered increased with nestling age, and tended to increase as the season progressed. Thus, because time of the season gave almost the same fit as nestling age, we cannot be conclusive as to whether the increase in daily rate of shrews delivered per nestling was caused by nestling age or by shrews being taken more throughout the breeding season because voles became less available (Korpimäki 1985, 1986). Environmental restrictions, such as low prey availability, may impair parental effort and optimal nestling development (e.g., Hakkarainen et al. 1997; Naef-Daenzer and Keller 1999; Naef-Daenzer et al. 2000; Mägi et al. 2009). However, parents may be capable of countering lower prey availability by increasing their parental effort or by switching to alternative prey to ensure optimal nestling development (e.g., Tremblay et al. 2005; Zarybnicka et al. 2009).

Overall, because the delivery rate of prey mass, as well as prey items, was better explained by the non-linear effect of nestling age than by the non-linear and the linear effect of time of season, our results suggest that the parents increased their parental effort as the nestling grew until a peak during the middle of the nestling period. The decrease in parental effort thereafter may have been caused by reduced food demands of the nestling, or by a reduced availability of voles. If the latter was the case, we would assume that, until the nestlings were about 2 weeks old, the parental provisioning was less constrained by the availability of voles. During this period, the male provides most of the prey, while later on the female may also hunt to ensure sufficient amounts of food for the whole family (cf. Durant et al. 2004).

## Conclusion

In conclusion, the daily rate of prey mass delivered by parent Kestrels was highly associated with nestling age. It peaked only marginally later than the predicted point where nestling growth is “settling down”, and also matched the predicted peak in the nestlings ME intake. This indicates that the parents adjusted their feeding effort to the changing needs of the nestlings. The daily rate of the number of prey items delivered peaked later than did the rate of prey mass delivered, because the daily average body mass of prey items declined linearly with nestling age. The latter is the opposite to what has been found in most passerine birds, where prey size increases with nestling age because the ingestion ability of the young improves as they grow (Slagsvold and Wiebe 2007). Like other raptors, Kestrel

parents are able to dismember large prey, and are therefore relieved from this swallowing constraint. However, when the nestlings start to feed unassisted, their lower dismembering skill, and reduced ingestion ability, may affect parental prey choice (cf. Steen et al. 2010). This may explain why we found smaller prey items when the nestlings handled prey unassisted than when they were fed by the female. However, we cannot decide whether the decrease in average body mass of prey delivered during the late nestling phase was caused by nestling age, or by a decrease in vole availability. Thus, future studies should measure the instant availability of small mammals to Kestrels continuously throughout the breeding season.

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