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Abstract
The growth and the food requirements of the European barn owl (Tyto alba) were studied in three groups of captive chicks. One group of chicks, raised in ad libitum food conditions by their parents, was used to measure body mass and linear growth of a number of structural body components at their characteristic growth rate. A second group of chicks, hand-raised with food ad libitum until fledging, was used to measure food requirement at the characteristic growth rate. A third group, hand-raised with restricted feeding, was used to specify the plasticity of growth and food requirements still compatible with a normal development at fledging. Chicks of both sexes of the first two groups experienced an overshoot in body mass (maximum of 391 g) when approximately 40 days old, followed by a decrease (to a mass of 314 g) until fledging at 60 days old, giving a mass distribution with age in the form of a bell-shaped curve. The daily food intake also showed a bell-shaped curve with a peak value of 80 ± 10 g of fresh mice/day when the body mass was maximum. The decrease of food intake preceding fledging was spontaneous. The average daily food intake was 67 ± 17 g/day between the ages of 20 and 60 days. In the restricted feeding group, however, the same timing for linear growth and fledging was achieved with a 17% reduction of daily food intake. For the same fledging body mass as the ad libitum fed group, there was a flattening of the body mass curve. The significance of the overshoot in body mass and food intake is discussed in terms of the chick’s and brood’s advantages and in terms of parental investment in this species with hatching asynchrony.

Key words: Tyto alba, raptors, hatching asynchrony, brood requirement, logistic model

INTRODUCTION
In numerous bird species, the postnatal growth shows a bell-shaped curve of body mass characterized by a peak body mass heavier than that of an adult and a subsequent decrease prior to fledging (review in Ricklefs, 1968). This peak has been interpreted as a fat accumulation (Lacombe, Bird & Hibbard, 1994) that must be reduced prior to fledging by a reduction of food intake (Ricklefs, 1968; Ricklefs & Schew, 1994). The accumulation of body reserves has been considered as an adaptation to stochastic variation in foraging experienced by parents (the energy insurance hypothesis). However, there is no direct data to assert that the starvation period prior to fledging is not an endogenous phenomenon independent of the chicks’ food availability.

Hatching asynchrony, which is a breeding strategy often observed in raptors, is generally interpreted as an adaptation to stochastic variation in food availability (brood reduction hypothesis; Lack, 1968). Different species also show the characteristic bell-shaped growth curve. In the American kestrel Falco sparverius (Lacombe et al., 1994) it was demonstrated that a 10% reduction of energy intake causes a disappearance of the overshoot of body mass without any consequence for body mass or body lengths at fledging time. In raptors with a large clutch size (e.g. barn, snowy or short-eared owl) and asynchronous hatching, we might expect the effects of fluctuations in food availability to be intricate since it could affect each chick according to birth rank. In these situations, the possibility of modifying the growth could be an advantage for chick survival and/or for parental effort.

In the barn owl (Tyto alba), the fledglings (yearly mean range 1.5–5.0; Taylor, 1994) leave the nest after more than two months of growth. Interestingly, fledging occurs about 20 days after attainment of peak body mass (at 40 days of age: Pickwell, 1948; Schönfeld & Girbig, 1975; Baudvin, 1986; Wilson, Wilson & Durkin, 1987; Langford & Taylor, 1992; Taylor, 1994). Barn
owls are also known for yearly fluctuations of breeding success (number of breeding pairs, second clutches, clutch size) and nest mortality (Baudvin, 1978; Wilson, Wilson & Durkin, 1986; Taylor, 1994).

We investigated the food requirements of captive chicks during growth and the consequences of food restriction on their growth parameters and growth curve shape. Studies in captivity allow measuring growth at its characteristic rate, which is possible only when food availability is high (Ricklefs, 1973; Lenton, 1984). To understand the influence of food intake on chick growth, we compared groups of chicks raised with food ad libitum with another group restricted in feeding. The major objectives of this study were: (i) to study the chick growth and the corresponding food intake in situations of high food availability; (ii) to learn if the decrease in body mass observed before fledging is spontaneous or results from a lessening of food availability; and (iii) to determine the influence of restricted feeding on chick development and the impact of this food restriction on the foraging investment of the parents.

MATERIALS AND METHODS

This study was performed on 30 barn owl chicks from a breeding programme conducted since 1985 in the laboratory. The breeding programme was begun with 3 chicks born in captivity from road-injured birds kept in a rescue centre. Whenever possible, new individuals of the same origin were added. Each pair of owls was housed in outside aviaries where a nest box was installed. The pairs bred at least once each year.

According to the type of rearing, we have constituted 3 groups of chicks as explained below.

Groups of birds

The growth of 50 chicks was followed for a first group. Subgroups were constituted after fledging, based on the possibility of getting correct weighings (see below). We selected 10 females out of 21 and 10 males among 29. In this first group (Control group, \( n = 20 \)), chicks were raised by their parents. The 10 males came from 5 different broods and 3 pairs of adults. The 10 females came from 6 different broods and 4 pairs of adults. Brooding occurred between March and July in outside aviaries (5 \( \times 4 \times 2.5 \) m), the temperature ranging from 10–28°C. Since the chicks were raised by their parents, they were considered wild. This group was used as the Control group. In fledging barn owls, sexing by external features is not always reliable (Taylor, 1994; Handrich, pers. obs.). Thus, when necessary, sexing was made by laparoscopic examination of gonads under halothane anaesthesia. The procedure complied with current laws of French authorities: Authorization of the Ministère de l’Agriculture et de la Forêt followed by acceptance of the research programme by the Ministère de l’Environnement.

In the second group (Ad libitum group, \( n = 5 \)), the chicks (2 males and 3 females) came from 3 different broods and 3 pairs of adults. Examination of the daily food intake began when the chicks were 20 days old, the age of thermal emancipation (Taylor, 1994). It was then possible to house the chicks separately and alone in open-topped nest boxes (25 \( \times 25 \times 50 \) cm) without the need of female constant care. The boxes were put in a climatic chamber that maintained the natural photoperiod (experiment conducted in June) and an ambient temperature of 25±1°C. The thermal neutrality zone of the barn owl is 22.5–33°C (Johnson, 1974; Edwards, 1987).

In the third group (Restricted group, \( n = 5 \)), the chicks (3 males and 2 females) came from 3 different broods and 3 pairs of adults. The chicks were raised under the same conditions as the Ad libitum group except that they were raised alone from their 12th day.

This corresponds to the time when the female starts to forage during bad food years (Taylor, 1994). To limit potential heat loss, cotton was added inside the nest boxes.

Feeding

Chicks of the Control group were fed by their parents with laboratory mice (Mus musculus). Daily, live mice were put in the aviary at 16:00. At the same hour, we checked food availability in the nest boxes so that we could adjust the number of mice given.

Chicks of the Ad libitum group were also provided with freshly killed mice at 16:00 each day. At 20 days old, when the experiment started, they were able to eat an entire mouse on their own (Taylor, 1994). Since mice were always available when food was added, they were considered fed ad libitum.

Chicks of the Restricted group were fed by hand with pieces of fresh mice and thus the experiment could be begun on 12-day-old chicks. In contrast with the Ad libitum group, the meals were given 3 times daily during daytime only (09:00, 12:30 and 16:00). The food was ad libitum during meals only and not between. During night-time (16:00–09:00), the chicks were given no food. Since the meal-to-pellet interval for owls is 10–13 h (Duke, Evanson & Jegers, 1976), and is certainly less for chicks fed with torn mice, the feeding was not ad libitum but restricted. At the age of 20 days, the chicks could feed by themselves and eat the food stored inside the nest. Prior to 20 days old, the chicks need to be fed by the female. As a consequence, chicks younger than 20 days have no food available when the female forages. They will be fed only when the female stays in the nest to rest during daytime (Durant, pers. obs.). This situation was simulated in the Restricted group.
Measurements

Body mass

The chicks were weighed to the nearest 0.1 g using a Sartorius scale every day before the meal at 16:00 for the Ad libitum group and the Restricted group but only once every 2 days at the same hour for the Control group. We verified by checking the nest box before the weighing that the last pellet was made. When no pellet was found, the chick’s belly was gently felt. This superficial examination was done with great care and no apparent consequences were observed for the birds. Unreliable weighings (weighing with either pellet or meal in stomach) were discarded.

Body size

Body length (humerus, tarso-metatarsus, tibia, rectrix and remex) were measured with callipers to the nearest mm on the Ad libitum and Control groups during the afternoon weighing. Feather length corresponded to the measurement of feathers plus the remnant of the sheath which sticks out of the epidermis. Remex length was taken to be the length of the tenth primary remex (P10). Rectrix length was the length of the sixth rectrix from the right (R1).

Growth curves and statistical analysis

To compare the growth data among groups and chicks, we used the graphical method of Ricklefs (1967). A logistic equation was fitted to both body mass and linear growth data for each individual (SigmaPlot 5.0 software from Jandel Scientific). Even if the logistic equation does not describe a bell-shaped curve, we used it for comparison purposes with other studies. Since the body mass curve is bell-shaped, and because the logistic equation describes a sigmoid curve, we divided the data into 2 parts. The cut was made at the peak of body mass, the 2 delimited parts approximating to a sigmoid form well described by the logistic equation:

\[ Y(t) = A \left[ 1 + e^{-K (t - t_i)} \right]^{-1} \]

where \( Y(t) \) = body mass (g) or length (mm) of the chick at age \( t \) (days), \( A \) = asymptotic body mass (g) or component length (mm), \( K \) = growth constant (1/day), \( t_i \) = inflection point of the growth curve (days).

The comparisons were made with the 3 parameters obtained with the fitting (\( A, K \) and \( t_i \)) for each individual. The mean values of individual parameters and their standard deviations were then calculated.

Statistical analyses were performed with non-parametric tests because of the small group sizes. The Mann–Whitney U-test (MWU-test) was used for the comparisons between sexes, the Kruskal–Wallis test to compare the different groups and the Wilcoxon test to compare changes in the same group.

RESULTS

Growth in the Control group

Body mass differences between sexes

Although females tended to have an asymptotic body mass greater than males (Table 1 and Fig. 1), the chicks exhibited no significant sex differences for the fitted parameters (MWU-test, \( P>0.5 \)). Data for males and females were therefore pooled (Table 2 and curve in Fig. 1).

Body mass growth

The chicks were hatched with a body mass of 13.9±1.4 g. The gain of mass was almost linear between the 8th and 27th day (growth rate of 14.3±1.3 g/day). Near the 40th day, the body mass reached a maximum value of 391.0±11.5 g (Table 2). Chicks grew from 10 to 90% of their maximum weight in 25 days (the \( t_{10-90} \) index of Ricklefs, 1968). Between the 40th day and fledging (60 to 65th day; Pickwell, 1948; Taylor, 1994), the birds lost weight. Fledging body mass (314.4±26.5 g) was significantly less (Wilcoxon test, \( P<0.001 \)) than the maximum weight.

Linear growth

Bone and feather growth (Table 1) exhibited no
significant difference in the fitted parameters between sexes (MWU-test, \( P > 0.1 \) for the bones and \( P > 0.1 \) for the feathers). Therefore, data for males and females were pooled (Table 2 and Fig. 2).

Humerus, tibia and tarso-metatarsus lengths were \( 12.0 \pm 6.4 \), \( 15.2 \pm 5.4 \) and \( 11.6 \pm 4.4 \) mm, respectively, at hatching. The three bones had nearly finished their growth when the chicks were at their maximum weight (98, 98 and 95\% for humerus, tibia and tarso-metatarsus, respectively) and had reached full size at fledging. The remex (P10) began to grow out of the skin near the 7th day and continued until the chicks left the nest. At fledging, the remex had reached only 80\% of the asymptotic length. The rectrix (R1) began its growth later than the remex at around the 17th day but grew more quickly, with a length equal to 88\% of the asymptotic value at fledging. At the maximum of body mass, the two types of feathers had reached only 47\% (P10) and 50\% (R1) of their final length.

**Food intake and effect of diet on growth rate**

There was also no significant difference for the fitted parameters between the Control and Ad libitum groups (MWU-test, \( P > 0.1 \) in Table 3). We therefore considered the Ad libitum group instead of the Control group, for which we did not have the measurement of food intake, as the reference for the relationship between food intake and the characteristic growth.

The mean daily food intake was calculated over 4-day intervals (Fig. 3a). In the Ad libitum group, daily food intake increased, respectively, from the 20th to the 31st day from hatching from \( 63 \pm 5 \) to \( 80 \pm 10 \) g/day. There was then a spontaneous decrease to \( 60 \pm 9 \) g/day around the 60th day. The maximum and the minimum values of food intake were significantly different (Wilcoxon test, \( P < 0.001 \)).

In the Restricted group, there was no significant change of daily food intake during the studied period of

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**Table 2.** Fitted parameters obtained by the logistic equation for different growth variables in the Control group (\( n = 20 \)). The equation was fitted to each individual chick. \( A \) is the asymptote, \( K \) the growth constant and \( t_i \) the inflection point. The values are means ± S.D.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter</th>
<th>( A ) (g, mm)</th>
<th>( K ) (day(^{-1}))</th>
<th>( t_i ) (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>390.6 ± 11.5</td>
<td>0.177 ± 0.003</td>
<td>17.18 ± 1.35</td>
<td></td>
</tr>
<tr>
<td>Humerus length</td>
<td>91.59 ± 0.65</td>
<td>0.150 ± 0.003</td>
<td>12.41 ± 0.18</td>
<td></td>
</tr>
<tr>
<td>Tarso-metatarsus length</td>
<td>73.35 ± 0.61</td>
<td>0.132 ± 0.004</td>
<td>12.64 ± 0.22</td>
<td></td>
</tr>
<tr>
<td>Tibia length</td>
<td>96.57 ± 0.61</td>
<td>0.140 ± 0.003</td>
<td>11.37 ± 0.16</td>
<td></td>
</tr>
<tr>
<td>Rectrix length (R1)</td>
<td>109.5 ± 0.60</td>
<td>0.140 ± 0.003</td>
<td>40.33 ± 0.17</td>
<td></td>
</tr>
<tr>
<td>Remex length (P10)</td>
<td>201.9 ± 0.83</td>
<td>0.099 ± 0.001</td>
<td>40.37 ± 0.15</td>
<td></td>
</tr>
</tbody>
</table>

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**Fig. 1.** Body mass (a) from hatching to maximum weight and (b) from maximum weight to 90 days of age (data for 10 males and 10 females of the Control group and the logistic curve is for the sex-pooled data). The cross-hatched part of (b) represents data already shown in (a).
growth (maximum vs. minimum food intake, Wilcoxon test, $P = 0.09$), despite a high value of $57 \pm 15$ g/day on the 36th day. On a daily basis, the food intake of the Restricted group was significantly lower than in the Ad libitum group (MWU-test, $P < 0.001$). The food intake during the studied period from age 20 to 60 days in the Ad libitum group was on average $67 \pm 17$ g/day, i.e. 17% higher than the Restricted group with a maximum difference of 28.5% at the Ad libitum peak of food intake. The major influence of the restricted diet on body mass growth was the flattening of the bell-shaped curve observed with the ad libitum diet (median asymptote significantly lower, Kruskal–Wallis test, $P < 0.003$; Dunn’s test $P < 0.05$; no significant difference for the growth parameters $K$ and $t_i$, Kruskal–Wallis test, $P = 0.051$ and $P = 0.651$, respectively). Body mass at fledging time was calculated using the fitted equation for each chick. For the Restricted group, the value was $298.9 \pm 10.6$ g and for the Ad libitum group $317.7 \pm 23.9$ g. There was no difference in fledging body mass or its timing (MWU-test, $P > 0.1$ and Fig. 3b). The body mass loss between the asymptote and the fledging mass was $72.9 \pm 17.8$ g for the Ad libitum group which is significantly different from the $39.7 \pm 13.3$ g of the Restricted group (MWU-test, $P = 0.016$). Feather growth parameters showed no significant difference between the two groups (MWU-test; $A$, $P = 0.305$; $K$, $P = 0.176$; and $t_i$, $P = 0.176$).

### DISCUSSION

Compared to previous data (Wilson, Wilson & Durkin, 1987; Langford & Taylor, 1992; Taylor, 1994), the new information brought by the present study on barn owls was the measurement of the chicks’ food intake during their growth. Our data enhance our knowledge on the significance of the bell-shaped curve encountered in many species of birds (Ricklefs, 1968; Olendorff, 1974; Korpimäki, 1981; Dijkstra, 1988; Lessells & Avery, 1989; Holt, Melvin & Steele, 1992; Hamer & Hill, 1993; Lacombe et al., 1994; Starck, König & Gwinner, 1995; Kristan, Gutiérrez & Franklin, 1996) by showing:

I. That the decrease in body mass that occurs before fledging is not due to a reduction of parental care but results from a spontaneous reduction of food intake.

II. That a normal development occurs when the bell-shaped growth curve, i.e. the overshoot, is flattened by a reduction of food availability.

### Characteristic growth rate of the barn owl

Field data are available on body mass and linear growth for various subspecies of barn owls (Pickwell, 1948; Ricklefs, 1968; Schönfeld & Girbig, 1975; Lenton, 1984; Wilson et al., 1987) and for the present subspecies, *Tyto alba* (Guérin, 1928; Bunn, Warburton & Wilson, 1982; Baudvin, 1986; Langford & Taylor, 1992; Taylor, 1994). There is no difference between our data and those found in other studies conducted on a larger number of birds for the same subspecies (for parameters calculated from Guérin’s data 1928; for the asymptotic body mass, Baudvin, 1986; Langford & Taylor, 1992; Taylor, 1994; for the $t_{10-90}$ index, De Jond in Wijnandts, 1984). Therefore, we may conclude that our Ad libitum group exhibited the normal, characteristic, growth rate (Ricklefs, 1973; Lenton, 1984).

### Table 3

<table>
<thead>
<tr>
<th>Group</th>
<th>$n$</th>
<th>Adult body mass (g)</th>
<th>$A$ (g)</th>
<th>$K$ (day$^{-1}$)</th>
<th>$t_i$ (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>20</td>
<td>317</td>
<td>$390.6 \pm 11.5^a$</td>
<td>$0.177 \pm 0.003^a$</td>
<td>$17.18 \pm 1.35^a$</td>
</tr>
<tr>
<td>Ad libitum</td>
<td>5</td>
<td>337</td>
<td>$390.6 \pm 35.0^a$</td>
<td>$0.174 \pm 0.016^a$</td>
<td>$17.67 \pm 1.37^a$</td>
</tr>
<tr>
<td>Restricted</td>
<td>5</td>
<td>317</td>
<td>$338.7 \pm 8.26^b$</td>
<td>$0.215 \pm 0.053^a$</td>
<td>$16.26 \pm 2.03^a$</td>
</tr>
</tbody>
</table>

Fig. 2. Linear growth of various bones and feathers expressed as a percentage of asymptote or in mm for the Control group (logistic curves).
Our growth constant (K, body mass) for the European barn owl was 0.177 which is low if we consider the adult body size of the bird (Ricklefs, 1968). The European barn owl nests inside buildings which give a protection against predators and climatic variations. Furthermore, the female stays continuously with her brood during the first 20 days of development. Ricklefs (1968) found that hole-nesting birds such as barn owls usually have a lower growth rate than open-nesting birds. This could explain the difference of growth rate encountered with other owl species of similar size (Asio otus, Wijnandts, 1984, or Asio flammeus, Holt et al., 1992). On the other hand, the characteristic growth rate certainly has an endogenous origin. The barn owl is a species originating from warm climates (Taylor, 1994). This could explain its low growth rate and longer breeding period in comparison with more northern species such as the short-eared or the long-eared owl.

The Restricted group's diet simulates food intake of the youngest chick of a wild brood

In barn owls, 20 days is a critical age in development. Chicks become thermally emancipated (Taylor, 1994) and begin to eat prey by themselves. Before 20 days, the chicks need female care to be fed with torn prey. The female starts to forage for long periods at night when her youngest chick is between 12 and 20 days old (Bunn et al., 1982; Taylor, 1994) and still unable to eat by itself. Consequently, when the female is foraging, the youngest chick may suffer food restriction because of its incapacity to eat the food available in the nest. The youngest chick can take its first meal of the day only when the female stays in the nest at the end of the night to rest, a period when chicks seldom eat (Durant, pers. obs.). The youngest chick will then eat only during daytime (female resting period) like the chicks of our Restricted group. Thus, our Restricted group reproduces the situation experienced by the youngest chick in the wild. Since there was no apparent influence of this hypocaloric diet on the timing of development in this experimental group, we may also assume that there is none for the youngest fledgling of a wild brood in a year of normal prey availability.

Food intake of captive birds is lower than in the field

For chicks fed ad libitum, we calculated the average daily food intake to be 67 ± 17 g/day (Fig. 3a). This average value is overestimated because the calculation was made from the age of 20 days to fledging, therefore not taking into account the period of lesser food intake the first few days after hatching. From field observations (Durant, Gendner & Handrich, 1996), we estimate the average number of prey brought to the nest per chick to be 2.9/day. With an average prey's mass of 23.6 g (Durant, pers. obs.), each chick could obtain 68.4 g a day, which is nearly the same as the average daily food intake we calculated. The main prey of the European barn owl during the brooding period in eastern France is the common vole Microtus arvalis (Muller, 1991). Using the average caloric values for laboratory mice of 7.35 kJ/g (Handrich, Nicolas & Le Maho, 1993) and for the common vole of 7.74 kJ/g (Wijnandts, 1984), we could calculate energy intake. The gross energy intake for wild chicks (529.4 kJ/day) was then 7.4% greater than for captive chicks (493 kJ/day). This difference might be due to an over-estimation of the number or size of prey actually delivered to a chick in the field. Indeed, food storage is frequently observed in the nest (Baudvin, 1980; Bunn et al., 1982; Taylor, 1994).

Another explanation could be a problem of dehydration for the wild chicks because the temperature in certain nest sites (garrets, roofs or other protected locations) can be more than 10°C higher than the outdoor ambient temperature (Durant, pers. obs.). Dehydration could increase the chicks’ requirements, especially if they consume stored, and thus also partially dehydrated, prey. As a consequence, food efficiency might be lower (rate of increase in body mass per unit food intake; Björntorp & Yang, 1982; Brownell et al., 1986) in the field than in captivity.

Growth overshoot and spontaneous drop in food intake

Our results on barn owls in captivity support the idea that the overshoot of body mass does not seem indispensable for the fledgling (for petrels, Ricklefs & Schew, 1994; for kestrels, Lacombe et al., 1994). Why then do chicks undergo such a development? Lacombe et al. (1994) demonstrated that, despite the same developmental timing, chicks fed ad libitum and having a peak body mass were fatter than underfed chicks at fledging. This observation is consistent with the energy insurance hypothesis (Ricklefs & Schew, 1994), which predicts that chicks accumulate fat as insurance against periods of poor feeding conditions. On the other hand, Lacombe et al. (1994) found a difference in fat reserves only for chicks reared with at least a 30% food restriction. The difference of overshoot between our two groups may not be only the result of the accumulation of energy reserves because we experimented with a food restriction of only 17%. At the body mass peak, the feather growth is at its maximum (ti in Table 2) and requires abundant protein and water (Murphy & King, 1991; Dietz, Daan & Masman, 1992). The reserves could be either proteins or water but the water loss when feather synthesis ends cannot explain the decrease in food intake we observed. Nevertheless, it could be advantageous to constitute reserves when possible instead of depending only on food supply when the need is the most important. When 50% of the feather growth is completed (ti), the chicks may start using the reserves to reduce the body mass for the fledging. Since the feather development was normal in the Restricted group, the energy, protein and water inputs were sufficient. Thus, the reserves may be more a protection against a period of hypothetical food scarcity.
(Ricklefs & Schew, 1994) than an accumulation of protein and/or water for the period of maximum growth rate. In times of food scarcity, the barn owl changes its diet (Taylor, 1994), which would change the intake of essential amino acids, e.g. cysteine (Murphy & King, 1991) for feather synthesis. In such a case, the limitation for feather growth would be the availability of the essential amino acids (protein). It would then be advantageous for a chick to have stored essential amino acids. Such a chick would experience normal growth at the same time that a chick with no overshoot would experience growth delay. The composition of the energy, water and protein reserves could be measured by body composition throughout the growing period. Apparently such a study has never been done. The amount of overshoot could also have an effect on the post-fledging survival, a period when the young are forced to hunt by themselves. Since no difference was found for body mass and size at fledging, the effect of the overshoot on subsequent survival could be due to only internal factors. Consequences of the overshoot value can be assessed only by body composition analysis.

The present work demonstrates that the body mass decrease in ad libitum conditions, consecutive to the peak of body mass, is the consequence of a spontaneous decrease of food intake. What would be the advantage of this kind of growth for parental investment? We can calculate the brood requirement for a hypothetical brood fed ad libitum (Fig. 4; calculation made for a brood of four chicks with a hatching asynchrony of 2.5 days). The two-day period of maximum brood requirement (Fig. 4) in ad libitum conditions is obviously an important parameter of parental investment which cannot be modified. It depends only on the delay of the hatching asynchrony (in a synchronized brood, the duration for the maximum requirements would be 16 days). The short duration of the peak brood requirement is, in addition to the hatching asynchrony, a consequence of the spontaneous reduction of chick food intake when the asymptotic body mass is reached (Fig. 3a, b).

For the brood, the energy that becomes available by the spontaneous decrease of food intake of a given chick could be transferred to its younger siblings at their maximum food requirement period. Resources would therefore not be wasted on the first hatched chicks but used to improve the growth of younger siblings. Moreover, the maximum food requirement is dispatched over a longer period of time (Peak load hypothesis; Mock & Schwagmeyer, 1990). As a consequence, brood reduction would not occur before a more severe food restriction.

For the female, shortening the time of the peak brood requirements allows the transfer of a part of the food supply, i.e. the male investment, from the brood to the restoration of her body reserves in preparation for an eventual second brood. This would be an important benefit in a species like the barn owl where a second
brood could overlap with the end of the first brood (Muller, 1990). Thus, for the parents, an advantage of the bell-shaped growth curve that gives a greater flexibility of chick requirements could be a decrease of the influence of food availability on parental investment. If a comparison is made between the hypothetical brood fed ad libitum and another one fed with the restricted diet used in the present study (Fig. 4), we would expect a 20% decrease of the peak food intake (calculation made for a four-chick brood with a hatching asynchrony of 2.5 days). The parents could have raised at least one more chick with the restricted diet, but the youngest chick would experience a growth delay whenever there is a decrease of food supply (Lacombe et al., 1994). Because of this growth delay, even if the food shortage is of short duration, the youngest chick could suffer from starvation when the female is foraging. Moreover, the whole brood could suffer a growth delay if the food restriction lasts longer. Thus, this margin in food intake can be interpreted as a safety asset against small fluctuations of food supply without brood reduction.

CONCLUSION

The food intake of barn owls in captivity undergoes a spontaneous decrease after the body mass has reached its maximum value. This spontaneous reduction of food requirement of the oldest chicks of a brood when the youngest are at their peak requirement could be an advantage for raising a brood successfully.

A reduction of food availability does not seem to affect the development of barn owl chicks before fledging except for a reduction of the maximum body mass. The body reserves that contribute to the overshoot of body mass seem to be a security against periods of food scarcity. As a consequence, a short period of food restriction would have no effect on the development (growth delay, brood reduction) since the reserves will cover the needs (energy, water and protein).

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