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WINTER STARVATION IN CAPTIVE COMMON BARN-OWLS: PHYSIOLOGICAL STATES AND REVERSIBLE LIMITS

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ABSTRACT.—Among birds, the Common Barn-Owl (*Tyto alba*) is considered to be particularly sensitive to winter-induced starvation. Yet, there are no detailed data on the metabolic response of this species to long-term food deprivation in the cold. Therefore, eight captive Common Barn-Owls (*T. a. alba*), including both males and females, were fasted at 5°C ambient temperature, until there was a clear increase in the rate of body mass loss. In wild birds, which fast spontaneously, such an increase (reflecting increased protein utilization) is associated with a triggering of refeeding that anticipates a lethal depletion in body fuels. Weighing the barn-owls every 8 h and collecting excreta for 24-h periods, we found that even after only 0.7 day of starvation, body-mass and nitrogen loss reached low and constant values (at 8.6 ± SD of 1.0 and 0.17 ± 0.01 g/day, respectively), which were maintained for 7.2 ± 1.6 days. This was calculated to correspond to energy equivalents of body-mass loss and daily energy expenditure of 24.3 ± 1.9 kJ/g and 213 ± 22 kJ/day, respectively. Based on these data, the contribution of proteins to energy expenditure was as low as 8.7 ± 1.6%. In contrast to what could be expected, when compared to the prefasting level, mean daily energy expenditure per unit body mass was not significantly reduced. Presumably, this was due to the maintenance of a high locomotor activity during the first part of the night, as revealed by a rate in body mass loss two-fold higher than during the light phase. The fast was stopped after 1.3 ± 0.1 days of increased body-mass loss. The shift to an increased protein utilization was indicated by a 3.5-fold rise in nitrogen excretion associated with a rise in plasma uric-acid concentration from 0.34 ± 0.08 mmol/L up to 1.75 ± 0.13, and a drop of plasma free fatty acids from 1.3 ± 0.3 mmol/L to 0.11 ± 0.10. Despite the initially heavier females, this metabolic shift occurred simultaneously after 7.9 ± 1.7 days of starvation for both sexes. Accordingly, at the time of refeeding, the females weighed 240.0 ± 5.0 g and the males 217.8 ± 7.2 g (i.e. the initial difference in body mass was maintained). At this time, the barn-owls were still able to fly and refeed by themselves. However, based on data for wild Common Barn-Owls that presumably died from starvation, it can be estimated that the rise in nitrogen loss precedes death by less than 2.5 days. *Received 3 October 1991, accepted 5 May 1992.*

STARVATION IS an important cause of mortality in raptors (Hirons et al. 1979, Newton 1979, Ratcliffe 1980, Hardy et al. 1981), particularly in the Common Barn-Owl (*Tyto alba*) during winter, when prey are scarce due to deep snow cover (Dobinson and Richards 1964, Glue 1973, Marti and Wagner 1985, Shawyer 1987). Marti and Wagner (1985) attributed the high sensitivity of this bird to winter starvation to two physiological causes: (1) a low level of body stores when compared with other middle-sized nocturnal raptors (Piechoki 1960, 1962, Schönfeld et al. 1977, Hardy et al. 1981); and (2) the relatively high value of their lower critical temperature (25°C based on Johnson 1974). Thus, even when ambient temperature is not extremely low, the effect of winter food scarcity is aggravated by increased thermogenesis.

However, there is little available information concerning the maximum possible length of total food deprivation for Common Barn-Owl in the wild. Data available indicate that, after eight days of at least 10 cm deep snow cover, most Common Barn-Owls (*T. a. guttata*) die when body mass reaches a value between 200 and 240 g (Piechoki 1962, 1964, Schönfeld et al. 1977).

To determine the resistance of Common Barn-Owls (*T. a. alba*) to winter starvation, we studied the metabolic responses of captive birds to fasting in the cold and compared these to data on emaciated wild specimens found dead of starvation. Obviously, such an experiment on captive birds has to be limited to the stage that is still physiologically reversible. The difficulty in determining this critical limit is overcome through knowledge of the different physiolog-

TABLE 1. Sex, age, and body mass of individual Common Barn-Owls before experimental starvation.

Bird	Sex	Age (years)	Body mass[a] (g)		
			Initial	Anorexia	Feeding
1	M	>2	292.3	282.1	291.6
2	M	>1	291.7	262.9	300.7
3	M	<1	294.0	266.8	307.3
4	M	<1	305.1	269.8	282.7
5	F	>2	359.0	339.1	355.5
6	F	<1	348.9	324.2	341.0
7	F	<1	374.2	308.6	344.2
8	F	<1	348.8	307.7	325.8
$\bar{x} \pm$ SD	M		295.9 ± 6.2^{a}	270.4 ± 8.3^{c}	295.6 ± 10.7^{a}
$\bar{x} \pm$ SD	F		357.7 ± 11.9^{b}	319.9 ± 14.9^{d}	341.6 ± 12.3^{bd}

[a] Body mass measured at 1500 GMT (pellet expelled) on individual birds: (initial) just before being housed in metabolic cage; (anorexia) at lowest body mass reached during anorexia (spontaneous fast during habituation to individual cages); (feeding) at onset of experimental starvation, after birds had reached a steady state in body mass lasting for five days (i.e. on last day of feeding). Two values labeled by similar letter not significantly different at $P < 0.01$.

ical states encountered by wild birds during spontaneous prolonged starvation (Cherel et al. 1987, 1988, Robin et al. 1988). These studies have shown that feeding behavior is triggered when there is a rapid but still reversible increase in the rate of body-mass loss and in muscle-protein utilization (Le Maho et al. 1988). Experimentally fasted animals are still in a reversible stage during this further rise in body-protein utilization (Belkhou et al. 1991). While this rise would inevitably lead to death if starvation were prolonged further, it is not initially associated with weakness.

Thus, for experimental investigations, this easily characterized metabolic shift has served as a good criterion for adjusting the length of the imposed starvation to a physiological limit. In addition, an advantage of studying the Common Barn-Owl is that comparisons may easily be made with wild specimens for which death can be attributed to starvation. Moreover, as this species is frequently hit by cars, it is possible to obtain data from emaciated specimens that were still able to fly at the time of their death. It then becomes possible to determine the safety margin of Common Barn-Owls after the rise in protein utilization.

In order to characterize the successive states undergone during the imposed fast, we followed the changes in the level of lipid and protein catabolism by measuring daily nitrogen excretion (Robin et al. 1987) and plasma concentrations of free fatty acids and uric acid (Cherel and Le Maho 1985, Le Ninan et al. 1988). The reversibility of the state reached by the barn-owls in the present experiment was confirmed by the complete restoration of their initial body mass (Handrich et al. 1993).

MATERIALS AND METHODS

Experimental procedure.—Our study was conducted in Strasbourg during the 1989-1990 winter, on four males and four females of the Common Barn-Owl selected from a small breeding colony in the laboratory. They were kept in a 5.0 × 4.0 × 0.5 m outside aviary. The experimental birds were chosen with a maximum range in age and body mass (Table 1) to increase the range of interindividual response to starvation. They were housed in individual 0.7 × 0.8 × 1.1 m metabolic cages in a climatic chamber that maintained natural photoperiod and an ambient temperature of 5 ± SD of 1°C. Although freshly killed mice were given *ad libitum*, all barn-owls showed a decrease in body mass when first moved to the climatic chamber. Some birds did not feed at all for two or three days. At the beginning of the experiment, after three weeks of acclimatization, the birds had a new steady body mass, but had not necessarily regained their initial outdoor body mass (see Table 1).

The experimental procedure consisted of a five-day period of steady-state body mass, food being available *ad libitum*, followed by a period of total starvation that was prolonged until a well defined acceleration in body-mass loss ($dm \cdot dt^{-1}$) occurred. The fast was stopped when the specific rate of body-mass loss ($dm \cdot m^{-1} \cdot dt^{-1}$ calculated for 8-h periods) reached a limit value of 7% per day (i.e. 7 g/[100 g·24 h]). This criterion was chosen by reference to our observations on the magnitude of changes in body-mass loss in other species (Cherel et al. 1988, Robin et al. 1988, Belkhou et al. 1991). The birds then were allowed to refeed *ad libitum* until initial body mass was restored and a new steady-state value achieved (see Handrich et al. 1993). The birds had no water available through-

TABLE 2. Length and daily loss in body mass ($\bar{x} \pm$ SD) for different phases of starvation.

	Male ($n = 4$)	Female ($n = 4$)
Phase length (days)		
Phase I	0.49 ± 0.18	0.75 ± 0.25
Phase II	6.83 ± 1.41	7.61 ± 1.88
Phase III	1.10 ± 0.12	1.39 ± 0.07
Complete starvation	8.43 ± 1.61	9.75 ± 1.84
Daily body mass-loss[b] (g/day)		
Phase I	20.20 ± 5.02[a]	20.90 ± 7.10[a]
Phase II	8.27 ± 0.99[c]	8.96 ± 1.09[c]
Phase III	11.34 ± 1.87[b]	14.89 ± 2.98[b]
Mean	9.33 ± 1.19	10.60 ± 1.42

Two values labeled with similar letter not significantly different at $P < 0.05$.

out the experiment, as is usually the case for barn-owls under captive conditions.

In prefasting condition, food was given at 1500 GMT. The urine, feces, and remaining food were collected the day after at 0700. On these two occasions (i.e. during the light phase), body mass was determined to the nearest 0.1 g. During fasting, the birds were also weighed at 2300, so that the 24-h cycle could be divided into three 8-h intervals, essentially corresponding to the resting diurnal stage (lights-on at 0600 and off at 1600 in December or February) and two successive periods of the nocturnal stage.

Sampling and analysis.—Excreta were collected daily, using a technique previously developed in our laboratory (Robin et al. 1987) and adapted for use with barn-owls. Urine and feces were directly drained through a wire-mesh floor via a polyethylene-covered funnel into a glass vial. Pellets were retained by the wire mesh. Each vial contained 10 ml sulfuric acid 0.1 N and was kept in crushed ice, to limit ammonium evaporation and microfloral activity. Using distilled water, traces of feces were scraped from the wire mesh and polyethylene sheet into the vial. Homogenized aliquots of 15 ml were stored at −20°C. Nitrogen content was directly determined on liquid aliquots by Kjeldahl's method. Another aliquot was freeze-dried for measurement of dry mass. For each day, dried aliquots of all individual birds were pooled for measuring the average energy content of the daily excreta of the eight birds. Energy content was measured on a 0.5- to 1.0-g dry sample using an adiabatic Parr calorimeter. Corrections were made for sulfuric and nitric acid.

For blood sampling, a volume of 0.5 to 0.7 ml was obtained from the brachial vein. A corresponding amount of water was given orally to compensate for the decrease in body mass and possible dehydration. Successive samples were obtained for each barn-owl: at the onset of the fast; every two days thereafter; at the beginning of phase III; and, finally, at the onset of refeeding. Sampling was always between 1300 and 1500, except for the last sample (i.e. at onset of refeeding) obtained at 0700, 1500 or 2300. Blood was withdrawn in heparinized syringes and immediately centrifuged in polyethylene microtubes at 5°C. Uric acid (see methods in Sheibe et al. 1974) and free fatty acids (FFA, using C-Test Wako kit for nonesterified fatty acid) were assayed on whole plasma using enzymatic methods.

Statistics.—Means and standard deviations are presented throughout the paper. Statistical analysis of differences among group means were performed with Peritz' *F*-test (Harper 1984). Linear-regression analyses were performed with SigmaPlot software (Jandel Scientific) and slope statistical analysis with Student's *t*-test. The same software was employed to determine the length of the three starvation phases using a best-fit procedure.

RESULTS

Characteristics of different phases of fasting.—The fast was characterized by three successive and well-delimited phases: phase I (lasting less than one day) of high daily loss in body mass ($dm/dt = 20.5 \pm 5.7$ g/day); phase II corresponding to the major part of the fast (7.2 ± 1.6 days) with a mean dm/dt of 8.6 ± 1.0 g/day; and phase III characterized by an abrupt increase of dm/dt to 13.1 ± 3.0 g/day just before refeeding. The mean duration of each phase of fasting and the corresponding dm/dt were not significantly different between sexes (Table 2).

The specific rate of body mass loss (i.e. proportion of body mass lost per day; $dm \cdot m^{-1} \cdot dt^{-1}$) remained constant during phase II, equal to 3.2 ± 0.1 g/(100 g·24 h) (see Fig. 1). It increased dramatically during phase III ($P < 0.01$), reaching 6.2 ± 1.5 g/(100 g·24 h) at the onset of refeeding, a mean value also significantly higher than in phase I.

Since the birds were weighed every 8 h, it was possible to calculate $dm \cdot m^{-1} \cdot dt^{-1}$ on intervals shorter than one day, allowing us to more closely specify the duration and characteristics of the different fasting phases (Fig. 2). The duration of fasting phases was then calculated with a 0.2-day accuracy, using a best-fit procedure. Throughout starvation the eight barn-owls showed a well-synchronized circadian rhythm, characterized by an oscillation of the rate of body-mass loss between a maximum value during the first part of the dark phase (1500–2300), and a minimum value during the two other parts of the 24-h period. During phase II, the mean was 4.4 ± 0.7 g/(100 g·24 h) for the 1500–2300 interval, and 2.6 ± 0.4 for the two other intervals pooled together (see Fig. 2). However,

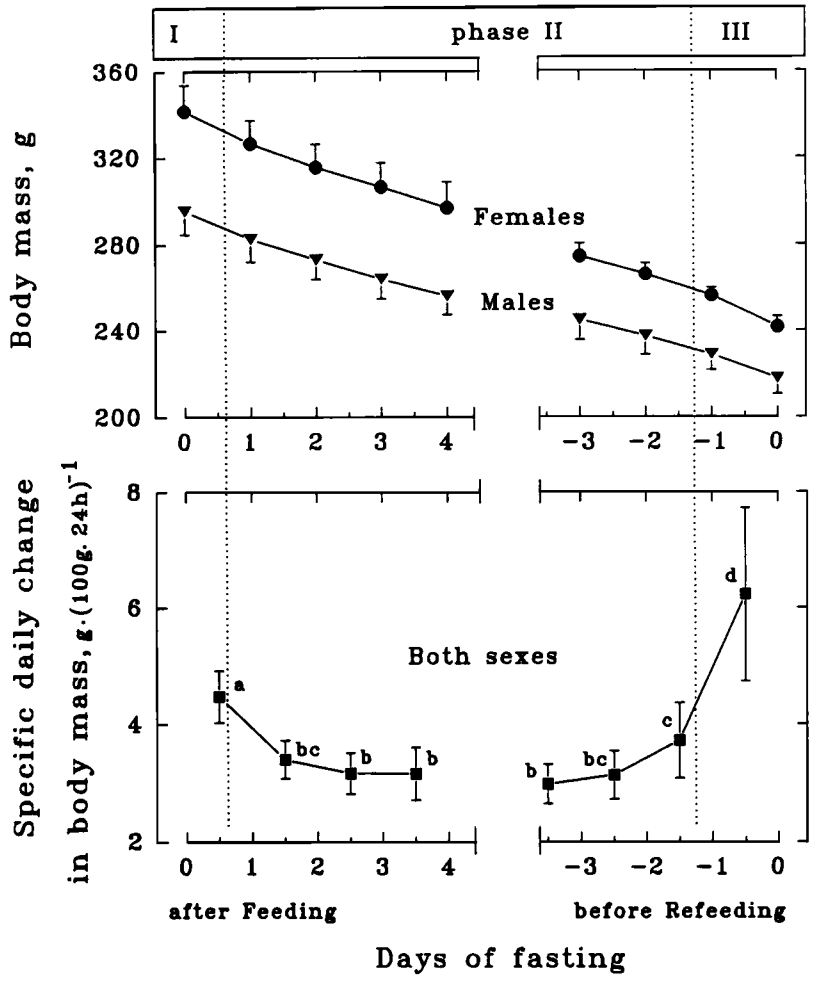

Fig. 1. Changes in body mass (upper panel) and in specific rate of body-mass loss (lower panel) throughout three successive phases of fasting. Data from four male and four female Common Barn-Owls. Bars indicate standard deviations. Individual data synchronized, starting forward from first or backward from last day of fasting. Two values labeled with same letter are not significantly different at $P < 0.01$.

the rate of body-mass loss during the first part of the night (1500–2300) progressively decreased during phase II (Fig. 2) until it reached the value for the two other parts of the 24-h period. During phase III, both night and day $dm \cdot m^{-1} \cdot dt^{-1}$ values increased. Before refeeding, these values finally exceeded those previously observed during the early part of the night at the beginning of phase II.

Total duration of starvation and body-mass changes.—The mean duration of the experimental fast in the eight captive barn-owls was 9.1 ± 1.8 days; data for males and females are shown in Table 2. There was considerable variation among birds (from 6 to 12 days) that was independent of their sex, although the mean pre-fasting body mass was 16% (i.e. 46 g) higher in females (Table 1).

This initial difference in body mass was still evident at the end of starvation (Fig. 1), as there was no difference between sexes in the duration of starvation or in the rate of body-mass loss (Table 2). The body mass reached at the beginning of phase III was 30 g lower in males than in females, and still 22 g lower at the end of starvation: 217.8 ± 7.2 g in males versus 240.0 ± 5.0 g in females. The combined values for males and females represent a relative reduction of 22.9% in initial body mass at the transition between phase II and III, and 28.0% at

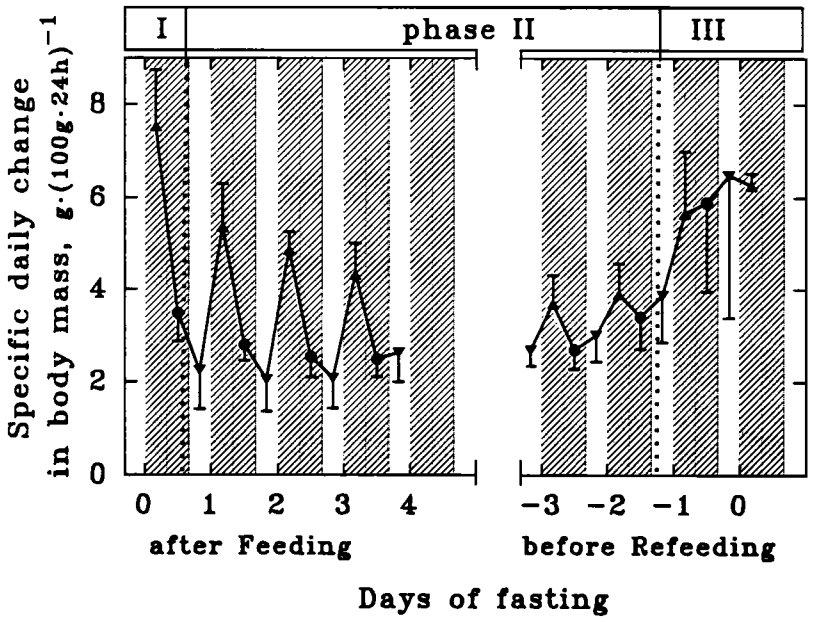

Fig. 2. Change in circadian cycle of specific rate of body-mass loss during fasting determined over three intervals per 24 h. Data taken for periods of 8 h: between 1500 and 2300 GMT (triangle point up); between 2300 and 0700 (circle); and between 0700 and 1500 (triangle down). Dark phase delimited with hatched box. Data obtained from eight synchronized birds and plotted as mean values (with SD bars).

the end of experimental starvation (Table 3). At that time, all of the barn-owls still were able to fly and to refeed by themselves (Handrich et al. 1993).

Changes in nitrogen excretion.—Before starvation, the mean daily loss in dry excreta was 4.7 ± 0.4 g/day, corresponding in nitrogen to 1.2 ± 0.2 g/day. During phase II, daily nitrogen loss was steady and as low as 0.17 ± 0.01 g/day. This value was more than two times lower than during phases I or III, and seven times lower than during the prefasting period (Fig. 3). The nitrogen and caloric content of dry excreta were at a maximum value in prefasting condition, equal to 23.4 ± 1.3% and 9.3 ± 0.2 kJ/g, respectively. During starvation, changes closely paralleled those in daily body-mass and nitrogen loss (Figs. 2 and 3). Interestingly, the color

TABLE 3. Critical body mass and body-mass reduction during starvation.[a]

	Male (n = 4)	Female (n = 4)
Body mass (g) at end of		
Feeding	295.6 ± 10.7^{a1}	341.6 ± 12.8^{a2}
Phase I	286.2 ± 9.3^{a1}	327.3 ± 10.6^{a2}
Phase II	230.1 ± 7.3^{b1}	260.6 ± 6.5^{b2}
Phase III	217.8 ± 7.2^{c1}	240.0 ± 5.0^{c2}
Body-mass loss (g) during		
Phase I	9.4 ± 1.7^{a1}	14.3 ± 2.8^{a2}
Phase II	56.1 ± 10.5^{c1}	66.7 ± 8.5^{c2}
Phase III	12.3 ± 0.7^{b1}	20.6 ± 3.6^{b2}
Complete starvation	77.8 ± 11.8^{d1}	101.6 ± 9.1^{d2}
Relative body-mass loss (%) at end of		
Phase I	3.2 ± 0.5^{a}	4.2 ± 0.7^{a}
Phase II	22.1 ± 3.1^{b}	23.7 ± 2.0^{b}
Phase III	26.3 ± 3.2^{b}	29.7 ± 1.8^{b}

[a] $\bar{x}$ ± SD. Two values labeled with same letter or number not significantly different at $P < 0.05$ (a, b, c, d between phases; 1, 2 between sexes).

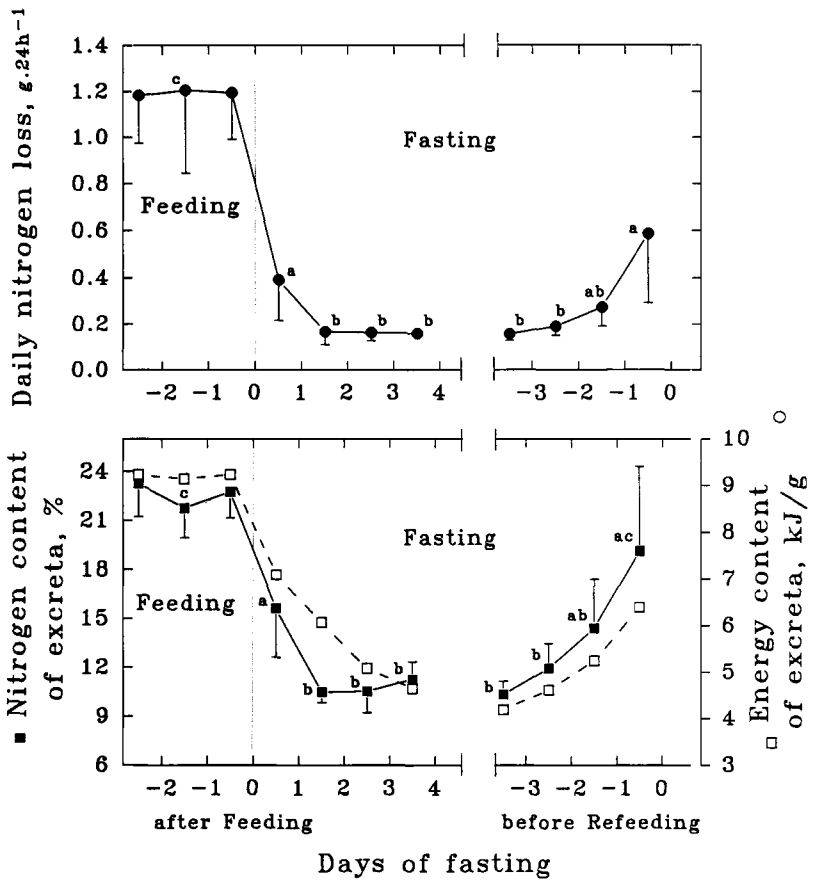

Fig. 3. Upper panel shows daily nitrogen loss before and during fasting. Lower panel indicates composition of excreta, in nitrogen (filled squares) and energy (open squares), before and during fasting. Nitrogen data obtained from eight synchronized birds and plotted as mean values (with SD bars). Energy content measured on mixed sample of the eight birds. Two values labeled with same letter not significantly different at $P < 0.01$.

of the excreta changed with the successive phases of fasting: white cream during feeding and phase I; greenish and increasingly translucid during phase II; milklike with a brown color in phase III.

Changes in plasma metabolites.—Plasma concentration of uric acid was 0.52 ± 0.17 mmol/L just before the onset of fasting (Fig. 4). This value is in agreement with values obtained in granivorous birds (Robin et al. 1987), but substantially lower than those for piscivorous birds (1.3 mmol/L; Robin et al. 1988, Le Ninan et al. 1988). The value for day 0 corresponds in our work to postabsorptive condition during the resting phase. This value is in close agreement with the 0.44 mmol/L mean value found in Eagle Owls (*Bubo bubo*) during daylight, although in that nocturnal bird it increases to 0.92 mmol/L during the dark phase (Garcia-Rodriguez et al. 1987b). This explains why we did not find any significant decrease in plasma concentration of uric acid during the early fast in barn-owls (Fig. 4), as was previously found in the Common Buzzard (*Buteo buteo;* Garcia-Rodriguez et al. 1987a).

Throughout phase II, plasma uric-acid concentration was maintained at a low value of 0.34 ± 0.08 mmol/L. In contrast, there was a sharp increase during phase III (Fig. 4). At the time of refeeding, plasma uric acid reached a mean of 1.75 ± 0.13 mmol/L, a fivefold increase over phase II (Fig. 4).

Plasma concentration of free fatty acids (FFA) averaged 0.18 ± 0.09 mmol/L in the prefasting

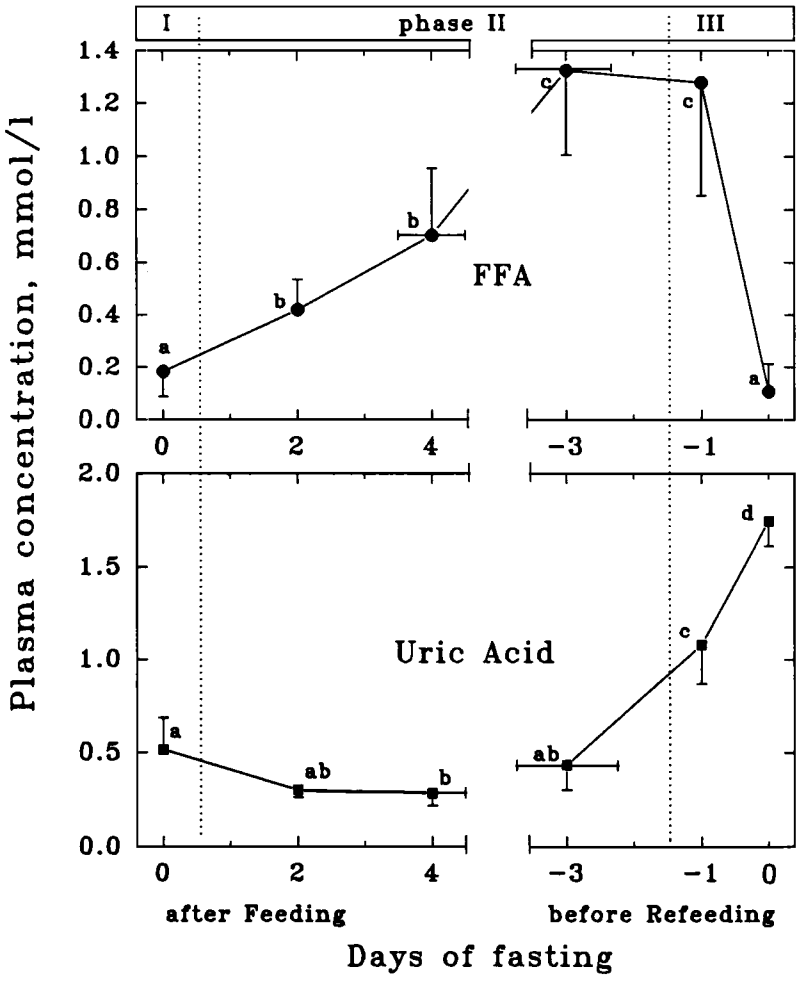

Fig. 4. Changes in concentrations of two plasma metabolites during fasting. Samples synchronized except at middle of phase II, depending on length of fasting. Mean value (with SD) indicated for the eight barn-owls. Two values labeled with same letter not significantly different at $P < 0.01$.

state and progressively increased during phase II, reaching a mean of 1.3 ± 0.3 mmol/L (see Fig. 4). It presumably peaked at the transition between phase II and phase III (between day −3 and day −1 of refeeding). A drop to 0.11 ± 0.10 mmol/L was observed at the time of refeeding, a value lower than in the prefasting condition (day 0 of fasting).

DISCUSSION

Our study demonstrates that emaciation is still reversible in the Common Barn-Owl after eight days of experimental fasting, a finding in accord with previous observations that wild Common Barn-Owls can tolerate one week of complete food deprivation in winter (Piechoki 1962, 1964, Schönfeld et al. 1977). We also characterized three successive phases during the fast on the basis of changes in body-mass loss rate and body-fuel catabolism. The characterization of the phases II and III of fasting enables getting simple criteria (rate of body-mass loss, blood metabolites, color of droppings) of the nutritional condition of a Common Barn-Owl (i.e. whether or not the bird has reached a critical stage). It also provides a better understanding of the influence of physiological or behavioral factors on the capacity of a Common Barn-Owl to survive long periods of food deprivation in the field.

TABLE 4. Body-fuel utilization and daily energy expenditure during Phase II.[a]

	Male ($n = 4$)	Female ($n = 4$)
Cumulative nitrogen loss (g)	0.98 ± 0.16	1.31 ± 0.18
Relative contribution (%) of body fuels to		
Body-mass loss		
Proteins	10.9 ± 1.6^{a1}	12.6 ± 0.8^{a2}
Lipids	59.6 ± 5.8^{b1}	53.3 ± 3.1^{b2}
Energy expenditure		
Proteins	7.8 ± 1.8^{a1}	9.7 ± 1.1^{a2}
Lipids	92.2 ± 1.8^{b1}	90.3 ± 1.1^{b2}
Energy equivalent of body-mass loss (kJ/g)	25.4 ± 2.0	23.2 ± 1.1
Daily energy expenditure (kJ/day)	213.3 ± 33.3	213.1 ± 19.6

[a] $\bar{x}$ ± SD. Two values labeled with same letter not significantly different at $P < 0.05$ (a, b between phases; 1, 2 between sexes).

To ascertain the reversibility of our experimental fast, all of the barn-owls were refed. In Handrich et al. (1993), we show that the eight owls, independent of their particular duration of fasting, restored their initial body mass within eight days and reached a normal steady-state level of feeding after six more days. Furthermore, two of the pairs involved started laying eggs in an outside aviary, one five weeks after and the other eight weeks after the fasting period. Members of one of these pairs were two years old. They had the same clutch and brood size as the previous year, with a delay of only 11 days in the laying date.

Metabolic aspects during steady-state body-mass loss.—Daily losses of both body mass and nitrogen were constant during phase II, which is in accord with the concept of a metabolic steady state during this period of fasting (Groscolas 1988, Robin et al. 1988). Thus, this phase is characterized by protein and lipid utilization in constant proportions. Using a conversion factor to tranform nitrogen mass into protein mass (6.25) and assuming a constant water content in fat-free tissues throughout starvation (73%, Groscolas et al. 1991), loss in protein tissue (PTL) can be calculated from the cumulative loss of nitrogen (CNL) during phase II:

$$PTL = 6.25CNL/(1 - 0.73). \quad (1)$$

By subtraction from the parallel loss in body mass, the total amount of catabolized fat tissue can be estimated.

Results of these calculations are presented for each sex in Table 4. Proteins are spared during phase II, contributing only 11.8 ± 1.5% of total loss in body mass versus 56.4 ± 5.5% for lipids. Since the energy capacity of protein is less than one-half that of lipids in ureotelic animals (17.8 kJ/g for protein and 39.3 for lipids; Schmidt-Nielsen 1979), the contribution in proteins was still lower in terms of energy (8.7 ± 1.6% for proteins vs. 91.3 ± 1.6% for lipids). One good criterion for adaptation to prolonged starvation is the ability to conserve protein during phase II. There is, however, an incompressible minimum limit of protein utilization during starvation, which represents 3 to 5% of the total energy expenditure (Le Maho and Groscolas 1990, Belkhou et al. 1989), as reached for example in the Emperor Penguin (*Aptenodytes forsteri*), which can fast for four months (Robin et al. 1988). Another expression of protein conservation during starvation is the energy equivalent of body-mass loss in phase II. The value of 24.3 ± 1.9 kJ/g found in the Common Barn-Owl (Table 4) is very close to that found in the Emperor Penguin (25.5 kJ/g), although such a high value is considered to be typical of a large and fat bird (Groscolas 1988, Groscolas et al. 1991).

A further adjustment to prolonged fasting is the reduction of daily energy expenditure, mainly through a reduction of locomotor activity (Le Maho et al. 1981, Cherel et al. 1988, Le Maho and Groscolas 1990). The daily energy expenditure during phase II, calculated from the daily loss in body mass and the energy equivalent of body-mass loss, was 213 ± 32 kJ/day (see Table 4), significantly lower than the 275 ± 31 kJ/g mean value measured under normal feeding conditions ($P < 0.01$; Handrich et al. 1993). Expressed per unit body mass, this decrease was however not significant, suggesting that there is no reduction of daily energy expenditure in the fasted Common Barn-Owl, in contrast to the others species studied. In the other studies (e.g. of the American Kestrel [*Falco*

sparverius]; Shapiro and Weathers 1981), the birds were exposed to a thermoneutral ambient temperature. Thus, pending confirmation by direct body-composition analysis, our data indicate that fasted Common Barn-Owls in captivity are able to conserve body protein as efficiently as birds well adapted to long-term fasting, without significantly reducing mean energy expenditure during the period of steady-state body-mass loss.

As for penguins (Cherel and Le Maho 1985, Robin et al. 1988), the protein conservation during phase II was reflected in the Common Barn-Owl by a low plasma concentration of uric acid (Fig. 4). However, this may not be true for other bird species. In fasting geese (*Anser anser*) and Common Buzzards, uric-acid concentration was not maintained at a low and steady value (Robin et al. 1987, Garcia-Rodriguez et al. 1987b).

Interestingly, the protein conservation of phase II was associated in the Common Barn-Owl with a lower proportion of nitrogen in excreta, a lower caloric content (Fig. 3), and a color change of droppings. The disappearance of the milklike color of droppings reflects the drop in uric-acid excretion (with a high caloric value of more than 3 kJ/g). Instead, the greenish color appearance may be attributed to an increasing proportion of biliary compounds (with a low caloric value, below 1 kJ/g).

Acceleration of protein utilization with prolonged starvation.—The late 3.5-fold rise in daily nitrogen excretion (Fig. 3) associated with the 1.5-fold rise in $dm \cdot m^{-1} \cdot dt^{-1}$ (Fig. 1) suggests an increase in body-protein utilization and/or daily energy expenditure. Changes in FFA and uric-acid concentrations are good indices, respectively, for the mobilization of stored triglycerides and for protein catabolism (Cherel et al. 1988). As in other species studied, the rapid changes of both their plasma concentrations at the transition between phase II and phase III (see Fig. 4) provide evidence for the reorientation of the catabolism of body reserves. Moreover, the observation that plasma FFA concentration only fell during late phase III is consistent with other observations that lipid reserves are not completely exhausted at the time of the acceleration of protein catabolism (Robin et al. 1988, Belkhou et al. 1991). The plasma uric-acid concentration measured just before refeeding (1.75 mmol/L) was higher than the maximun value found earlier during prolonged starvation (1.5 mmol/L; Robin et al. 1988). Conversely, the FFA concentration was the lowest ever recorded (0.11 vs. 0.3 mmol/L; Cherel and Le Maho 1985). This suggests that, despite the reversibility of the prolonged starvation, an extreme limit of body reserves depletion had been reached by the owls in the present study.

As for phase II, the color of droppings reflected body-protein utilization. The droppings were again milklike during phase III (i.e. as in the fed state), which can be attributed to a higher uric-acid content in excreta during the rise in nitrogen excretion (Fig. 3). The brown color of droppings just before refeeding may be attributed to an increasing proportion of biliary and/or pyloric-ceaca compounds. Thus, in the context of field investigation or of the rehabilitation of raptors, very simple criteria can be used to determine the nutritional condition of fasting birds (i.e. particularly whether they have reached the further stage in body-protein utilization).

Factors of starvation tolerance.—Surprisingly, the observed variability in fasting duration (7.0 to 12.3 d) was not related to the initial body mass (when considering the initially heavier females). This initial difference between sexes was maintained at the time of increasing body-mass loss (critical body mass) and upon refeeding. Was this apparent sex-related difference in critical body mass the result of sampling? In a further experiment (unpubl. observ.) during which the initial body mass of females was only 310 g (n = 4), a mean value similar to that of males in the present study, the mean critical body mass at the end of phase II was still the same as we found (255.5 g). There appears to be a sex-dependent critical body mass for entering phase III that is independant of the initial body mass. In the present study, the initial and final sex difference in body mass was then presumably due to a difference in body size and protein mass, and to the proportion of stored fat. Thus, based on these data, wild female barn-owls despite being heavier will not have a greater capacity than males to avoid winter starvation.

The four females, which were not heavier than males (mean = 310 g), reached phase III within only 4 to 5 days compared to 7 to 12 days in the present study. This demonstrates that, for each sex, the fasting capacity of Common Barn-Owls also depends on initial body condition. In the wild, body composition may be more subject to variation than in captivity, especially during winter. Assuming a constant

rate of body-mass loss (9.5 g/day), a realistic 70-g range in the initial body mass (260–330 g in males and 290–360 g in females; i.e. 30–100 g of potential body reserves in both sexes) would result in both sexes in a minimum of eight days (range 3 to 11 days) of fasting tolerance.

Obviously, duration of starvation also depends on the ability of individuals to decrease the rate of body-mass loss during phase II. The variability (7.4–9.9 g/day) among individuals was not correlated ($P > 0.05$) with daily nitrogen loss, suggesting that individual dm/dt was not purely related to the ability to conserve protein, but also to the overall daily energy expenditure. The circadian variation of $dm \cdot m^{-1} \cdot dt^{-1}$ we observed in the barn-owls (Fig. 2) indicates a circadian variation in energy expenditure. This may result from two main causes: (1) a circadian variation in body core temperature (Chaplin et al. 1984, Shapiro and Weathers 1981); (2) a circadian variation in locomotor activity.

The second factor presumably predominates. As soon as phase III was initiated, the daily rate of body-mass loss calculated during the light phase (0700–1500; see Fig. 2) rapidly increased up to the nocturnal level (i.e. in accordance with increase in locomotor activity observed in the rat [*Rattus norvegicus*] at the phase II–phase III transition; Koubi et al. 1991). However, during the first part of the night the progressive decrease in the rate of body-mass loss during phase II (Fig. 2) varied between individuals, in correlation with the pattern of spontaneous fasting observed when the barn-owls were individually housed in the metabolic cage before the experiment (Table 1); a higher loss of body mass in this period of habituation to individual cages was associated with a reduced amplitude of the circadian variation of rate loss in body mass during the experimental fast, irrespective of the minimum value during the light phase. This could be interpreted as a habituation to captivity, and/or to a previous episode of reduction of body reserves. Increased activity during the first part of the night could be to find food, but habituation to captivity is presumably associated with a progressive drop in this foraging behavior.

In the field, when Common Barn-Owls are exposed to episodes of snow cover, they apparently do not hunt more during daytime. They must then select between two survival strategies: (1) continue hunting all throughout the dark period (active strategy); or (2) reduce nocturnal activity to the low diurnal level (waiting strategy). Depending on these opposite strategies, the rate of body-mass loss could vary between 6 and 11 g/day, resulting in a fasting duration from 8.5 to 14.5 days for a 350-g female. Thus, the combined influences of sex, initial body conditions, and locomotor activity may result in a starvation tolerance ranging between 3 and 15 days for wild owls.

"Safety margin" between acceleration of protein loss and lethal state.—Road casualties indicate that the lowest body mass at which a Common Barn-Owl is still able to hunt is between 200 and 230 g (Piechoki 1960, 1962), with several values as low as 175 g (Shawyer 1987). However, from reliable data concerning several wild specimens (*T. a. alba*) for which death could be attributed to starvation in winter, minimum body mass was 190 g for males and 212 g for females (C. Riols pers. comm.). Since daily loss of body mass was 15 to 20 g/day in phase III, it would have only taken 1.0 to 1.5 days for our experimental animals to reach the average minimum body mass observed in the wild.

Even though an animal can still hunt, is it still able to digest prey? Several emaciated road casualties were characterized by a black tarry bilelike liquid in the gut (Shawyer 1987), similar to what we found in the dropplings of three of our experimental birds in the last 8 h before refeeding. In our laboratory, a starving male that weighed 212 g, and was still able to fly, was refed 16 h after having exhibited droppings of this type. The first meal was entirely regorged 10 h later in the form of a nearly undigested pellet with a strong smell of fermentation. By giving a new skinned mouse, the process of digestion started again and the bird's initial body mass was restored within 10 days of refeeding. This suggests that at least some of the emaciated birds that are killed by cars while still hunting may already have lost the ability to digest prey.

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