The Auk 110(3):470-480, 1993

WINTER STARVATION IN CAPTIVE COMMON BARN-OWLS: BIOENERGETICS DURING REFEEDING

YVES HANDRICH,[1] LAURENT NICOLAS,[2] AND YVON LE MAHO[1]
[1]*Centre d'Ecologie et Physiologie Energétiques,*
Centre National de la Recherche Scientifique 67087 Strasbourg, France; and
[2]*Fonds d'Intervention pour les Rapaces, 29 rue du Mont Valérien, 92210 St Cloud, France*

ABSTRACT.—The bioenergetics of eight captive Common Barn-Owls (*Tyto alba alba*) acclimated at 5°C were studied during the restoration of a 30% reduction in body mass following a period of total food deprivation. The eight-day period during which body mass was restored (Refeeding I) was compared with a five-day prefasting period (Feeding), corresponding to steady body mass and a six-day period (Refeeding II) of stabilization at a new steady state. Food was given *ad libitum* throughout the feeding periods. During Refeeding I, the rate of increase in body mass (13.9 ± SD of 1.0 g/24 h in females and 9.2 ± 0.8 g/24 h in males) was close to the maximum value for growth of captive or wild owlets. It was achieved by a 1.63-fold increase in gross energy intake and daily metabolized energy, respectively, of 370 ± 42 and 275 ± 31 kJ/d during Feeding. In contrast to the clear increase in food assimilation efficiency observed in other species during refeeding, the high rate of energy intake and body mass restoration in the Common Barn-Owl was associated with only a slight increase in assimilation efficiencies: 52.0 ± 2.2% versus 49.1 ± 1.0% during Feeding for dry mass; and 75.5 ± 1.1% versus 74.1 ± 0.6% for energy. This slight increase could only be attributed to a reduction of the energy lost in pellet production (i.e. to a higher effectiveness in gastric digestion). The energetic cost of daily change in body mass was estimated in both sexes and both feeding periods, and appeared to be constant (10.8 ± 1.1 kJ/g fresh body mass). Using this value, the part of the daily metabolized energy invested in the existence metabolism was calculated. After four days of refeeding, existence metabolism paradoxically appeared similar or even higher than before fasting, while the body mass was still lower than the initial value. Thus, in contrast to the laboratory rat (*Rattus norvegicus*) or humans, the Common Barn-Owl is unable to enhance restoration of body reserves by minimizing existence requirements when refed *ad libitum* after a period of starvation. This might be partly due to the maintenance of a high locomotor activity throughout starvation and refeeding. *Received 3 October 1991, accepted 5 May 1992.*

IN THE COMMON BARN-OWL (*Tyto alba alba*), severe winters with cold weather and extensive cover of deep snow are well known to result in declines in population density and/or in reduction of further breeding success (Honer 1963, Frylestam 1972, Schönfeld et al. 1977, Baudvin 1975, 1976, Bunn et al. 1982, Marti and Wagner 1985, Muller 1987, Shawyer 1987).

In addition to mortality due to winter-induced starvation (Handrich et al. 1993), poor breeding success may be due to an insufficient restoration of body stores (Hardy et al. 1981). Presumably, this restoration not only depends upon food availability, but also on the extent of depletion of body fuels and on the physiological ability to convert food into energy reserves. These points are still largely ignored in the literature on birds. After fasting in man and laboratory rats (*Rattus norvegicus*), a greater proportion of the ingested energy during refeeding can be used for restoration of energy reserves. This has been attributed to a decrease of existence energy requirements during refeeding. This decrease is proportional to the severity of reduction in body mass or to the degree of food restriction during refeeding (Hill et al. 1984). It does not seem to be due to a reduction in locomotor activity (Boyle et al. 1981), but to a drop in basal metabolic rate.

Such an increase of food conversion into energy reserves in a wild animal would improve the capability for body-mass restoration in an environment where food is not available *ad libitum*, and where this limitation itself contributes to increasing the cost of foraging, and accordingly the existence metabolism.

All studies on the energy requirements of raptors that involved determination of gross energy intake, existence metabolism, and energy assimilation efficiency (EAE) have been conducted on captive birds at constant body mass. The EAE is a factor often calculated in studies on the bioenergetics of wild species, as it is essential to establish the relationship between the level of food intake of a species in the field and its energy expenditure. As EAE is always determined under captive conditions, for extrapolation to the field it has been assumed to be constant, whatever the level of food intake. Furthermore, constant body mass corresponds to an idealistic situation for a wild species, which naturally encounters periods of food scarcity.

For mammals, in which gastrointestinal wastes are easily separated from urine, the calculation of EAE can be made independently of the excreta so that it represents the efficiency of the digestive tract. However, for birds, because urine cannot be separated from feces, the EAE also takes into account a part of the energy loss that is independent of digestion (i.e. energy loss in urine that reflects intensity of metabolic rate). Accordingly, it can be expected that EAE will vary with both the amount of food intake and subsequent change in body mass. EAE then, should increase if existence metabolism remains at the low fasting level during refeeding.

The aim of our study was to determine the EAE and the relative importance of existence metabolism in captive Common Barn-Owls during different feeding conditions: steady state in body mass; and refeeding *ad libitum* after starvation (see Handrich et al. 1993). Throughout the investigation, ambient temperature (5°C) was below thermoneutrality (lower critical temperature, LCT = 25°C; after Johnson 1974) to mimic a winter condition. In this paper, during feeding and refeeding after fasting, the following energetic parameters were compared in captive birds: gross energy intake, daily metabolized energy, existence energy requirement, and dry mass or energy assimilation efficiencies.

MATERIALS AND METHODS

Three weeks before the experiment, four males and four females were individually housed in a climatic room at 5°C. Freshly killed mice were provided *ad libitum*. At the beginning of the experiment, the birds had a steady body mass, but not necessarily at the same level that was previously maintained in the outside aviary in which they were raised (Handrich et al. 1993:table 1).

A five-day period of steady body mass, food being available *ad libitum*, was followed by a period of total starvation that was prolonged until a critical but still reversible state was reached (Handrich et al. 1993). The birds then were allowed to refeed *ad libitum*, until the prefasting food intake was restored two weeks later. The experimental birds did not have water available throughout fasting or feeding periods, which is the usual situation for our breeding colony of captive birds.

During prefasting and refeeding periods, food was given at 1500 GMT and remaining food, urine and feces were collected at 0700 the day after. On these two occasions, body mass was determined to the nearest 0.1 g. The last pellet corresponding to the preceding nocturnal meals was usually expelled before the weighing at 1500. If not, the pellet was found at the beginning of the night and its mass subtracted from the body mass at 1500. With this procedure, there was a good day-to-day correspondence between daily change in body mass, amount of food eaten, amount of feces, and excreta collected.

To ensure that food was given *ad libitum*, enough food was available so that at least one intact mouse was left. Every morning, the uneaten food was divided into three parts: intact mice; mice partially eaten; and viscera, which often were removed from an animal and scorned by the barn-owls. Often, there was partial dessication of the scorned food; therefore, the amount of food eaten was calculated on the basis of dry mass. Partially eaten mice and viscera were dried at 70°C for 48 h in a still-air oven and weighed separately to the nearest 0.01 g. All of the partially eaten mice and viscera collected throughout the experiment were pooled into two samples (using a high-speed grinder; Retch ZM1). The dry mass and energy content were measured for the 10 freshly killed mice, the sample of partially eaten mice, and the viscera sample. The daily food intake in dry mass could then be calculated using the following formula:

$$(M_{FM} - I_{FM})C_{DM} - P_{DM} - V_{DM}, \qquad (1)$$

where M_{FM} was the fresh mass of the meal, I_{FM} the fresh mass at 1500 of intact mice not eaten, C_{DM} the dry mass content of fresh mice, P_{DM} the dry mass of partially eaten mice, and V_{DM} the dry mass of viscera. Gross energy intake was calculated using the same procedure.

Pellets were collected daily, dried at 70°C for 48 h, and weighed to the nearest 0.01 g. Two consecutive periods (eight and six days long, respectively) were characterized during refeeding, based on the changes in body mass (see Results and Fig. 1). For each barn-owl the pellets were mixed, ground and homogenized into three samples, corresponding to the feeding period and the two periods of refeeding. Energy content of each sample was measured.

Feces and urine were collected daily, with particular precautions to avoid nitrogen evaporation or bacterial fermentation (see methods in Handrich et al. 1993). An aliquot was freeze-dried for measurement of dry mass. The eight dried aliquots of each day were pooled for energy measurements. Nitrogen content was measured directly on the liquid samples.

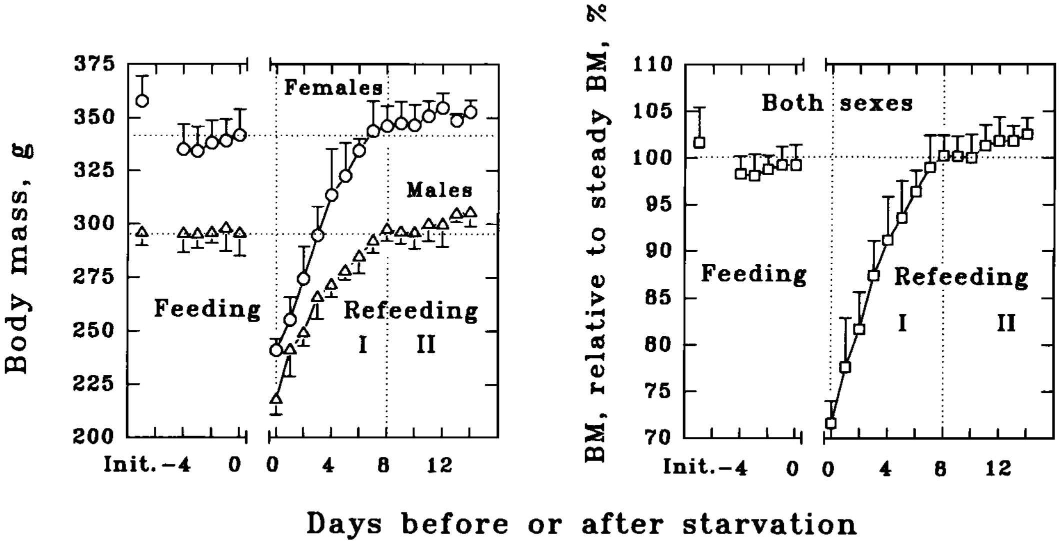

Fig. 1. Change in body mass of eight owls before and after fast. Time indicated on abcissa up to initiation of starvation (left of break) or from beginning of refeeding (right of break). Two phases defined during refeeding relative to rate of increasing body mass (vertical dotted lines). For each owl, a reference value for steady body mass calculated as mean of 12 values obtained in steady body-mass conditions: first day of housing in metabolic cage; five days of Feeding; and six days of Refeeding II (horizontal dotted line). Left panel has males and females plotted separately. Right panel has mean reference steady body mass for corresponding sex taken as 100%. Squares correspond to mean relative body mass of eight owls.

Total nitrogen was determined by Kjeldahl's method. Energy content was measured in a 0.5- to 1.0-g dry sample, using an adiabatic Parr calorimeter. Corrections were made for sulfuric and nitric acid.

The gross energy intake (GEI), corresponding to the amount of ingested energy (in W or kJ/day), was calculated by subtracting the energy content of the food scraps from the energy of the food provided. The daily metabolized energy (DME) was determined following Kendeigh (1949), as the net amount of energy obtained from the food eaten, after subtracting from GEI the gastrointestinal and urinary wastes (pellets, feces and urine).

As pointed out in Wijnandts (1984), existence metabolism is the sum of the basal metabolic rate (BMR), temperature regulation cost, heat increment of feeding (SDA), and cage locomotor activity. It only corresponds to the daily metabolized energy (DME) when body mass is constant. The slope of the relationship between DME and the daily change in body mass (DBMC) gives an estimation of the cost of unit daily change in body mass (Owen 1970). The existence metabolism and its relative proportion in the total DME can then be calculated by subtracting from DME the energy cost of the corresponding daily body mass change. The EAE, as defined in Gessaman (1972), was calculated as 100·DME/GEI. Using the same calculation with the dry mass data, the corresponding assimilation efficiency could be calculated.

Statistics.—Mean values ± SD are presented. Statistical analyses of differences among group means were performed with Pertiz' F-test (Harper 1984) and slope statistical analysis with Student's t-test. Linear regressions were performed with SigmaPlot software from Jandel Scientific.

RESULTS

Body-mass restoration.—In contrast to their considerable individual variability in fasting duration (4 to 13 days; Handrich et al. 1993), the eight refed barn-owls returned to their initial body mass in essentially the same amount of time (i.e. 8.0 ± 0.5 days; Refeeding I period). The next six days corresponded to a period of stabilization of body mass (Refeeding II period). Throughout the Feeding or Refeeding II periods, body mass varied by less than 1%. Therefore, these two periods were considered as periods of steady body mass. During Refeeding I, the daily increase in body mass was significantly greater in females (13.9 ± 1.0 g/day) than in males (9.2 ± 0.8 g/day; $P < 0.05$; Fig. 1).

Constitution of diet and waste.—The laboratory mice constituting the food of the barn-owls had a relatively high energy content of 23.1 kJ/g

TABLE 1. Components and energetic values of pellets during different periods.[a]

Pellets	Feeding (5 days)	P	Refeeding I (8 days)	P	Refeeding II (6 days)
Dry pellet loss[b] (g/day)	3.41 ± 0.54 (7)	**	5.03 ± 0.65 (7)	**	3.66 ± 0.41 (7)
Pellet dry mass[b] (g/pellet)	1.80 ± 0.30 (7)	**	2.71 ± 0.42 (7)	**	1.85 ± 0.37 (7)
Water content[c] (%)	58.6 ± 4.1 (5)		61.7 ± 5.2 (22)		57.9 ± 7.0 (14)
Dry energy content[d] (kJ/g)	15.2 ± 0.7 (7)	**	14.1 ± 0.6 (7)		14.7 ± 0.4 (7)

[a] $\bar{x}$ ± SD (n). Values separated by asterisks are significantly different (*, $P < 0.05$; ** $P < 0.01$).

[b] Means of individual means for seven owls.

[c] Measured for pellets collected at moment of regurgitation.

[d] For each bird and each defined period, measurements made on pooled homogenized samples.

compared with the 22.6 kJ/g found by Tollan (1988) or the 21.1 kJ/g of Hamilton (1985). The larger body mass (29.7 ± 0.7 g) and lower protein content (56.1 ± 4.7 %) in the mice we used indicated greater fat content.

Viscera were almost entirely removed and not eaten by the barn-owls; the viscera constituted 73% and 97% of uneaten food items in males and females, respectively. The incompletely eaten mice had a higher relative energy content than the intact ones (23.7 ± 0.1 vs. 23.1 ± 0.1 kJ/g), although the difference was not significant. The unconsumed viscera were probably rich in crude fiber, as indicated by their significantly lower energy and protein content (22.2 ± 0.1 kJ/g and 48.2 ± 0.4%, respectively).

Characteristics of pellets.—Data on pellets were available for only seven birds. As there was no difference in the composition of pellets between sexes, the results for the seven birds were pooled (Table 1) for each of the three feeding periods. The energy content of dry pellets (15.2 ± 0.7 kJ/g) in the Feeding period was slightly higher than the 13.4 kJ/g previously given by Hamilton (1985) for Common Barn-Owls acclimated to the same temperature and eating the same diet as birds in our study.

There were no significant differences in the characteristics of pellets between the two periods of steady-state body mass. The number of pellets expelled per day (1.89 ± 0.22 in Feeding) was unchanged during refeeding periods. During Refeeding I, the mean dry mass of pellets was significantly higher than in Feeding, but the energy content of pellets was significantly lower (see Table 1).

Characteristics of excreta.—The composition of the droppings (i.e. excreta) of the eight birds was compared during the three feeding periods (Table 2). The energy content of dry excreta was lower than values previously reported for the species: 9.3 ± 0.2 kJ/g versus 11.4 in Hamilton (1985), 11.5 in Graber (1962), and 12.8 in Kirkwood (1979). In this latter case, the food eaten was day-old cockerels.

No significant difference was found in the characteristics of the excreta between the two periods of steady body mass. However, there was a 1.45-fold increase in dry excreta loss per day during the Refeeding I period, with a corresponding 10% increase in the excretory energy content. Nitrogen content was unchanged during refeeding, suggesting that nitrogen was excreted in higher-energy molecules, or that nitrogen-free energetic molecules appeared during the active phase of refeeding. This could be related to an increase in the proportion of feces in droppings during the first period of refeeding, as suggested by the brown color of the excreta. During Refeeding II, the color of

TABLE 2. Components and energetic values of excreta during different periods.[a]

Excreta	Feeding (5 days)	P	Refeeding I (8 days)	P	Refeeding II (6 days)
Dry excreta loss[b] (g/day)	4.67 ± 0.40 (8)	**	6.80 ± 1.57 (8)	**	5.47 ± 0.60 (8)
Dry nitrogen content[b] (%)	23.4 ± 1.3 (8)		23.5 ± 1.8 (8)		24.1 ± 1.5 (8)
Dry ash content[c] (%)	9.3 ± 0.7 (5)		9.8 ± 0.9 (8)		10.1 ± 0.4 (6)
Dry energy content[c] (kJ/g)	9.3 ± 0.2 (5)	**	10.2 ± 0.6 (8)	*	9.4 ± 0.2 (6)

[a] $\bar{x}$ ± SD (n). Values separated by asterisks are significantly different (*, $P < 0.05$; ** $P < 0.01$).

[b] Means of individual means for eight owls.

[c] For each day, measurements made on pooled homogenized samples.

TABLE 3. Balance of dry matter and energy during different periods.[a]

Dry matter and energy	Feeding (5 days)	P	Refeeding I (8 days)	P	Refeeding II (6 days)
Dry matter intake (g/day)	16.0 ± 1.8	**	25.0 ± 3.5	**	17.7 ± 2.0
Waste[b] (%)	13 ± 6		11 ± 5		13 ± 6
Dry pellet loss[c] (%)	21.3 ± 1.1		20.3 ± 0.5		20.8 ± 0.6
Dry excreta loss[c] (%)	29.7 ± 1.3		27.7 ± 1.8	*	31.3 ± 1.4
Dry matter assimilation efficiency[c] (%)	49.1 ± 1.0	*	52.0 ± 2.2	**	47.9 ± 1.7
Gross energy intake (kJ/d)	370 ± 42	**	578 ± 82	**	409 ± 48
Pellet energy loss[d] (%)	14.0 ± 0.7	**	12.3 ± 0.4	**	13.3 ± 0.4
Excretory energy loss[d] (%)	11.9 ± 0.6		12.2 ± 0.8		12.7 ± 0.6
Energy assimilation efficiency[d] (%)	74.1 ± 0.6	*	75.5 ± 1.1	**	74.1 ± 0.8
Daily metabolized energy (DME, kJ/d)	275 ± 31	**	438 ± 68	**	304 ± 37

[a] $\bar{x}$ ± SD of individual means of seven owls. Values separated by asterisks are significantly different (*, $P < 0.05$; ** $P < 0.01$).
[b] Percentage of the meal.
[c] Percentage of dry matter intake.
[c] Percentage of gross energy intake.

excreta was cream as usually is the case during feeding (i.e. reflecting a high proportion of uric acid).

Dry matter and energetic balances.—The losses of dry matter in the form of pellets and excreta (in percentage of daily dry matter intake; Table 3) were higher in our study than those calculated from the data of Hamilton (1985) on the American subspecies (*T. a. pratincola*): 17.5% for pellets, and 16.1% for excreta. Since this subspecies is approximately 1.5-fold heavier than the European subspecies (Marti 1990), it should have a more complete digestion of bones in pellets, as suggested by Duke et al. (1975, 1976) in their comparison of pellet composition among owl species of different body sizes. However, the discrepancy in these excreta results may be due to differences in collection procedure, evaporation, or fermentation. In our case, considerable attention was given to ways of circumventing this problem (see methods in Handrich et al. 1993). Consequently, the assimilation efficiency of dry matter in our study (49.1 ± 1.0%) is considerably lower than the 66.1% found by Hamilton (1985) and, to a lesser degree, than the 54.4% found by Kirkwood (1979).

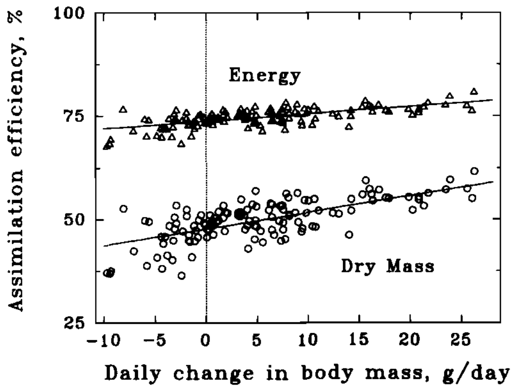

Fig. 2. Assimilation efficiency in dry mass (DMAE, %) and in energy (EAE, %), calculated for each owl (n = 7) and for each day (n = 19), plotted against daily body-mass change (DBMC, g/day). Linear regressions: DMAE = 47.7 + 0.405·DBMC; EAE = 73.7 + 0.179·DBMC.

However, EAE (74.1 ± 0.6%) is similar to the 75% mean value for carnivorous birds (Castro et al. 1989), and to the available values for barn-owls (78.4 in Hamilton 1985, 77% in Wijnandts 1984 or in Wallick and Barrett 1975, 75% in Ceska 1980).

Refeeding I was characterized by a significant 1.6-fold increase in GEI and DME. It was associated with a slight, but nevertheless significant, increase of 1.4% in EAE. There also was a significant increase in dry-matter assimilation efficiency, of less than 10% of the initial value, due to a slight reduction of the relative dry-matter loss in excreta and pellets. However, this was partially hidden by the increase in excretory energy content, so that the only factors that effectively contributed to enhance EAE were the parallel decreases in the energy content of pellets and their relative loss of dry mass. Refeeding II values tended to be intermediate between Feeding and Refeeding I, but the differ-

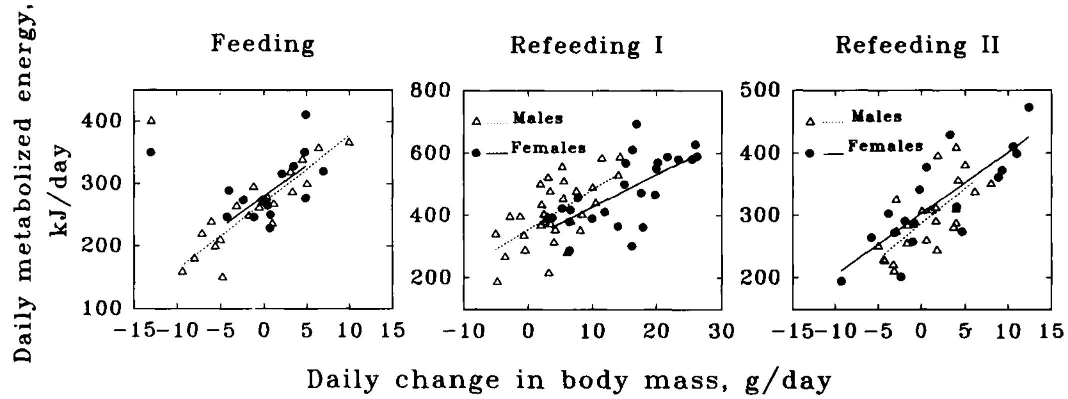

Fig. 3. Individual daily metabolized energy, calculated for each owl ($n = 7$) and for each day ($n = 19$), plotted separately for three periods of feeding. Linear regression analyses performed separately for males ($n = 4$) and females ($n = 3$; see Table 4).

ences between the two steady-body-mass stages were not significant (Table 3).

Using the energy contents of consumed mice, expelled pellets, and excreta calculated in the different feeding periods, we calculated the individual daily energy factors (GEI, DME and EAE) from the individual daily balances in dry mass ($n = 233$; 7 owls; 5, 8, and 6 days, respectively). There was a positive correlation with daily body-mass change (DBMC) for the dry mass assimilation efficiency (DMAE, $r = 0.73$, $P < 0.001$) and for the energy assimilation efficiency (EAE, $r = 0.71$, $P < 0.001$). The slope of linear regression for DMAE versus DBMC was 0.405 ± 0.033%$\cdot$(g/day)$^{-1}$; for EAE versus DBMC it was 0.179 ± 0.016%$\cdot$(g/day)$^{-1}$ (see linear regressions in Fig. 2).

Cost of daily change in body mass and existence metabolism.—The relation between daily metabolized energy and daily change in body mass was tested for both sexes with the individual data shown in Figure 3 for each period of feeding. The intercepts of the regression equations correspond to the existence metabolism, whereas the slopes refer to the energy cost of 1 g of daily change in body mass (Table 4). This energy cost showed no significant difference between sexes, or among feeding periods, despite higher values during Refeeding I. During Refeeding I, although the body mass was still lower than before starvation, the mean existence metabolism was surprisingly higher in both sexes (1.32-fold higher in males and 1.16 in females; Table 4).

TABLE 4. Existence metabolism (EM) and energy cost of daily change in body mass (K).[a]

	Feeding (5 days)		Refeeding I (8 days)		Refeeding II (6 days)	
	Males ($n = 20$)	Females ($n = 15$)	Males ($n = 32$)	Females ($n = 24$)	Males ($n = 24$)	Females ($n = 18$)
Existence metabolism[b] (EM), kJ/day	270.0 ± 7.1	280.2 ± 10.0	355.2 ± 1.8	324.4 ± 4.7	286.8 ± 9.6	303.1 ± 7.9
Energy cost of daily change in body mass[b] (K), kJ/g	10.8 ± 1.4	10.0 ± 3.6	12.8 ± 3.2	10.4 ± 2.7	11.2 ± 3.1	9.8 ± 1.2
Correlation coefficient, r	0.89	0.63	0.59	0.65	0.65	0.81
P	0.001	0.01	0.05	0.05	0.01	0.001

[a] $\bar{x}$ ± SD.

[b] EM and K values obtained from linear regressions for each sex and each period, using the equation: DME = EM + K$\cdot$DBMC, where DME and DBMC, respectively, are daily metabolized energy and daily change in body mass. Existence metabolism differed significantly ($P < 0.01$) between sexes in the three periods of feeding and among these periods for each sex. The energy cost of daily change in body mass was not significantly different between sexes or between periods of feeding.

DISCUSSION

Several studies using laboratory rats have shown that food is more efficiently processed into body reserves after a period of forced depletion in energy intake (Björntorp and Yang 1982, Brownell et al. 1986). Based on increase in food efficiency and decrease of existence metabolism, these data mean that EAE increases during refeeding in the rat. The key question obviously is the extrapolation of laboratory data to the field. Still, for wild animals, it is currently assumed that EAE is constant whatever the gross energy intake and daily change in body mass. Quite unexpectedly our data support this assumption, since there was no more than 1% change in EAE among the three periods of feeding. Such a slight change is indeed negligible in comparison to the effects of ambient temperature (Gessaman 1972, Stalmaster and Gessaman 1982), age (Raczynski and Ruprecht 1974, Wijnandts 1984), or diet composition (Duke et al. 1973, Stalmaster and Gessaman 1982, Wijnandts 1984, Tollan 1988, Castro et al. 1989). Therefore, the question is why EAE increases in the rat, whereas it does not under our experimental conditions in the Common Barn-Owl.

Body-mass restoration and daily-food intake.—The overall GEI of the barn-owls for the total duration of the experiment was compared to the theoretical GEI that the birds would have ingested if, instead of being fasted, they had maintained their initial daily-food intake during that time (which includes the duration of starvation; see Handrich et al. 1993). The experimental birds used 81 ± 1% of the food eaten by birds in the theoretical control group, calculations being made individually for each barn-owl. This means that there is an overall energetic advantage in starving and then restoring body reserves, even though the EAE is not strongly affected during refeeding.

The barn-owls used 35 ± 0.12% more energy (GEI) during Refeeding I than if they had maintained the initial prefasting daily-food intake during the same time. This represents a major difference from findings for laboratory rats, in which the restoration of initial body composition is achieved without a large increase in food intake (Hill et al. 1984). To compare the food efficiency of rats before and after fasting, a coefficient has been introduced, which corresponds to the rate of increase in body mass per unit of food intake (Björntorp and Yang 1982, Brownell et al. 1986). This rate is higher during refeeding, therefore indicating an increased food efficiency. It can only be attributed to a decrease in existence metabolism (Hill et al. 1984), since as indicated above there is only a slight increase in food intake during refeeding. Because the prefasting body mass of the barn-owls in our study was at steady state, such a coefficient that assumes continuous growth cannot be calculated. The question was then to determine whether a change in existence metabolism accompanies the increase of food intake during refeeding in the Common Barn-Owl. Since the cost of daily change in body mass was calculated in this study, the existence metabolism (DME at constant body mass) could indeed be determined during Refeeding I.

Cost of daily change in body mass.—This cost includes the cost of biosynthesis and the energy equivalent of accumulation of body reserves (Brown 1987). If the energy cost of biosynthesis is assumed to be constant (Ricklefs 1974), the latter obviously depends on the composition of the accumulated energy (i.e. proportion of lipids versus proteins). Another key factor that largely influences the relation between daily changes in body reserves and in body mass is fluctuations in water balance. However, our data indicate that there is no significant change in the cost of daily change in body mass between the period of increasing body mass and the two periods of steady state. Still, the mean cost of daily change in body mass, when taking into account all values for both sexes and all feeding stages, was 10.8 ± 2.1 kJ/g, slightly lower than the 13.5 kJ/g found in the Long-eared Owl (*Asio otus*) during normal feeding (Wijnandts 1984).

No decrease of existence metabolism during refeeding.—Using the 10.8 kJ/g calculated mean value of the energetic cost of daily change in body mass, the fraction of the existence metabolism in DME was calculated for the seven owls pooled on each day of the experiment (Fig. 4). Since there was no reduction of existence metabolism during refeeding, the only way to restore the body mass was to increase food consumption. After the third day of refeeding, the existence metabolism had reached the prefasting feeding values, whereas the body mass was still 50 g (14%) below the steady-state value. From the allometric relationship of caged metabolized energy (at constant body mass) for nonpasserine birds of a given body mass W (EM

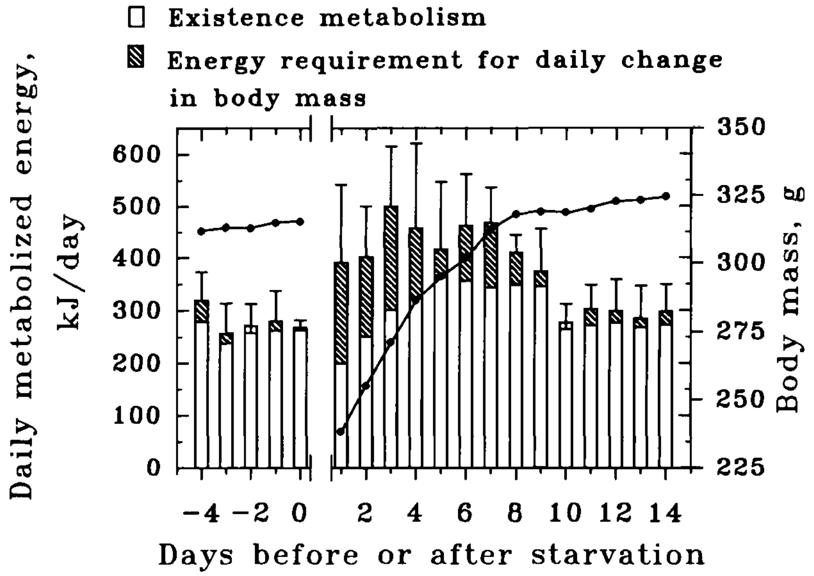

Fig. 4. Daily metabolized energy (DME; $\bar{x} \pm$ SD, $n = 7$ owls) throughout three feeding periods as arithmetic sum of existence metabolism (open bars) and energy requirement for daily change in body mass (hatched bars). Existence metabolism for given day calculated as mean of individual differences between DME and energy requirement for corresponding change in body mass ([10.8 kJ/g]·DBMC). Closed circles indicate mean body mass.

$= 11.41W^{0.592}$; Kendeigh et al. 1977), a reduction of 9% would have been predicted. Already after the fourth day of refeeding (Fig. 4), the increment in DME compared to the prefasting level was partly due to an enlarged existence metabolism. Furthermore, after the steady state in body mass had been restored in the Refeeding II period, the existence metabolism still remained higher than before fasting, even for the males where the body mass did not exceed the prefasting value (see Fig. 1).

Finally, these data indicate that existence metabolism increases in proportion with the increase in daily food consumption. Therefore, it is not surprising to find only a slight increase in EAE during refeeding. The only way to enhance EAE in such conditions is through greater digestive efficiency. This seems to be confirmed by the observed decrease of the relative energy loss in the form of pellets during Refeeding I.

Existence metabolism and body mass.—The large variation in body mass for the individual barn-owls during Refeeding I enabled us to determine the allometric relationship between existence metabolism and body mass (calculated by correcting DME according to the cost of daily change in body mass; Fig. 5). The allometric coefficient (slope of Ln/Ln relationship) was greater than unity for both sexes. It is also remarkable that we found a similar slope (1.5) by plotting our present data obtained for females during the normal period of feeding and the mean value obtained in the same situation of feeding and temperature on females of the larger North American subspecies (Hamilton 1985). Thus, there is an influence of body mass on caged existence metabolism that is larger than predicted, both within individuals and within subspecies. Such a large value for the allometric coefficient, higher than unity, has also been found in the Eurasian Kestrel (*Falco tinnunculus*), a diurnal raptor (Daan et al. 1989). For these kestrels, basal metabolic rate (BMR) varied in the individual birds to $W^{1.67}$ when body mass (W) was reduced using different hypocaloric diets. This important decrease in BMR was partly explained by a decrease in core temperature during the resting phase. However, circadian variation of core temperature appears lower in nocturnal raptors (Chaplin et al. 1984).

Existence metabolism, thermoregulation and locomotion.—The existence metabolism is the sum of basal metabolic rate (BMR), energy requirement for temperature regulation, heat increment of feeding (SDA), and locomotor activity. During a period of increasing body mass, if DME

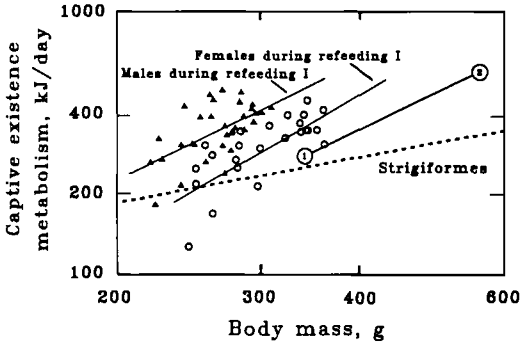

Fig. 5. Existence metabolism (i.e. daily metabolized energy [DME in kJ/day] at constant body mass) plotted against body mass (log-log units; filled triangles for males, $n = 32$, $r = 0.55$, $P < 0.01$; hollow circles for females, $n = 24$, $r = 0.75$, $P < 0.001$). Symbols in both sexes are individual calculated values of existence metabolism during period of body mass restoration (i.e. Refeeding I). Allometric coefficients (slopes in log-log units) of 1.56 ± 0.42 and 1.73 ± 0.33 for males and females, respectively, were not significantly different. Numbered circles indicate mean DME of female barn-owls at a steady body mass at 5°C. Circled 1 corresponds to experimental birds during Feeding period and circled 2 to value obtained on heavier North American subspecies (*Tyto alba pratincola*; Hamilton 1985). Dashed line represents corresponding allometric relation for Strigiformes (allometric coefficient 0.58; Wijnandts 1984).

is the sum of the existence metabolism and the energy cost of the new reserves and their biosynthesis, a part of the energy for food processing itself contributes to the increase in existence metabolism—the so-called heat increment of feeding. It should also partly explain the increase of existence metabolism during refeeding in the Common Barn-Owl. However, the additional heat liberated by the SDA of food digestion could have been used to reduce thermoregulatory cost (Tollan 1988). This explains the positive effect of cold on EAE found in other birds (Gessaman 1972, Stalmaster and Gessaman 1982).

In rats, the low existence metabolism during refeeding seems independent of a reduction in locomotor activity (Boyle et al. 1981). Inversely, a rapid increase of locomotor activity at the end of fasting or no decrease during fasting (see Handrich et al. 1993) would explain a large part of the surprisingly high value of the existence metabolism during Refeeding I in the captive barn-owls.

Extrapolation to the field.—It may seem paradoxical that a wild species such as the Common Barn-Owl, which naturally encounters periods of food scarcity, is unable to conserve its energy better during refeeding, apparently in contrast to laboratory rats and even humans. In the wild, the ability to restore body reserves after a long period of starvation depends upon this physiological response, but also on environmental factors such as prey availability and hunting cost.

Considering the maximum capacity to refeed and restore body mass, it is of interest that Kirkwood (1983) has developed an allometric relation to predict the maximum limit of DME for mammals or birds of a given body mass (1,713 $kJ/kg^{0.72}$). In our study, this limit was reached during Refeeding I in only two cases. For example, on day 4 of refeeding, a female weighing 305 g ate four mice (120 g of fresh mass, 891 kJ), providing a DME of 693 kJ (equal to 95% of the theoretical limit). This maximum amount of daily food intake is similar to the maximum values found in the field, based on pellet analyses of barn-owls: 6 to 7 short-tailed voles (*Microtus arvalis*) or 13 common shrews (*Crocidura* sp.) in a single pellet for the day, corresponding to 120 to 140 g of fresh mass (Bunn et al. 1982). Using values for body composition of prey in Wijnandts (1984), this corresponds approximately to the same maximum value of GEI (910 kJ/day).

Although in our study the food was given *ad libitum* during the feeding periods, a high daily food intake close to the theoretical maximum limit was only found in two cases. Thus, the mean relative value during Refeeding I was only 63% of the theoretical limit. Therefore, a larger GEI theoretically should still be possible, and then a higher rate of restoration of the initial body mass after starvation. However, it is remarkable that the mean rate of increasing body mass during Refeeding I (13.9 g/day in females versus 9.2 g/day in males) was very close to the mean growth rate of young owls in captivity (13.9 g/day in females versus 12.5 g/day in males during the linear part of their growth, between 10 and 30 days after hatching; unpubl. data) or to the 12.5 g/day value calculated from Guerin (1928), who studied a brood of wild Common Barn-Owls during a year at the time voles pullulate.

Let us assume that, as for DME, there is an upper limit for the rate of biosynthesis of body reserves and, thus, for the rate of restoration of body mass. In this case, Common Barn-Owls are able to reach this upper limit in captivity without reaching a maximum food intake rate. Similarly, in the wild, where the hunting cost represents an important part of DME, a rate of 10 to 13 g/day for restoration of the body mass is a possible maximum, whatever the prey availability may be.

Considering the influence of hunting on the rate of body-mass restoration, it is unfortunate that quantitative data on the bioenergetics and of the foraging energy expenditure in wild raptors usually are not available for the same species. Using data from Wijnandts (1984) and Masman et al. (1988a, b), the hunting costs of 1 kJ of captured prey in winter are 0.30 kJ/kJ for the Long-eared Owl and 0.21 kJ/kJ for the Eurasian Kestrel. For the Long-eared Owl, DME was 252 kJ/day, EAE was 72%, and daily hunting expenditure was 104 kJ/day. For the kestrel, DME was 273 kJ/day, EAE was 67%, and the daily hunting energy expenditure was 87.1 kJ/day. The hunting modes of these two species are similar to that of the Common Barn-Owl, with both exhibiting a mixture of active and sit-and-wait hunting modes (Jaksic and Carothers 1985). Let us assume that for Common Barn-Owls in winter, as for Long-eared Owls (Wijnandts 1984), the extra energy spent in the field in comparison to the metabolized energy in captivity (DME_c) is due to hunting energy expenditure. It is then possible to evaluate the daily metabolized energy (DME_f) of a wild Common Barn-Owl to restore its initial body mass with the maximum rate measured in captivity. Using an energetic hunting yield of 25% and the 75.5% EAE value measured during Refeeding I, the DME_f should be 1.5-fold higher than DME_c (i.e. $DME_f = 75.5/[75.5 - 25.0] \cdot DME_c$). Using the mean measured DME_c in Refeeding I (438 kJ/day), the value of DME_f should be approximately 650 kJ/day. The interest in this extrapolated value is that the corresponding GEI (860 kJ/day) is still below the maximum GEI in the field (910 kJ/day) estimated by pellet analyses.

Finally, providing food is readily available during the phase of restoration of body mass, the maximum rate of increase in body mass measured in captivity is still possible for a wild Common Barn-Owl.

ACKNOWLEDGMENTS

The authors thank A. Malan and R. R. Stewart for help in editing the manuscript.

LITERATURE CITED

BAUDVIN, H. 1975. Biologie de reproduction de la Chouette Effraie (*Tyto alba*) en Côte d'or. Premiers résultats. Le Jean le Blanc 14:1–51.

BAUDVIN, H. 1976. Biologie de reproduction de la Chouette Effraie (*Tyto alba*) en Côte-d'or. Premiers résultats. *Addendum*. Le Jean le Blanc 15: 29–32.

BJÖRNTORP, P., AND M-U. YANG. 1982. Refeeding after fasting in the rat: Effects on body composition and food efficiency. Am. J. Clin. Nutr. 36:444–449.

BOYLE, P. C., L. H. STORLIEN, A. E. HARPER, AND R. E. KEESEY. 1981. Oxygen consumption and locomotor activity during restricted feeding and realimentation. Am. J. Physiol. 241:R392–R397.

BROWN, C. R. 1987. Energy requirements for growth and maintenance in Macaroni and Rockhopper penguins. Polar Biol. 8:95–102.

BROWNELL, K. D., M. C. R. GREENWOOD, E. STELLAR, AND E. E. SHRAGER. 1986. The effects of repeated cycles of weight loss and regain in rats. Physiol. & Behav. 38:459–464.

BUNN, D. S., A. B. WARBURTON, AND R. D. S. WILSON. 1982. The Barn Owl. T. & A. D. Poyser, Calton, United Kingdom.

CASTRO, G., N. STOYAN, AND J. P. MYERS. 1989. Assimilation efficiency in birds: A function of taxon or food type? Comp. Biochem. Physiol. A Comp. Physiol. 92:271–278.

CESKA, V. 1980. Untersuchungen zu Nahrungsverbrauch, Nahrungsnutzung und Energie-haushalt bei Eulen. J. Ornithol. 121:186–199.

CHAPLIN, S. B., D. A. DIESEL, AND J. A. KASPARIE. 1984. Body temperature regulation in Red-tailed Hawks and Great Horned Owls: Responses to air temperature and food deprivation. Condor 86:175–181.

DAAN, S., D. MASMAN, A. STRIJKSTRA, AND S. VERHULST. 1989. Intraspecific allometry of basal metabolic rate: Relations with body size, temperature, composition, and circadian phase in the Kestrel, *Falco tinnunculus*. J. Biol. Rhythms 4:267–283.

DUKE, G. E., J. G. CIGANEK, AND O. A. EVANSON. 1973. Food consumption and energy, water, and nitrogen budgets in captured Great-horned Owls (*Bubo virginianus*). Comp. Biochem. Physiol. A Comp. Physiol. 44:283–292.

DUKE, G. E., O. A. EVANSON, AND A. A. JEGERS. 1976. Meal to pellet intervals in 14 species of captive raptors. Comp. Biochem. Physiol. A Comp. Physiol. 53:1–6.

DUKE, G. E., A. A. JEGERS, G. LOFF, AND O. A. EVANSON. 1975. Gastric digestion in some raptors. Comp. Biochem. Physiol. A Comp. Physiol. 50:649–656.

FRYLESTAM, B. 1972. Über Wanderungen und Sterblichkeit beringter Skandinavisher Scheiereulen *Tyto alba*. Ornis Scand. 3:45–54.

GESSAMAN, J. A. 1972. Bioenergetics of the Snowy Owl (*Nyctea scandiaca*). Arc. Alp. Res. 4:223-238.

GRABER, R. R. 1962. Food and oxygen consumption in three species of owls (*Strigidae*). Condor 64: 473-487.

GUERIN, P. 1928. Contribution à l'étude d'une avifaune régionale. La vie des Chouettes. Régime et croissance de l'Effraie commune *Tyto alba alba (L.)* en Vendée. P. & O. Lussaud, Fontenay-Le-Comte, France.

HAMILTON, K. L. 1985. Food and energy requirements of captive Barn Owls *Tyto alba*. Comp. Biochem. Physiol. A Comp. Physiol. 80:355-358.

HANDRICH, Y., L. NICOLAS, AND Y. LE MAHO. 1993. Winter starvation in captive Common Barn-Owls: Physiological states and reversible limits. Auk 110:458-469.

HARDY, A. R., G. J. M. HIRONS, AND P. I. STANLEY. 1981. The relationship of body weight, fat deposit and moult to the reproductive cycles in wild Tawny Owls and Barn Owls. Pages 159-163 *in* Recent advances in study of raptor diseases (J. E. Cooper and A. G. Greenwood, Eds.). Chirons Publications, Keighley, United Kingdom.

HARPER, J. F. 1984. Pertiz' *F* test: Basic program of a robust multiple comparison test for statistical analysis of all differences among group means. Comput. Biol. Med. 14:437-445.

HILL, J. O., S. K. FRIED, AND M. DIGIROLAMO. 1984. Effects of fasting and restricted refeeding on utilization of ingested energy in rats. Am. J. Physiol. 247:R318-R327.

HONER, M. R. 1963. Observation on the Barn Owl (*Tyto alba guttata*) in the Netherlands in relation to its ecology and population fluctuations. Ardea 51:159-195.

JAKSIC, F. M., AND J. H. CAROTHERS. 1985. Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. Ornis Scand. 16:165-172.

JOHNSON, W. D. 1974. Bioenergetics of the Barn Owl, *Tyto alba*. M.S. thesis, California State Univ., Long Beach.

KENDEIGH, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk 66:111-127.

KENDEIGH, S. C., V. R. DOLNIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pages 127-204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge Univ. Press, Cambridge.

KIRKWOOD, J. K. 1979. The partition of food energy for existence in the Kestrel (*Falco tinnunculus*) and the Barn Owl (*Tyto alba*). Comp. Biochem. Physiol. A Comp. Physiol. 63:495-498.

KIRKWOOD, J. K. 1983. A limit to metabolisable energy intake in mammals and birds. Comp. Biochem. Physiol. A Comp. Physiol. 75:1-3.

MARTI, C. D. 1990. Sex and age dimorphism in the barn owl and a test of mate choice. Auk 107:246-254.

MARTI, C. D., AND P. W. WAGNER. 1985. Winter mortality in Common Barn-Owls and its effect on population density and reproduction. Condor 87: 111-115.

MASMAN, D., S. DANN, AND H. J. A. BELDHUIS. 1988a. Ecological energetics of the Kestrel: Daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. Ardea 76:64-81.

MASMAN, D., S. DANN, AND C. DIJKSTRA. 1988b. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. J. Anim. Ecol. 57:411-432.

MULLER, Y. 1987. Statut de la Chouette Effraie (*Tyto alba*) dans les clochers d'église en Alsace-Lorraine. Fluctuation des effectifs au cours de dix années d'études. Ciconia 11:1-22.

OWEN, R. B., JR. 1970. The bioenergetics of captive Blue-winged Teal under controlled and outdoor conditions. Condor 72:153-163.

RACZYNSKI, J., AND A. L. RUPRECHT. 1974. The effect of digestion on the osteological composition of owl pellets. Acta Ornithol. (Warsaw) 14:25-36.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Publ. Nuttall Ornithol. Club 15:152-292.

SCHÖNFELD, M., G. GIRBIG, AND H. STURM. 1977. Beitrage zur Populations Dynamik der Schleiereule *Tyto alba*. Hercynia 14:303-351.

SHAWYER, C. R. 1987. The Barn Owl in the British Isles. Its past, present and future. The Hawk Trust, London.

STALMASTER, M. V., AND J. A. GESSAMAN. 1982. Food consumption and energy requirements of captive Bald Eages. J. Wildl. Manage. 46:646-654.

TOLLAN, A. M. 1988. Maintenance energy requirements and energy assimilation efficiency of the Australian Harrier. Ardea 76:181-186.

WALLICK, L. G., AND G. W. BARRETT. 1975. Bioenergetics and prey selection of captive Barn Owls. Condor 77:139-141.

WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). Ardea 72:1-92.