BODY COMPOSITION OF THE EUROPEAN BARN OWL DURING THE NONBREEDING PERIOD[1]

SYLVIE MASSEMIN, RENÉ GROSCOLAS AND YVES HANDRICH

Centre d'Ecologie et Physiologie Energétiques, CNRS UPR 9010, associé à l'Université Louis Pasteur,
23 rue Becquerel, 67087 Strasbourg Cedex 2, France, e-mail: massemin@c-strasbourg.fr

Abstract. The body composition of Barn Owls (*Tyto alba*) killed on motorways in the northeastern part of France during autumn and winter was studied in relation to their age, sex, body size, and season. Body composition differed greatly among individuals. In mature and immature birds of both sexes, body mass and body lipid were highest in early winter, whereas body protein did not show seasonal changes. Thus, body mass increase was due to accumulation of body lipid. Maximum (14%) and average (10%) adiposity of males and females were very similar, but body protein was higher in females than in males. This difference is explained by the larger skeletal size of females, and it disappears after size-adjustment. Relative to other data on captive fed or fasted Barn Owls, and based on body lipid, 54, 40 and 6% of the present birds were considered as nondepleted, partly-depleted and emaciated, respectively. The adiposity of nondepleted males and females and of mature and immature individuals were similar and averaged 12.5%, intermediate compared to other bird species. In contrast to previous suggestions, we conclude that Barn Owls accumulate lipid reserves as frequently as do other bird species, in anticipation of cold weather and food scarcity. During mild winters, most of the road-killed Barn Owls were in good nutritional condition. We found no evidence for a sex difference in the energy strategy of Barn Owls during the nonbreeding period.

Key words: Barn Owls, body composition, structural size, nonbreeding period, Tyto alba.

INTRODUCTION

During the winter season, the survival of birds in adverse climatic conditions can be greatly affected by nutrient reserves (Blem 1990, Suter and van Eerden 1992). Whereas this aspect of bird biology has been largely investigated in passeriformes, shorebirds and waterfowl, little work has concerned the nutrient reserves of sedentary raptors. To study the influence of low temperatures and food scarcity during winter on population size of raptors, we are using the Barn Owl (*Tyto alba*) as a model system. Among raptors, the Barn Owl is one of the few species for which many individuals can be obtained because of high mortality by road accidents (Baudvin et al. 1991, Taylor 1994). The Barn Owl is vulnerable to cold weather and prolonged snow cover, which is generally attributed to its inability to accumulate sufficient body reserves compared to other raptors of the same size (Piechocki 1960, Schönfeld et al. 1977, de Bruijn 1994). However, this assumption is based on results from a single study (Piechocki 1960) of the fat deposits in a sample of Barn Owls which included some individuals that had suffered nutritional stress.

A previous study on wild Barn Owls found dead on motorways during winter shows that their body mass is close to that of captive individuals fed ad libitum, and that it increases in early winter (Massemin et al., in press). This suggests that a majority of these killed birds was not affected by nutritional stress. However, it is well known that besides being related to structural size, body mass changes according to levels of lipid and/or protein reserves. In many bird species, seasonal variation of body lipid, such as an accumulation before winter in anticipation of cold weather and food scarcity, have been observed (King and Murphy 1985, Blem 1990). Body protein also can be used to cope with energetic stress (Witter and Cuthill 1993) or can be stored at particular periods of the annual cycle, such as before molt (Cherel et al. 1994) or migration (Piersma 1994). In winter, a trade-off would exist between an increase in body protein for the maintenance of thermogenesis during severe weather (Piersma 1994) and a decrease of body protein to improve ability to survive starvation during a period of food scarcity (Handrich et al. 1993b). The determination of the energy status and strategy of the Barn Owl during winter therefore requires the measurement of body size and reserves.
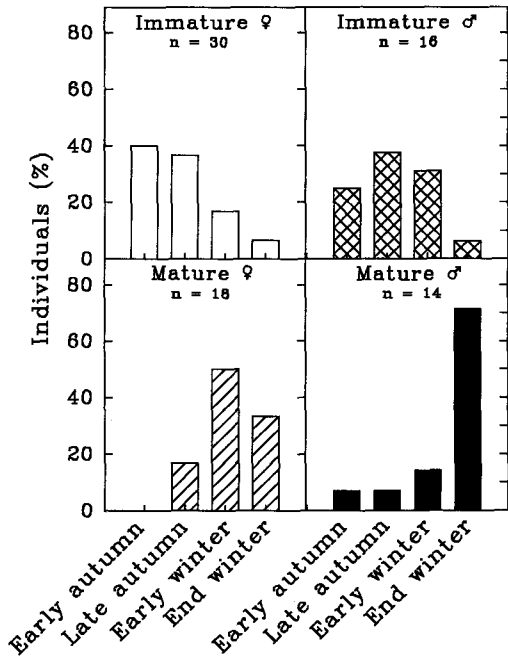
FIGURE 1. Seasonal distribution of killed Barn Owls in four age and sex categories.

This article focuses on body composition of Barn Owls during the nonbreeding period. Its main objectives are to characterize the seasonal changes in body composition according to sex and age, compare the body composition of males and females and determine how it relates to structural size, and estimate nutritional status from body composition. This was done through the study of a large sample of Barn Owls killed on motorways.

METHODS

BIRD SAMPLING

Barn Owls killed by cars on motorways were collected in the northeastern part of France (Al-sace-Lorraine from 1991 to 1993, Champagne and Rhône-Alpes in 1992) during autumn and winter nonbreeding periods. The weather was mild during these seasons with mean air temperature above $-1°C$ and duration of snow cover less than 3 days. The nonbreeding period was divided into four seasonal periods using the rule of Sturge (Scherrer 1984). The four seasonal periods studied were early (1 October–15 November) and late (16 November–31 December) autumn and early (1 January–15 February) and late (16 February–31 March) winter.

Birds selected ($n = 78$) were relatively intact individuals (not crushed) whose date of death was known. Sex was determined by gonad identification. Two age classes, immature and mature, were identified based on the bursa of Fabricius; individuals without a bursa of Fabricius were considered mature. The sample consisted of four categories: 30 immature females, 18 mature females, 16 immature males and 14 mature males. The distribution over the four seasonal periods of individuals belonging to each of these categories is shown in Figure 1. Immature females, and to a lesser extent immature males, were killed mostly in autumn. Mature males and females were killed mostly in winter.

DETERMINATION OF BODY COMPOSITION AND STRUCTURAL SIZE

Total body mass ($\pm$ 0.1 g) was defined as the mass of a bird after removal of the stomach contents, and body mass was defined as the mass of a bird after removal of the digestive contents and feathers. Total mass of body lipid and protein were predicted from the mass of different body components using linear regression equations developed in a previous study (Massemin et al., unpubl. data; Table 1). As a prerequisite, two types of birds have to be considered: non-emaciated birds with abdominal adipose tissue

TABLE 1. Regressions used to predict body lipid, body protein and skeletal ash in Barn Owls.

	Birds with AAT		Birds without AAT	
	R^2	Regression	R^2	Regression
Body lipid (g)	0.98	$\hat{Y} = -10.86 + 1.87DMS + 0.18RDBM^a$	0.96	$\hat{Y} = -0.01 + 13.84LLM^a$
Body protein (g)	0.89	$\hat{Y} = -0.02 + 0.78LDBM^a$	0.98	$\hat{Y} = -3.19 + 0.82LDBM^a$
Skeletal ash (g)	0.99	$\hat{Y} = 1.93 + 6.51AH + 18.36ACSC^b$		

AAT: Abdominal Adipose Tissue, R^2: coefficient of determination.
[a] These regressions were developed from a sample of wild Barn Owls ($n = 38$; Massemin. et al., unpubl. data).
[b] This regression was developed from a sample of captive Barn Owls ($n = 9$) and is valid for birds with and without AAT (Thouzeau. et al., unpubl. data).
DMS: Dry Mass of whole Skin; LLM: Lipids of Leg Muscles; RDBM: Remaining Dry Body Mass = dry body mass minus dry mass of whole skin; LDBM: Lean Dry Body Mass; AH: Ashes of Humerus; ACSC: Ashes of Coracoid, Scapula and Clavicle.

(AAT) and emaciated birds without AAT. To estimate body lipid, the specific excised tissues were the whole skin except toes (integument, subcutaneous adipose tissue, and adipose tissue deposits on muscles) in birds with AAT, and all muscles attached to the legs (femur and tibiotarse bones) in birds without AAT. These tissues and the remaining carcass were freeze-dried to determine their dry mass. Dry body mass corresponded to the sum of the dry masses of the above-mentioned tissues and of the remaining carcass. Body mass minus dry body mass yielded body water. Lean dry body mass was defined as dry body mass minus the predicted mass of body lipid. This variable allowed us to predict body protein in the two types of birds (Table 1). Leg muscles were ground into a fine homogeneous powder. Leg muscle lipids were measured by a gravimetric method after extraction according to Folch et al. (1957) and were used to predict body lipid in birds without AAT. For birds with AAT, the relative error of the estimation of body lipid and body protein is 5% and 2%, respectively; for birds without AAT it is 9% and 2%, respectively.

Wing span (with feathers), length of the trunk (from the first thoracic vertebra to the rump), humerus, bill, and claws were measured to the nearest mm. Skeletal ash was predicted from the mass of ashes of a few bones (humerus, coracoid, clavicle, and scapula, Table 1) obtained after heating at 500°C for 24 hr in a muffle furnace. The predicted skeletal ash is accurate (relative error of 1%), and mass of skeletal ash is constant, whatever the nutritional status of Barn Owls (Thouzeau et al., unpubl. data). The mass of skeletal ash therefore was used as an index of structural size.

CRITERIA FOR NUTRITIONAL STATUS

Birds were classified as having one of three nutritional statuses according to body lipid. We defined "nondepleted birds" as those whose body lipid or adiposity (body lipid/total body mass) was higher than or equal to that of the leanest individual among captive Barn Owls fed ad libitum during winter, i.e., 30 g of body lipid or 12% (Thouzeau et al. 1995). "Partly-depleted birds" were defined as individuals with AAT and < 30 g of body lipid. "Emaciated birds" were defined as individuals without AAT. Their body lipid mass was ≤ 14 g. The absence of AAT is a good criterion for a critical nutritional

state in birds (Dewasmes et al. 1980, Robin et al. 1991), including Barn Owls (Massemin et al., unpubl. data). During fasting, this critical state, called "phase III" (Le Maho et al. 1981), is characterized by an increase in protein breakdown following a threshold depletion of body lipid.

STATISTICAL ANALYSES

Student's t-test or analysis of variance (ANOVA) followed by the Student-Newman-Keuls test were used to compare means between two or more groups, respectively. When the normality test failed, a nonparametric test was used to compare two (Mann-Whitney U-test) or more groups (Kruskal-Wallis H-test). For comparison of proportions, arcsine transformation followed by the chi-square test was performed. The Spearman rank correlation was used for comparing time changes of two variables (Scherrer 1984). Principal component analysis (PCA) was used to determine which factors (size, sex, age, season) explained the range of Barn Owl body composition. PCA is an eigenvector ordination technique for displaying variables in a Pearson correlation matrix, which weights all variables equally. A variable with a high correlation with a principal axis explains a large part of inertia of this axis (STAT-ITCF, Dervin 1988). Values presented are means ± SE.

RESULTS

PRINCIPAL FACTORS OF BODY COMPOSITION VARIATIONS

Body mass of the 78 birds analyzed ranged from 186–295 g. There was considerable variability in body composition. Body lipid varied between 4 and 66 g, body protein between 40 and 60 g, and skeletal ash between 10 and 14 g. The results of the PCA on body lipid, body protein and skeletal ash are presented in Figure 2. The first principal component (A1) was highly correlated with body protein ($R^2 = 0.86$). The second principal component (A2) was uncorrelated with sex, age or season. Part of the variability in body protein was explained by the structural size (skeletal ash) of birds ($R^2 = 0.40, P < 0.001$). Birds with the highest masses of body protein were principally females. Their structural sizes also were the largest of the sample. In contrast, body lipid was not influenced by structural size ($R^2 = 0.06$). Considering the sample as a whole, there was a significant correlation between body
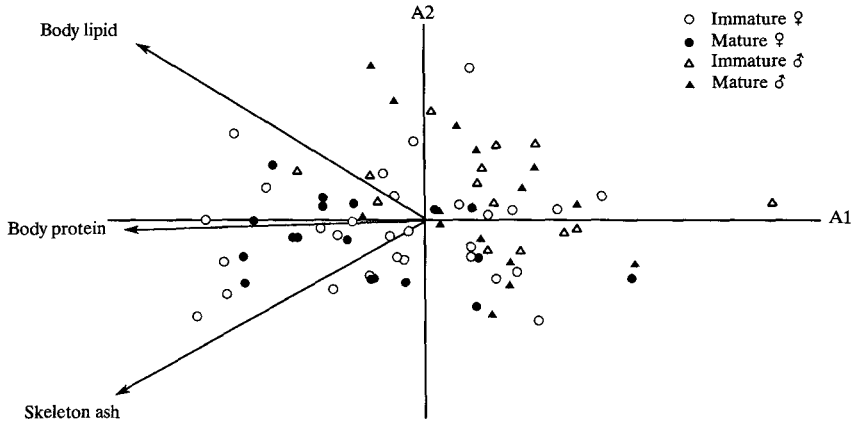
FIGURE 2. Biplot of the first two principal components of the masses of body lipid, protein and skeletal ash in Barn Owls. The first (A1) and second (A2) principal components explain 66% and 26%, respectively, of the variance of the data (together 92%).

lipid and protein ($R^2 = 0.34$, $P < 0.001$, $n = 78$).

SEASONAL VARIATION OF BODY MASS AND COMPOSITION ACCORDING TO AGE AND SEX

In each sex and age category, the same trends in seasonal changes of body mass were observed. Consequently, within each sex, values for mature and immature birds were pooled to allow comparison between males and females.
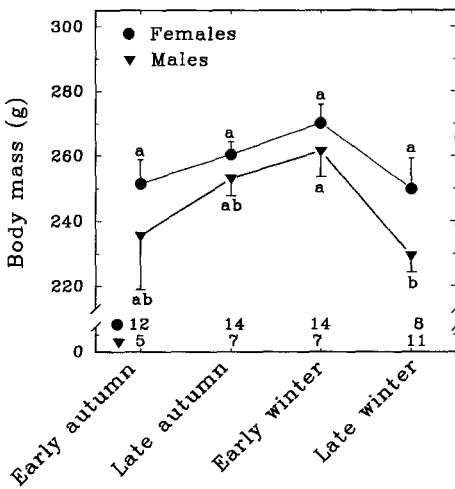

FIGURE 3. Seasonal changes in body mass of male and female Barn Owls during the nonbreeding period. The size of the sample used to calculate each mean is presented in the lower part of the graph. Values are means ± SE. Within each sex, mean values not sharing the same letter are significantly different ($P < 0.05$).

As shown in Figure 3, body mass exhibited significant seasonal changes in males ($F_{3,74} = 3.82$, $P < 0.05$), being maximum in early winter. The same trend was observed in females, although seasonal changes were not significant. At each of the four seasonal periods, there was no significant difference in body mass between males and females. Within each sex and age category, there was a tendency for body lipid to be higher in early winter than in the three other seasonal periods (Fig. 4). For example, in immature males body lipid was 120% higher ($F_{2,12} = 5.51$, $P < 0.01$) in early winter than in early autumn. In mature females, body lipid in early winter was 40 and 70% higher than in early autumn and late winter, respectively ($F_{2,15} = 10.21$, $P < 0.01$). Changes in lipid mass were similar in mature and immature females. Apparent differences between mature and immature males may be due to the small sample sizes at some periods. Consequently, values of body lipid from mature and immature birds were pooled. In early winter, body lipid was 50–130% (males) and 40–60% (females) higher than in the other three seasonal periods (males: $F_{3,26} = 7.71$, $P < 0.05$; females: $F_{3,44} = 5.14$, $P < 0.05$; Fig. 4, bottom). Peak adiposity (body lipid/total body mass) in early winter did not differ between males (14.1 ± 1.1%) and females (12.6 ± 0.9%) ($t_{19} = 1.04$). At each of the four seasonal periods there was no significant difference in body lipid between males and females. In both sexes, changes in body lipid paralleled those in body mass ($r_s =$
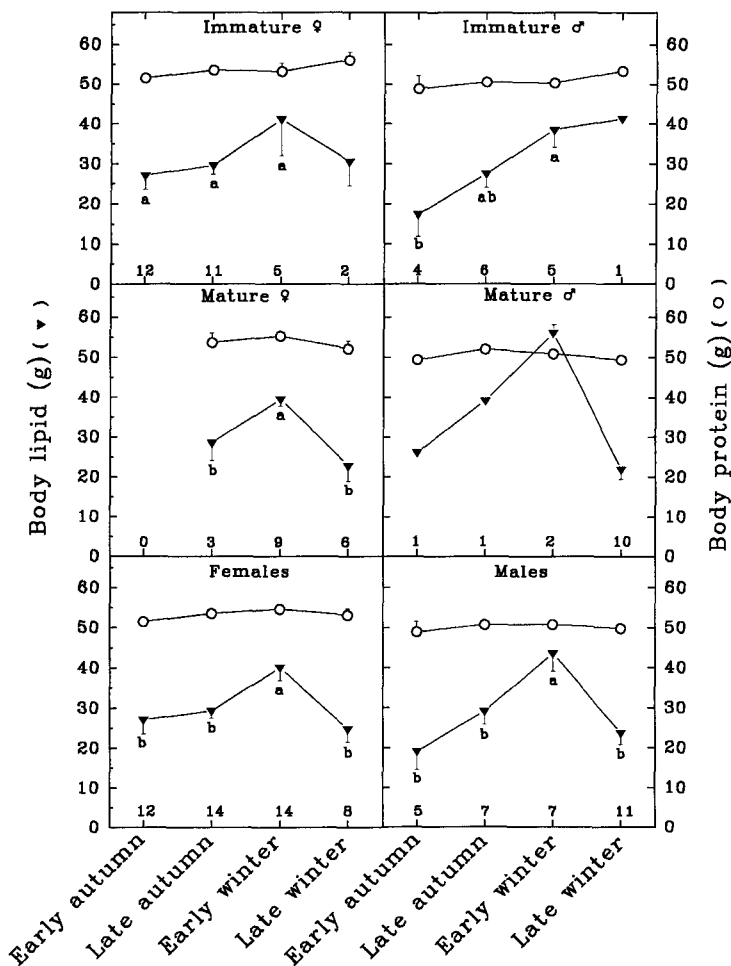
FIGURE 4.   Seasonal variations of body protein (open circles) and lipid (solid triangles) in Barn Owls according to age and sex. The size of the sample used to calculate each mean is presented in the lower part of each graph. Values are means $\pm$ SE. Mean values not sharing a common letter are significantly different ($P < 0.05$). Statistical analysis was not done if $n \leq 2$.

0.83 in males, $P < 0.01$; $r_s = 0.86$ in females, $P < 0.01$). Seasonal changes very similar to those described above also were found in mature and immature birds when sexes were pooled.

In contrast to body lipid, there was no significant influence of the season on body protein, either within the four sex and age categories or within the two sex categories (Fig. 4).

INFLUENCE OF SEX ON BODY COMPOSITION AND STRUCTURAL SIZE

Although body lipid showed significant seasonal changes, the average body composition of male and female Barn Owls during the nonbreeding period was calculated to allow a detailed comparison between sexes. Such a calculation does not introduce an important sampling bias because the pattern of the seasonal changes in body lipid was similar in males and females, and the number of birds killed at the peak of body lipid (early winter) represented approximately the same proportion of males (23%) and females (29%) in the total sample. These percentages also were close to 25%, the proportion that should be found in a nonseasonally biased sample obtained over four seasonal periods.

As shown in Table 2, average body lipid mass was not significantly different between males and females. Average adiposity was close to 10% in both sexes. On the other hand, average

TABLE 2. Means ($\pm$ SE) of body mass and composition of male and female Barn Owls during the nonbreeding period.

Compartment	Sex		t_{76}	P-value
	Male ($n = 30$)	Female ($n = 48$)		
Total body mass[a] (g)	286.9 $\pm$ 5.1	305.8 $\pm$ 3.5	3.18	< 0.05
Body mass[b] (g)	243.5 $\pm$ 4.5	259.3 $\pm$ 3.3	2.90	< 0.05
Body water (g)	150.7 $\pm$ 2.4	160.1 $\pm$ 1.5	3.58	< 0.05
Dry body mass (g)	92.9 $\pm$ 2.8	99.2 $\pm$ 2.2	1.79	< 0.05
Body lipid (g)	28.8 $\pm$ 2.4	31.1 $\pm$ 1.7		ns
Body lipid (%)[c]	9.8 $\pm$ 0.7	10.0 $\pm$ 0.5		ns
Body protein (g)	50.0 $\pm$ 0.6	53.2 $\pm$ 0.5	3.93	< 0.05
Body protein (%)	17.5 $\pm$ 0.2	17.4 $\pm$ 0.1		ns
Skeleton ash (g)	11.3 $\pm$ 0.1	12.1 $\pm$ 0.1	5.43	< 0.001

[a] Total body mass = mass without stomach contents.
[b] Body mass = Total body mass without digestive contents and feathers.
[c] % refers to total body mass.

body mass, dry body mass, body water, and body protein were significantly higher in females than in males. This could be due to a greater structural size, given that the mass of skeletal ash (Table 2) and the length of the trunk (10.6 $\pm$ 0.1 vs. 10.2 $\pm$ 0.1 cm; $t_{40} = 3.84$, $P <$ 0.001) were greater in females than in males. To test this structural size hypothesis, the relationship between body protein and skeletal ash was examined. Only nondepleted birds were used in the calculations to avoid potential bias due to

FIGURE 5. Relationship between body protein and skeletal ash in nondepleted male and female Barn Owls (male: y = 34.39 + 1.49x, $R^2 = 0.16$, $P < 0.05$, $n = 15$; Female: y = 24.37 + 2.50x, $R^2 = 0.44$, $P < 0.001$, $n = 27$). The slopes of these relationships were not significantly different ($t_{41} = 0.97$) and the average slope (2.81, $R^2 = 0.53$, $P < 0.001$) was used to adjust body protein (Y-adjusted) to structural size according to Lison (1968). The following equation was used: Y adjusted = Y − 2.81(X − 11.92). In this equation, X and Y represent individual skeletal ash and body protein, respectively, and 11.92 is the average mass of skeletal ash.

different proportions of emaciated and partly-depleted birds among males and females. A direct relationship was found between body protein and skeletal ash in both males and females (Fig. 5). Accordingly, body protein was adjusted to structural size. Size-adjusted body protein was not different between sexes ($U_{27,15} = 309$, ns).

THE NUTRITIONAL STATUS OF BARN OWLS DURING THE NONBREEDING PERIOD

Birds were classified as nondepleted, partly-depleted and emaciated according to the criterion defined in the Methods section. In nondepleted and partly-depleted birds, the different age and sex categories were represented in different proportions ($\chi^2_3 = 9.35$, $P = 0.05$). However, this mostly reflected the fact that marked differences in the seasonal distribution of killed birds exist among these categories, notably in the proportion of birds killed in early winter (see Fig. 1).

In nondepleted birds, the average adiposity (12.5 $\pm$ 0.4%; range 10–20%) was not significantly different between males, females, mature and immature birds. Partly-depleted and emaciated birds had significantly lower adiposity (7.5 $\pm$ 0.3 and 3.9 $\pm$ 0.7%, respectively, $H_2 = 58.7$, $P < 0.001$). Body protein was 50.6 $\pm$ 0.5 and 46.0 $\pm$ 2.1 g in partly-depleted and emaciated birds, respectively, i.e., 6 and 14% lower, respectively, than in the nondepleted owls (53.7 $\pm$ 0.5 g; $F_{2,77} = 17.7$, $P < 0.001$). The percentages of the killed Barn Owls considered as nondepleted, partly-depleted and emaciated were 54, 40 and 6%, respectively. In accordance with the seasonal changes in body lipid, 95% of the birds killed in early winter were nondepleted, whereas 45–68% of the birds killed in other seasonal pe-
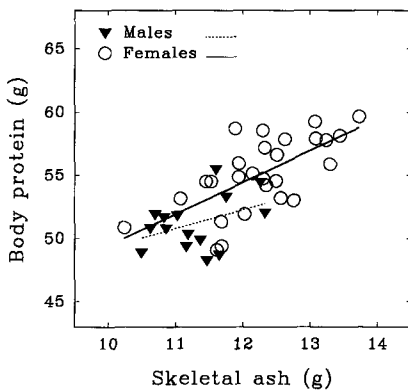
riods were partly-depleted. The few emaciated birds were found only in early autumn and late winter.

DISCUSSION

SEASONAL VARIATION OF BODY COMPOSITION AND ENERGY STRATEGY OF BARN OWLS DURING WINTER

As previously observed and discussed (Massemin et al., in press), we found that a different population was killed at different times of the nonbreeding period: mostly immature birds were killed in autumn, whereas mostly mature birds were killed in winter. These facts could affect the validity of our conclusions. For example, the increase in adiposity and body condition in early winter could have been artificial if immature birds were on average more depleted than mature birds. This was not the case because the level of adiposity and its pattern of seasonal changes were similar in mature and immature Barn Owls. Lastly, over half of the killed birds (54%) were nondepleted, indicating that the probability of collision was not restricted to depleted, and thus possibly weak, birds. Altogether these observations give no support to biased sampling as an explanation of the seasonal changes in body condition of Barn Owls.

The increase in body mass of Barn Owls in early winter was due only to an accumulation of body lipid; no seasonal changes in the amount of body protein was observed. Birds are often fatter and heavier during winter compared to summer (Witter and Cuthill 1993). In winter, an increase of body lipid is required to meet the potential energy deficits arising both from thermogenesis and insufficient food intake when snow cover is important (Andrews 1995). This increase in body lipid in early winter allows birds to survive longer periods of starvation. From the 7 g day^{-1} lipid loss calculated for Barn Owls fasting but hunting at 5°C (see below), it can be estimated that in early winter (body lipid = 41 g) birds are able to survive 6 days of starvation, whereas in autumn (body lipid = 27 g) they would die after 4 days of starvation. Thus, the increase in body lipid in early winter is a strategy that aids the survival of Barn Owls in a situation of food shortage.

Compared to males, females had larger structural size but not significantly different adiposity or size-adjusted protein mass. This is probably due to the low sexual dimorphism of Barn Owls,

as observed in this study and by others (Mlikovsky and Piechocki 1983, Taylor 1994). The similar adiposity between sexes also agrees with the observation that during winter, male and female Barn Owls have the same ability to survive an experimental fast (Handrich et al. 1993b). Thus, in this species, there seems to be no sexual difference in the strategy during the nonbreeding period. On the other hand, from the observation that the total body mass of breeding female Barn Owls is higher than that of breeding males, Korpimäki (1990) has suggested that females but not males adopt a "passive storage" strategy during the breeding period.

Compared to other bird species, the average adiposity of male and female Barn Owls (10% overall, 12.5% in nondepleted birds) may be considered as "intermediate": in winter the mean adiposity is 2% in Galliformes (Thomas 1982), 6% in Passeriformes (Newton 1969), 10–13% in Charadriiformes (Evans and Smith 1975, Marcström and Mascher 1979), 12–17% in Anseriformes (Ely and Raveling 1989), and 18–25% in Sphenisciformes (Robin et al. 1988, Cherel et al. 1994). Thus, in contrast to previous suggestions (Piechocki 1960), the reason for the vulnerability of the Barn Owl during winter does not seem to be a low lipid reserve. Considering (1) the resting energy expenditure of captive Barn Owls fasting at 5°C (213 kJ day^{-1}, Handrich et al. 1993b), (2) the additional energy cost of hunting in the field (95 kJ day^{-1}, Handrich et al. 1993a), (3) the relative contribution of body lipid to energy expenditure (91%, Handrich et al. 1993b), and (4) the energy equivalent of lipid (39.3 kJ g^{-1}, Schmidt-Nielsen 1979), it can be estimated that a fasting but active wild Barn Owl would use 7 g of lipid daily. Thus, wild birds with a 10% adiposity (30 g of body lipid, Table 2) have the potential to survive a 4–5 day total fast at a mild (5°C) winter temperature. This capacity could reach 9 days in the fatest birds (66 g of body lipid). Obviously, the potential to survive would be reduced at lower ambient temperatures, but it would be greater in situations of food restriction as compared with total fasting.

THE NUTRITIONAL STATUS OF BARN OWLS DURING THE NONBREEDING PERIOD

Fifty-four percent of the birds in our sample were classified as "nondepleted." They had probably been feeding ad libitum or at least they

had not faced prolonged periods of food restriction. Five individuals (6% of total sample) were considered emaciated. They were in a nutritional status equivalent to the so-called phase III of fasting (Handrich et al. 1993b) and must have undergone prolonged food shortage or total starvation. Forty percent of the birds were in an intermediate nutritional status, that is partly-depleted. The difference in the body energy content between nondepleted and partly-depleted Barn Owls was on average 93% due to lipid and 7% due to protein (calculated from body lipid and protein; energy equivalent of lipids and proteins equals 39.3 and 17.8 kJ g^{-1}, respectively; Schmidt-Nielsen 1979). These figures are close to the respective contributions of lipid and protein of 91% and 6% of the energy loss during the so-called phase II in totally fasting Barn Owls (Handrich et al. 1993b). This suggests that most of the partly-depleted Barn Owls were in a nutritional status equivalent to phase II of total fasting, which is characterized by the preferential use of body lipid as a fuel source and by the sparing of body protein (Le Maho et al. 1981, Handrich et al. 1993b). However, whether these birds were totally fasting or only food-restricted is not known. The possibility that some of the partly-depleted birds were well-fed and restoring their lipid reserves after an emaciated status (phase III) cannot be excluded.

Our conclusions on the nutritional status of Barn Owls during the nonbreeding period are based upon captive birds as reference and a sample of road-killed individuals. The question therefore arises as to what extent these conclusions apply to a free-living population. The captive Barn Owls used as reference belonged to a small population breeding in a large aviary exposed all year to natural climatic conditions and photoperiods. That these individuals were representative of the free-living ones from the point of view of body reserves is suggested by the observation that their annual cycle of total body mass (Handrich, unpubl. data) was similar to that reported by Taylor (1994) for a free-living Scottish population of Barn Owls. How the nutritional status of road-killed Barn Owls reflects that of the whole population has been assessed in only one study (Taylor 1994). Using total body mass as a criterion, Taylor found that most of the road-killed Barn Owls in winter were in a poorer condition than free-living birds. However, free-living birds were caught in nest-boxes

and were therefore most likely territorial mature birds whose body mass might be greater than the average of the whole population. The sample in the present study included immatures and thus probably mostly Barn Owls whose body mass could be more representative of the overall average. Thus, we can conclude that during mild winters most of the Barn Owls living in northeastern France are in good nutritional condition. This conclusion would be reinforced if, as suggested by Taylor (1994), emaciated birds were over-represented in our sample.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDREWS, J. F. 1995. Comparative studies on programmes for management of energy supply: torpor, pre-winter fattening and migration. Proc. Nutrit. Soc. 54:301–315.

BAUDVIN, H., J. C. GENOT, AND Y. MULLER. 1991. Les rapaces nocturnes. Sang de la terre, Paris.

BLEM, C. R. 1990. Avian energy storage. Current Ornithol. 7:59–113.

BRUIJN, O. DE 1994. Population ecology and conservation of the Barn Owl Tyto alba in farmland habitats in Liermers and Achterhoek (the Netherlands). Ardea 82:1–109.

CHEREL, Y., J. B. CHARRASSIN, AND E. CHALLET. 1994. Energy and protein requirements for molt in the King Penguin Aptenodytes patagonicus. Am. J. Physiol. 266:R1182–R1188.

DERVIN, C. 1988. STAT-ITCF (Institut Technique des Céréales et des Fourrages), Paris.

DEWASMES, G., Y. LE MAHO, A. CORNET, AND R. GROSCOLAS. 1980. Resting metabolic rate and cost of locomotion in long-term fasting Emperor Penguins. J. Appl. Physiol. 9:888–896.

ELY, C. R., AND D. G. RAVELING. 1989. Body composition and weight dynamics of wintering Greater White-fronted Geese. J. Wildl. Manage. 53: 80–87.

EVANS, P. R., AND P. C. SMITH. 1975. Studies of shorebirds at Lindisfarne, Northumberland. 2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. Wildfowl 26:64–75.

FOLCH, J., M. LEES, AND G. H. SLOANE STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226:497–509.

HANDRICH, Y., L. NICOLAS, AND Y. LE MAHO. 1993a.

Winter starvation in captive Common Barn Owls: bioenergetics during feeding. Auk 110:470–480.

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

KING, J. R., AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? Am. Zool. 25:955–964.

KORPIMÄKI, E. 1990. Body mass of breeding Tengmalm's Owls *Aegolius funereus*: seasonal, between-year, site and age-related variation. Ornis Scand. 21:169–178.

LE MAHO, Y., H. VU VAN KHA, H. KOUBI, G. DEWASMES, J. GIRARD, P. FERRÉ, AND M. CAGNARD. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting Geese. Am. J. Physiol. 241:E342–E353.

LISON, L. 1968. Statistique appliquée à la biologie expérimentale. Collection Science et Techniques d'aujourd'hui. Gauthier-Villars, Paris.

MARCSTRÖM, V., AND J. W. MASCHER. 1979. Weights and fat in Lapwings *Vanellus vanellus* and Oystercatchers *Haematopus ostralegus* starved to death during a cold spell in spring. Ornis Scand. 10:235–240.

MASSEMIN, S., Y. LE MAHO, AND Y. HANDRICH. In press. Seasonal pattern in age, sex and body condition of Barn Owls *Tyto alba* killed on motorways. Ibis.

MLIKOVSKY, VON J., AND R. PIECHOCKI. 1983. Biometrische untersuchungen zum geschlechts-dimorphismus einiger mitteleuropäischer Eulen. Beitr. Vogelkd. 29:1–11.

NEWTON, I. 1969. Winter fattening in the Bullfinch. Physiol. Zool. 42:96–107.

PIECHOCKI, R. 1960. Über die winterverluste der Schleiereule (*Tyto alba*). Vögelwarte 20:274–280.

PIERSMA, T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. Ph.D. diss. Univ. Groningen, Groningen, The Netherlands.

ROBIN, J. P., M. FRAIN, C. SARDET, R. GROSCOLAS, AND Y. LE MAHO. 1988. Protein and lipid utilization during long-term fasting in Emperor Penguins. Am. J. Physiol. 254:R61–R68.

ROBIN, J. P., T. ZORN, AND Y. LE MAHO. 1991. Résistance au jeûne hivernal et réalimentation chez le Canard Colvert: évolution des réserves énergétiques et de la prise alimentaire. Compte Rendu Acad. Sci., Paris 313:529–535.

SCHERRER, B. 1984. Biostatistique. Gaëtan Morin, Québec, Canada.

SCHMIDT-NIELSEN, K. 1979. Animal physiology: adaptation and environment. Cambridge Univ. Press, Cambridge, MA.

SCHÖNFELD, M., G. GIRBIG, AND H. STURN. 1977. Beiträge zur populationsdynamik der Schleiereule, *Tyto alba*. Hercynia 14:303–351.

SUTER, W., AND M. R. VAN EERDEN. 1992. Simultaneous mass starvation of wintering diving ducks in Switzerland and at the Netherlands: a wrong decision in the right strategy? Ardea 80:229–242.

TAYLOR, I. 1994. Barn Owls: predatory-prey relationships and conservation. Cambridge Univ. Press, Cambridge.

THOMAS, V. G. 1982. Energetic reserves of Hudson Bay Willow Ptarmigan during winter and spring. Can. J. Zool. 60:1618–1623.

THOUZEAU, C., Y. HANDRICH, AND Y. LE MAHO. 1995. Mobilisation des réserves énergétiques lors d'un jeûne hivernal chez la Chouette Effraie et seuils critiques de réversibilité. Arch. Physiol. Biochem. 103:D113.

WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. Phil. Trans. R. Soc. Lond. B 340:73–92.