Bunting (*Emberiza schoeniclus*). Nature 371:698–700.

DYBAS, L. K., AND H. S. DYBAS. 1981. Coadaptation and taxonomic differentiation of sperm and spermathecae in featherwing beetles. Evolution 35: 168–174.

GOMENDIO, M., AND E. R. S. ROLDAN. 1991. Sperm size and sperm competition in mammals. Proc. R. Soc. Lond. B 243:181–185.

HARTLEY, I. R., N. B. DAVIES, B. J. HATCHWELL, A. DESROCHERS, D. NEBEL, D., AND T. BURKE. 1995. The polygynandrous mating system of the Alpine Accentor, *Prunella collaris*. II. Multiple paternity and parental effort. Anim. Behav. 49:789–803.

MØLLER, A. P. 1988. Testes size, ejaculate quality, and sperm competition in birds. Biol. J. Linn. Soc. 33: 273-283.

MØLLER, A. P. 1991. Sperm competition, sperm depletion, paternal care and relative testes size in birds. Am. Nat. 137:882–906.

NAKAMURA, M. 1990. Cloacal protuberance and copulatory behaviour of the Alpine Accentor (*Prunella collaris*). Auk 107:284–295.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525–567.

SHELDON, B. C., AND T. R. BIRKHEAD. 1994. Reproductive anatomy of the Chaffinch in relation to sperm competition. Condor 96:1099–1103.

SCHULZE-HAGEN, K., B. LEISLER, T. R. BIRKHEAD, AND A. DYRCZ. 1995. Prolonged copulation, sperm reserves and sperm competition in the aquatic warbler *Acrocephalus paludicola*. Ibis 137:85–91.

WOLFSON, A. 1952. The cloaca protuberance—a means for determining breeding condition in live male passerines. Bird-Banding 23:159–165.

The Condor 99:969–971

HIGHER WINTER MORTALITY OF THE BARN OWL COMPARED TO THE LONG-EARED OWL AND THE TAWNY OWL: INFLUENCE OF LIPID RESERVES AND INSULATION?[1]

SYLVIE MASSEMIN AND YVES HANDRICH
Centre d'Ecologie et Physiologie Energétiques, CNRS, 23 rue Becquerel, 67087 Strasbourg, France, e-mail: massemin@c-strasbourg.fr

Abstract. The role of lipid reserves in winter mortality of the European Barn Owl (*Tyto alba*) was investigated by comparing its adiposity to that of two sympatric nocturnal raptors, the Tawny Owl (*Strix aluco*) and the Long-eared Owl (*Asio otus*), considered as less affected by winter mortality. Adiposity was similar for the three species. Feather insulation, diet, and hunting behavior may explain winter mortality of the Barn Owl.

Key words: Barn Owl, Long-eared Owl, Tawny Owl, adiposity, insulation, winter mortality.

The Barn Owl (*Tyto alba*), Long-eared Owl (*Asio otus*), and Tawny Owl (*Strix aluco*), all three middle-sized nocturnal raptors, are sympatric species in Europe. The Barn Owl and Long-eared Owl inhabit grasslands, whereas the heavier Tawny Owl inhabits forest (Mikkola 1983). In contrast to these other raptors, the Barn Owl in Europe is already at the northern limit of its geographical distribution (Taylor 1994). Harsh winters in Europe are responsible for the death of many Barn Owls (Schönfeld et al. 1977, de Bruijn 1994, Taylor 1994), and the number of Barn Owls found dead in winter is greater than that of Long-eared or Tawny Owls (Piechocki 1960, Guichon 1966).

The explanation usually given for the higher Barn Owl mortality is that the amount of adipose tissue, where major energy reserves (lipids) are stored (Blem 1990), is lower for Barn Owls compared to Long-eared Owls and Tawny Owls (Schönfeld et al. 1977, Marti and Wagner 1985, Baudvin et al. 1991). This assumption apparently is based on a single study in which some individuals that suffered a severe food scarcity were used (Piechocki 1960). To determine whether the Barn Owl should be considered as a "lean" species with little lipid reserve, we compared the adiposity of Barn Owls, Long-eared Owls, and Tawny Owls, none of which were emaciated or breeding. We also studied the insulative value of the plumage in the three species.

METHODS

Barn Owls, Long-eared Owls, and Tawny Owls killed by cars on motorways were collected in 1992–1994 in Alsace-Lorraine, northeastern France. We used intact specimens for which the sex was determined by gonad identification. Some birds reached a critical phase of starvation as evidenced by the absence of abdominal adipose tissue and were therefore excluded from this study. Only nine Long-eared Owls (five males, four females) and eight Tawny Owls (six males, two fe-

[1]Received 31 October 1996. Accepted 11 June 1997.

TABLE 1. Means (± SE) of body mass and body composition of three nocturnal raptors. Values in the same row not sharing a common letter are significantly different. Content refers to mass of carcass.

	Barn Owl	Long-eared Owl	Tawny Owl	Test	*P*-value
Mass (g)					
Body mass	288 ± 6b	277 ± 16b	453 ± 15a	$F_{2,26} = 60.1$	<0.001
Feather	39.8 ± 1.1b	40.6 ± 1.6b	55.5 ± 1.4a	$F_{2,26} = 41.3$	<0.001
Carcass	240 ± 5b	233 ± 21b	392 ± 15a	$H_2 = 17.8$	<0.001
Body lipid	26.7 ± 2.0	28.5 ± 6.5	43.8 ± 8.1	$H_2 = 5.9$	ns
Body protein	50.6 ± 1.1b	47.3 ± 1.8b	79.7 ± 3.0a	$F_{2,26} = 77.9$	<0.001
Content (%)					
Lipid	11.0 ± 0.7	11.6 ± 1.7	10.9 ± 1.7	$F_{2,26} = 0.1$	ns
Protein	21.0 ± 0.2	20.5 ± 0.5	21.0 ± 1.0	$H_2 = 2.7$	ns
Feather insulation (g cm^{-2})	4.8 ± 0.1b	4.9 ± 0.1b	5.5 ± 0.1a	$F_{2,26} = 8.0$	<0.001
n	12	9	8		

males) were used for this study. To obtain a comparable sampling of Barn Owls, 12 Barn Owls (6 males, 6 females) were randomly selected from non-emaciated Barn Owls found killed on motorways ($n = 38$). About one individual per month of each species was collected between November and May. All birds were nonbreeding individuals with undeveloped gonads.

Body mass was determined after removal of the stomach content. Carcass mass was defined as the body mass after removing the remaining digestive contents and feathers. After drying, carcasses were ground under liquid nitrogen into a fine homogeneous powder. Lipid contents (1 g aliquots) were measured by a gravimetric method derived from Folch et al. (1957) using chloroform/methanol (all classes of lipids were therefore extracted). Nitrogen content (100 mg aliquots) was determined by the Kjeldahl method and converted to protein by multiplying nitrogen by 6.25 (Schmidt-Nielsen 1979). Lipids and proteins of carcasses provided body lipid and body protein, respectively. Adiposity was defined as the ratio of body lipid to mass of carcass. We also determined feather insulation, defined here as the dry mass of body feathers (without wing feathers) per unit skin area. Skin area was calculated according to Walsberg and King (1978) ($S_{skin} = 10\ M^{0.667}$, with M defined as body mass in grams and S in cm^2).

Analysis of variance (ANOVA), followed by the Student-Newman-Keuls test, was used to compare differences between groups. When data failed the normality test, the Kruskal-Wallis test was performed followed by Dunn's test (Scherrer 1984).

RESULTS

Body and carcass mass, and body protein of Barn Owls and Long-eared Owls were significantly lower than those of Tawny Owls (Table 1). However, the mass of body lipid and adiposity (average 11%) did not differ significantly among the three nocturnal raptors. Thus, Barn Owls were not leaner than Long-eared Owls or Tawny Owls.

DISCUSSION

Our results are in contrast to those of Piechocki (1960), which has been extensively cited over the years (Schönfeld et al. 1977, de Bruijn 1994, Taylor 1994). Piechocki's samples included birds without abdominal adipose tissue. These birds were probably nutritionally stressed, because birds without abdominal adipose tissue are already relying on their body protein as an energy source (Dewasmes et al. 1980, Robin et al. 1991).

As demonstrated here, lipid reserves cannot be the main reason for the higher winter mortality of the Barn Owl. Furthermore, the adiposity of nocturnal raptors in occidental Europe does not appear to be related to their movements because the Tawny Owl, a sedentary species, has a similar adiposity as the two other raptors, which are both less sedentary (Mikkola 1983). Moreover, the Barn Owl could accumulate lipids before the winter (Massemin et al. 1997).

Because the daily energy expenditures of captive Barn Owls are higher compared to those of Long-eared and Tawny Owls (Wijnandts 1984), it can be concluded that the winter vulnerability of the Barn Owl is due to a higher metabolic rate. This might be related to the low efficiency of feather insulation as homeothermy would be difficult to maintain at low ambient temperatures. The insulation efficiency calculated with the feather mass scaled to skin area was significantly lower for the Barn and the Long-eared Owl than for the Tawny Owl (Table 1).

Importantly, the Barn Owl is the only species among the three for which the tarsi are sparsely feathered and the feet unfeathered (Grassé 1950). The low insulation efficiency of the Barn Owl may be a characteristic linked to the fact that this species generally inhabits tropical regions, although it also reaches temperate areas (Taylor 1994). In the northern limit of its geographical distribution, the Barn Owl could be more vulnerable to winter conditions. Thus, prey requirements for the Barn Owl in the field would be more important than for other raptors despite a similar assimilation efficiency of food (Kirkwood 1979, Wijnandts 1984). Diet also could influence energetic requirements. In France, Barn Owls usually prey upon voles, mice and shrews (Baudvin et al. 1991). The Long-eared Owl and the Tawny Owl also hunt small mammals but rely more heavily on birds than does the

Barn Owl (Baudvin et al. 1991). Accordingly, when snow covers the ground, the Barn Owl may have to spend more time hunting because small mammals are less accessible (Guichon 1966, Jacobsen and Sonerud 1993), whereas the Long-eared and the Tawny Owl may find food easily by eating other prey such as birds (Baudvin et al. 1991). Finally, the hunting mode of the Barn Owl seems to be a highly energy-consuming task because the Barn Owl hunts either flying or waiting on a perch, whereas the Long-eared and the Tawny Owl usually perch for hunting (Mikkola 1983, Jaksic and Carothers 1985).

Further studies should include the energetics of semi-captive and free-living birds, their hunting behavior, and availability of prey in order to understand the life history tactics of middle-sized nocturnal raptors during winter.

This study was supported by a grant from the Société des Autoroutes du Nord et de l'Est de la France (SANEF). We thank its personnel for the regular collection of dead Barn Owls. We are very grateful to C. A. Bost, Y. Le Maho and E. Challet for comments on the manuscript, and A. Pape for his editorial help.

LITERATURE CITED

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.

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. 49:888–896.

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

GRASSÉ, P. P. 1950. Traité de zoologie. Anatomie, systématique et biologie. Tome 15 Oiseaux. Masson, Paris.

GUICHON, J. 1966. Etude sur la Chouette Effraie (*Tyto alba*) et conséquences des froids de 1956 et 1966 sur cette espèce dans la région de Rougemont (Doubs). Bull. Soc. Hist. Nat. du Doubs 68:49–51.

JACOBSEN, B. J., AND G. A. SONERUD. 1993. Synchronous switch in diet and hunting habitat as a response to disappearance of snow cover in Tengmalm's Owl *Aegolius funereus*. Ornis Fennica 70: 78–88.

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.

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. 63A:495–498.

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.

MASSEMIN, S., R. GROSCOLAS, AND Y. HANDRICH. 1997. Body composition of the European Barn Owl during the nonbreeding period. Condor 99:789–797.

MIKKOLA, H. 1983. Owls of Europe. T. and A. D. Poyser, Carlton, UK.

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

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. C. R. 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.

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

WALSBERG, G. E., AND J. R. KING. 1978. The relationship of the external surface area of birds to skin surface area and body mass. J. exp. Biol. 76: 185–189.

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