ECOLOGICAL ENERGETICS OF THE LONG-EARED OWL (ASIO OTUS)

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CONTENTS

1. INTRODUCTION

1.1. BACKGROUND

With the growing interest in cost-benefit analyses the study of energy flow in the life of birds has entered a new phase, where the central problem is the interaction between time and energy as limiting factors determining the behaviour of the individual (King 1974). Until recently such studies were severely hampered on the income side because of the shortcomings of standard techniques when applied to the field situation, but a number of new avenues have opened up (Gessaman 1973, King 1974, Ebbinge *et al.* 1975, Kendeigh *et al.* 1977, Walsberg 1980). Raptorial birds offer advantages peculiar to their way of life, and from an early date attempts were made to quantify energy intake for free-living birds. Graber (1962) relied on deductions from pellet analysis to reconstruct daily energy intake for three owl species, but as we shall see several inferences basic to his method require revision. More recently Tarboton (1978) and Koplin *et al.* (1980) presented figures on daily energy intake in kites and kestrels where these pitfalls have been avoided, but their data cover only the winter period. The only data set for the entire annual cycle concerns the Common Buzard, *Buteo buteo*, but an inde-

Ardea 72 (1984): 1—92

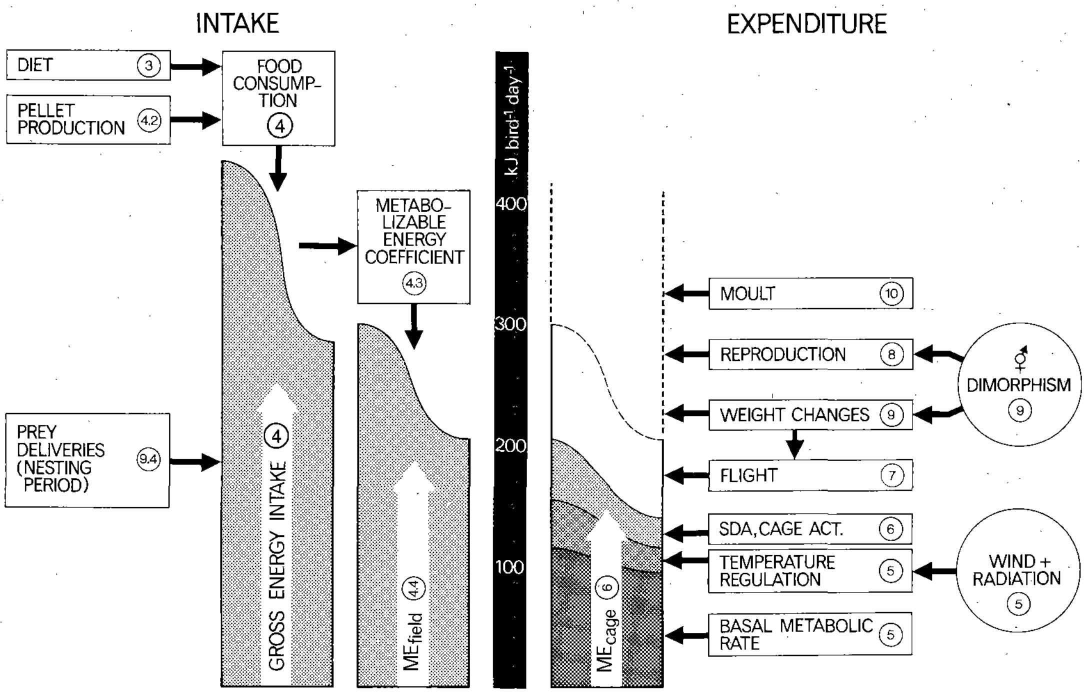


Fig. 1. Schematical overview of the energy budget of the Long-eared Owl, with methods followed in the estimation of food intake of free-living birds (left) and the components of energy expenditure (right). Numerals refer to the chapters (or chapter sections) in which the relevant material is presented; the bar graph shows the approximate values for the Long-eared Owl outside the breeding season.

pendent check on the reliability of the method is not included (Sylvén 1982).

The aim of the present study was to measure the daily gross energy intake (hereafter abbreviated GEI) throughout the annual cycle in the Long-eared Owl, *Asio otus*, by means of field and laboratory measurements of pellet production, the analysis of pellets collected in the field, and during the reproductive period indirect observation at the nest. Secondly, on the side of energy expenditure, a partitioning over the various functions was aimed at by a combination of field and laboratory techniques. The central assumption is that the energy-demanding functions (especially reproduction and moult) will be so timed in the annual cycle to result in an optimal seasonal allocation of energy (King 1974, Murton & Westwood 1977). The logical next step, bringing this quantification to bear on the timing of individual pairs, demands more detailed information on hunting success and foraging cost than can feasibly be collected on nocturnal hunters such as owls, and is being pursued by our group in a follow-up study on the kestrel (Rijnsdorp *et al.* 1981, Daan *et al.* in prep.).

1.2. ORGANIZATION OF THE PAPER

The concept of energy budgets as here employed involves the *energy intake* of individual birds (as determined from food consumption and utilization) as one side of the budget, and the partitioning of this income over the various categories of *energy expenditure* on the other (see Fig. 1, showing also the sequence of chapters).

Chapter 3 covers the composition of the diet and its seasonal variation, based on analysis of pellets collected in the field. Estimation of the amount of food eaten daily is presented in chapter 4, relying on deductions from a study of the rate of daily pellet production throughout the year (4.2. and 4.3.) supplemented by the direct observation of prey delivery at the nest for the reproductive period (9.4.). When converted in terms of energy (kJ = kilo-Joules) these data provide the daily gross energy intake (GEI).

Not all of this energy can be metabolized by the birds, and the metabolizable energy coefficient (MEC) was determined in trials with captive birds, where food intake and also excretion were quantified (4.3.). Taken together these data provide the annual pattern in daily metabolized energy (ME_{field}) for free-living owls (4.4.).

Turning now to the routes of energy expenditure, chapter 5 covers basal metabolic rate (BMR) and energy devoted to temperature regulation (TR), in both cases based on measurements of the oxygen consumption of individuals held at constant temperatures. Two other aspects of microclimate, wind and solar radiation, were also considered. Theoretically the ME for birds kept in small cages should consist of BMR and TR together with some energy used in locomotion and the heat increment of feeding (SDA = specific dynamic action), at least during periods of constant body weight. Approximation of this ME at constant weight was achieved using food balance trials (chapter 6), where the costs of adding increments to the body weight were also estimated.

Chapter 7 presents the winter energy budget using the foregoing elements. On the expenditure side no attempt was made to measure the cost of flight, but substitution in the data using the time spent in flight derived from radio-telemetry of free-living birds yields an estimate in close accord with predictive formulas on the basis of body weight and wing morphology as currently employed.

The two main productive processes of adult birds, reproduction and moult, are described in chapter 8 and 10. Included in chapter 8 is the energy budget of growing nestlings and fledglings. In all of these chapters the differences between the sexes are treated, and in chapter 9 I return to the problem of sexual dimorphism in body size and consider its implications for energy balance.

Chapter 11 comprises an integration of these processes in relation to the timing of the annual cycle. As background information chapter 2 provides a brief sketch of the natural history of the Long-eared Owl in the Netherlands.

1.3. STUDY AREA

Most of the field work was done in the province of Groningen and the northern part of Drente, situated in the north-eastern part of the Netherlands (see Fig. 3A).

This whole area is generally flat and can be divided in four characteristic parts. The northern part of Groningen is mainly agricultural land with very few wood lots. Only close to farms and villages are some small plantations found. The soil is mainly marine clay. The eastern and south-eastern part of Groningen is a typical fen-peat landscape. Outside the villages the land is largely farmland. There are some plantations, from a few to less than 100 ha. Scattered over the whole area are many locations where natural gas is brought to the surface, each up to a few ha in size and illuminated at night.

The landscape to the south of the city of Groningen and the northern part of Drente is much more wooded, but it is still mainly farmland (with an emphasis on dairy farming). Forests up to a few hundreds of hectares are found, especially on the poorest sand soils. In general these plantations are mixed, involving oaks and pines. Many oaks, often of considerable size, can be found along roads and lanes and around human settlements.

The south-western part of the province of Groningen consists mainly of meadows surrounded by wooded banks (especially alders). The soil is mainly cultivated peat bog with sand ridges. Towns and villages are scattered throughout these areas (Groningen city, Delfzijl, Assen, Hoogezand, Haren, Winschoten, Veendam, together comprise about

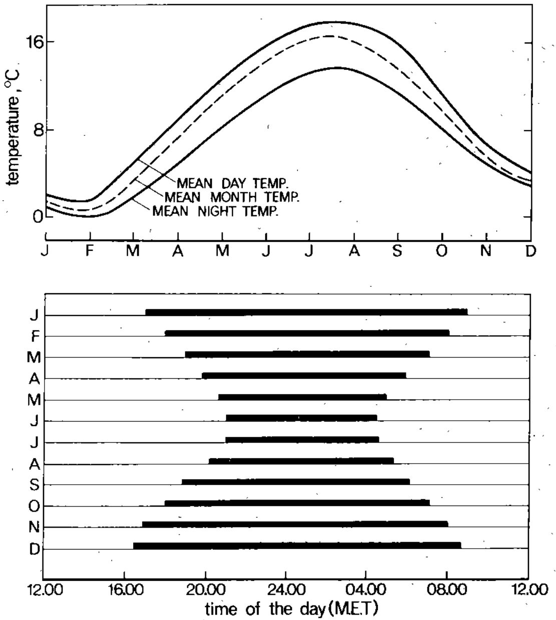


Fig. 2. Mean air temperature in the study area (Above, long-term means from station Eelde near Groningen, plotted with respect to month) and duration of the nocturnal period (Below, black bars run from sunset to sunrise for each month).

300.000 people). Winter concentrations of Long-eared Owls often occur in these settled areas (parks and churchyards in particular) and breeding sometimes occurs.

Climatic and weather data, when not measured at the location, were obtained from the local airport weather station (Eelde). Monthly temperature averages for the Eelde station were taken from the report for the period 1951—1960. These data are represented in Fig. 2. As the Long-eared Owl is almost entirely nocturnal the duration of the dark period is an important parameter in its way of life. The time of sunset and sunrise, and so the duration of the night, for the midpoint of each month is included in Fig. 2.

1.3. HOUSING AND GENERAL TECHNIQUES

The main part of the study was conducted in the period 1974—1979, but data from a pilot study in the winters of 1969—1971 will be included. For the laboratory experiments a number of owls were kept in captivity (14 in all), all housed on the terrain of the Zoological Laboratory at Haren (53° 11′ N, 6° 36′ E). When not used in the experiments the owls were generally housed in a large outdoor aviary (ground area 6 × 20 m, 3 m in height) but some were kept in individual outdoor cages (2 × 2 m and 2.5 high). There were several perches and there was shelter against rain.

Although sexing of Long-eared Owls is difficult the striation and colour tones of specific feathers (see chapter 9) provides a reliable method, as was tested on a large skin collection. Moreover for 8 captive owls sex was determined by measuring testosterone levels in the blood (radioimmuno assay technique, Sorin biomedical). Sex determinations of captive owls could be confirmed in early spring by the weight increase typical for females.

The standard diet for the owls was fresh or freshly frozen laboratory mice. Occasionally they were fed with young laboratory rats or one day old chicks. The owls received a surplus of food, given at the end of each day, between 15.00 and 17.00. All owls were generally captured and weighed once a week, between 16.00 and 18.00. They were weighed to the nearest 0.1 g on a balance.

During autumn and winter roosting sites of Long-eared Owls were searched for throughout the whole area. Pellets were collected from many winterroosts. Numbers of roosting owls, mostly determined during the period of exodus, were determined for a few roosts throughout the winter period.

In early spring breeding territories of Long-eared Owls were located at nighttime by listening to the female and male calls. Sometimes a taperecorder with the male ooh-ooh-call was used to stimulate male or female reactions. During daytime possible nestsites were investigated. Nests at favourable locations were used for night observations. These and other nests were used to obtain general reproduction data (as clutch size, egg weight, growth of nestlings). During the moult period known roosting places were searched for shed feathers (chapter 10).

For obtaining information on body weight, adult owls were regularly trapped especially in autumn and winter. Two techniques were used. Mist nets together with a decoy mouse were erected around roosting trees. Although early on a few owls were trapped on this way in general the results were disappointing. For this reason bal-chatris were later used with a mouse, sparrow or starling as a decoy. Generally the bal-chatris were placed very close to the roosting trees, just before the time of exodus. These traps were mostly observed from a car parked nearby. So the owls could be liberated within a minute after trapping. Owls were weighed to the nearest 5 g with a 300—500 g springbalance. They were sexed (where possible) and the wing chord (stretched method) was measured. After ringing with an aluminium ring they were liberated again. The whole procedure took only a few minutes.

More specialized techniques will be described in the relevant chapters. Mean values in text are given with ± standard deviation between brackets, unless otherwise stated.

2. NATURAL HISTORY OF THE LONG-EARED OWL

2.1. WINTER

During the winter Long-eared Owls spend the daytime on communal roosting sites. These winter roosts are often located in groups of evergreens (pine, spruce, fir or holly) but before the autumn leaf fall may also by found in deciduous trees (willows, poplars, or in orchards). Often the roosts are found close to breeding sites, but where parks or churchyards are utilized the nearest breeding territory may be as far as several kilometers. In our study area the majority of roosts comprise 2—15 owls, but sometimes up to 40 were counted (Fig. 3C). In August and September the first roosts are observed, generally with less than 8 owls, and probably formed by one or two pairs with their juveniles. These sites are used only 2—3 weeks, and definitive winter roosts are established during the last phase of moult of the flight feathers in October. Numbers increase up to mid-December and generally remain stable until early February when numbers fall. Most roosts are abandoned by the end of March or early April.

For one roost located in the southern part of the city of Groningen, the number of roosting owls was counted frequently (Fig. 4). In general, 15—20 owls were present during the December—January maximum, but during periods of heavy snow cover there was a sudden sharp increase (up to 27 in February 1976, and 40 in January-February 1979). In the 1979 snow period an increase at other roosts in or near towns was also found (Delfzijl, Hoogezand, Winschoten, see Fig. 3A). This tendency to concentrate near villages and cities in periods of bad weather has been commented on earlier (März 1965, Bruns 1965) and is seen as an adaptation to exploit prey concentrations occurring there in such periods (in particular, flocks of passerine birds).

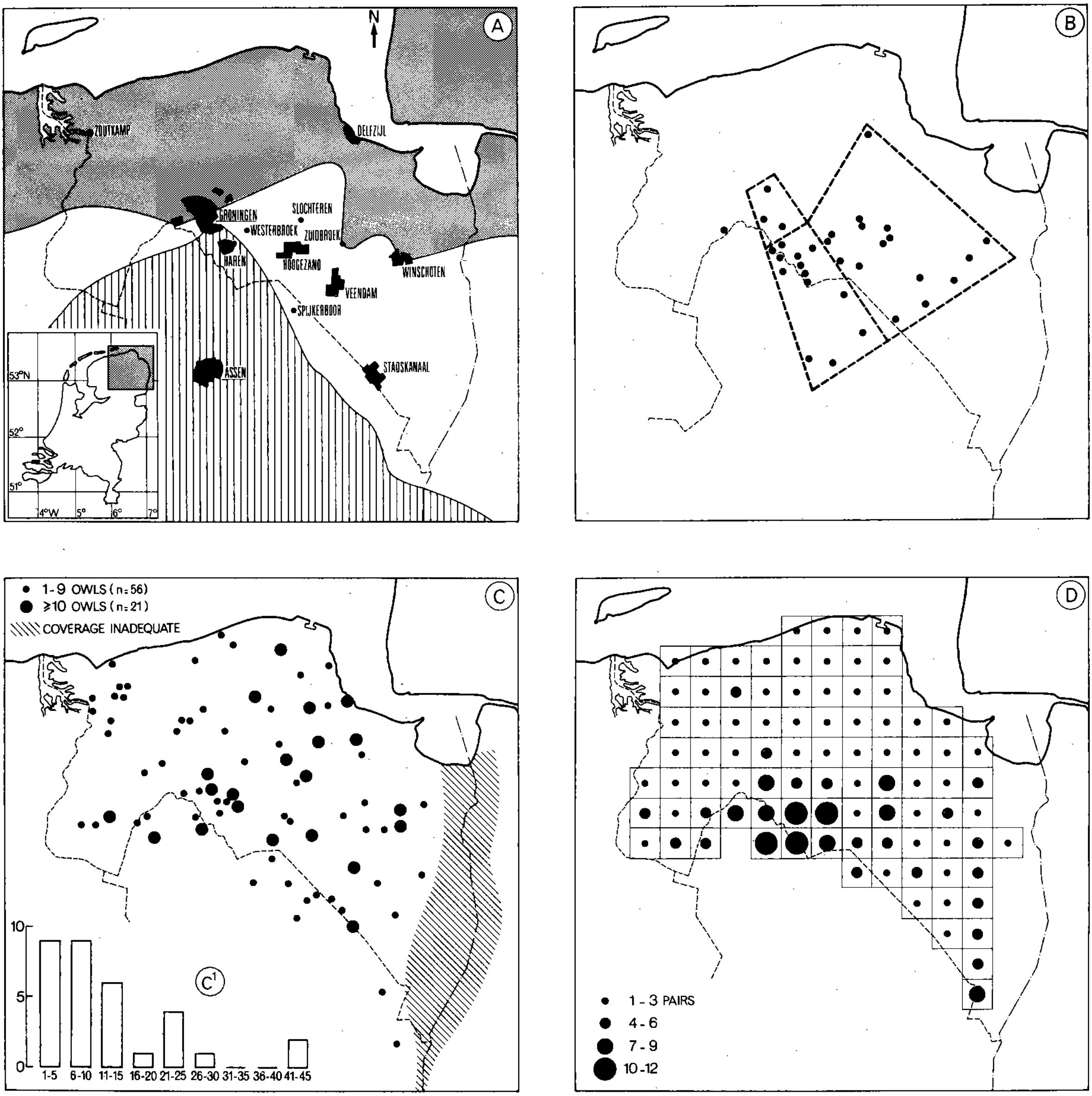


Fig. 3. (A) Main towns and villages mentioned in text and the physiographic regions within the study area, see text for explanation. (B) Localities where pellets were collected arranged according to physiographic region. (C) 1978/'79 winter census of roosts, inset shows percentage distribution of roost sizes. (D) Density of breeding pairs per 25 km² bloc.

Although we trapped and ringed 196 Long-eared Owls on the winter roosts it is difficult to determine the proportions of local residents as distinct from long-distance migrants. Fennoscandinavian and Russian Long-ears migrate in a SW direction during October and November (Hartwig & Vauk 1969, Glutz & Bauer 1980) but the extent of this movement probably depends on the local food situation. That long-distance migrants occur in our area was affirmed by the recovery of a winter-trapped individual the next summer in the USSR (2500 km away). The other 28 recoveries were all local (mean distance 28 km, while 22 of them were less than 10 km; the mean time interval between trapping and recovery was 379 days). Recoveries of all

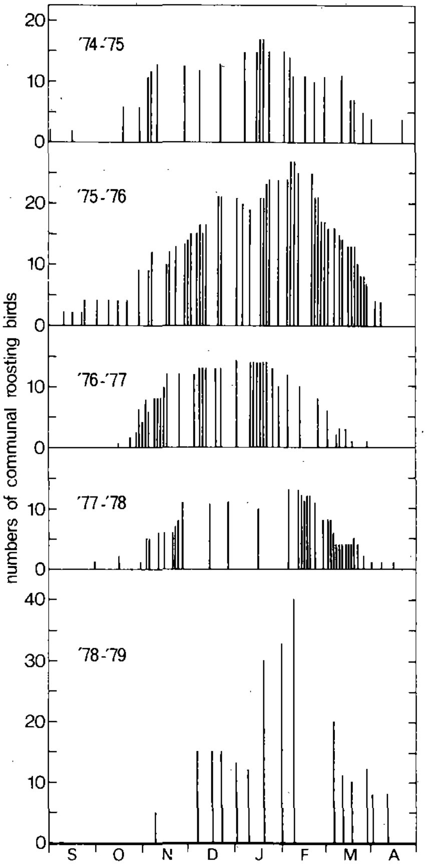


Fig. 4. Number of Long-eared Owls counted at the Helpman roost (suburb of Groningen) from September through April.

Long-eared Owls ringed as fully grown in the Netherlands (almost all of them at winter roosts) affirm that the majority are local residents (Fig. 5). Another line of evidence pointing in the same direction comes from census data. During January-February 1979 a complete census for the province of Groningen and the northern part of Drente was carried out (Fig. 3C). Although some roosts may have been missed, and movements between roosts (Stiefel & Stiefel 1970 and pers.obs.) are a source of error, a total of 750 roosting Long-eared Owls was found in the census area (2100 km²). In the same area a mean breeding density of 250—300 pairs was found (Fig. 3D), so this does not leave much scope for immigrants. On a smaller scale this is illustrated for two winter roosts in Fig. 6. In both cases the number of birds wintering is in agreement with the number of owls breeding

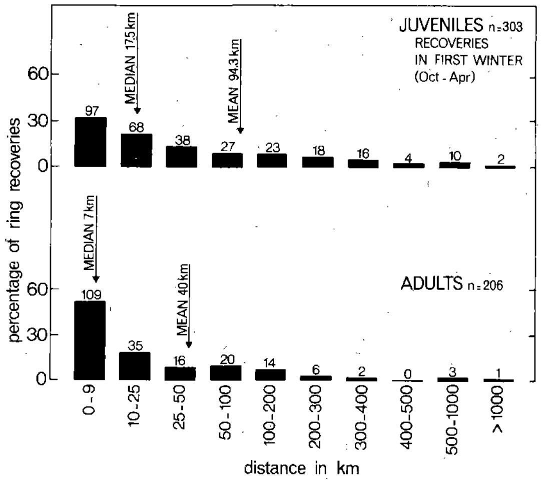


Fig. 5. Percentage distribution of recoveries of the Long-eared Owl ringed in the Netherlands with respect to distance from the ringing site. Juveniles above, adults below (data from Vogeltrekstation, Arnhem).

within a short distance of the roost, and for three marked pairs we could prove that they all originated within 3 km of the roost. In the spring, decline in numbers at the roost coincided with the occupation of the adjacent breeding territories.

The ringing recoveries and census data thus indicate that in our area the adult owls remain close to the breeding site the year round. In common with the pattern established for middle Europe (Glutz & Bauer 1980) the majority of juveniles however migrate in their first autumn.

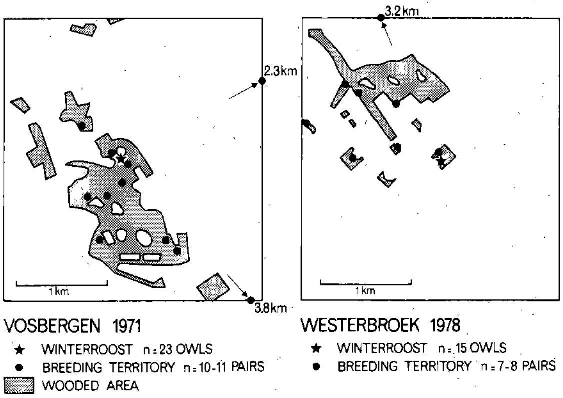


Fig. 6. Location of breeding territories in relation to the winter roost at two intensively studied sites (numbers at the winterroosts are maxima for December—January).

The distribution of recoveries reveals a greater extent of movement than in the adults (Fig. 5). This pattern of greater dispersion in juveniles than the more resident adults has been found in other owls and raptors (Cavé 1968, Newton 1979, Galushin 1974).

2.2. HOME RANGE DURING AUTUMN AND WINTER

Information on the size and utilization of the home range was derived from radio telemetry. Miniaturized radio transmitters were attached to the owls, and by taking bearings every ten minutes from two motor cars simultaneously it was possible to follow the movements of the owls (for methods see chapter 7). As detailed in Table 1, five individuals were intensively tracked for periods of 1—3 weeks. All five tracking locations were situated in open farming country dominated by meadows and ploughed fields interspersed with small woodlots.

In this landscape home ranges varied from 1135 to 2560 ha (mean 2025, see Table 1). Only about 20% of the home range was utilized each night (Table 1, and see the sample plot for owl I in Fig. 7). A more systematic approach to determining the intensity of utilization of the hunting area is undertaken for owl I and owl II (Fig. 8). The bearings have been plotted in blocs of 25 ha, and the intensity of use given in per cent of "active bearings" (= in-flight determinations). As summarized in Table 2, the intensively exploited hunting area (defined here as containing 75% of the active bearings) comprised only 10—20% of the total home range.

The question arises if these smaller areas are

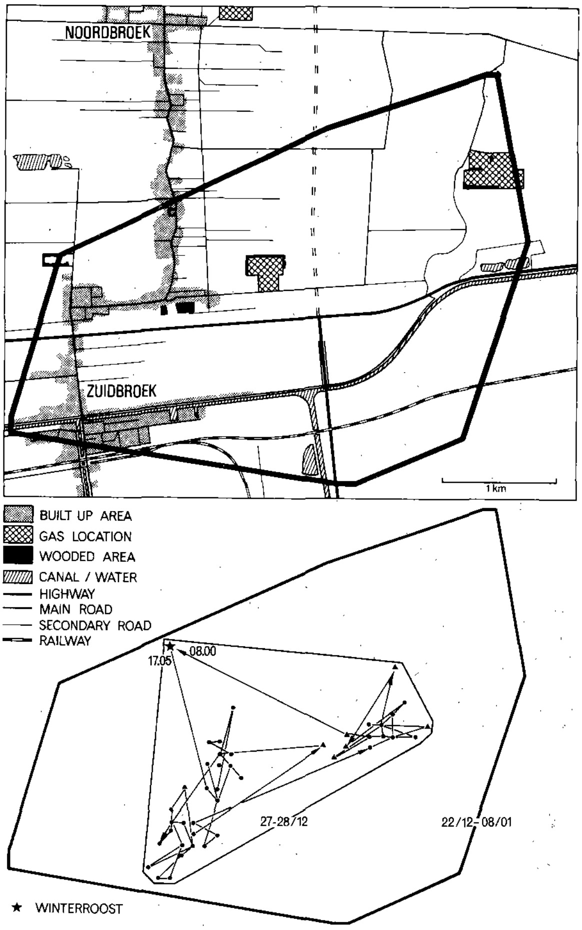


Fig. 7. Home range of Long-eared Owl no. I, based on radio telemetry from 22-12-76 until 08-01-77 (polygon connects the extreme observations). Lower panel shows movements on one night, fixes being obtained every 10 minutes (triangles show bearings taken during flight, dots temporary roosts).

Table 1. Homeranges of Long-eared Owls measured by means of radio telemetry

Owl number	Location*	Tracking period	Sex	Total homerange** (ha)	Maximum distance from roost (km)	Mean nightly range** (ha)
I	Zuidbroek	221276—080177	♀	1136	3.4	323 (206— 462)
II	Zuidbroek	150277—010377	♂	2059	4.3	393 (129—1051)
III	Zoutkamp	041077—121077	♂	2445	9.0	644 (105—1919)
IV	Westerbroek	181177—121277	♀	1924	4.8	251 (67— 621)
V	Spijkerboor	300478—180578	♂	2560	6.0	— —
				x̄ = 2025	x̄ = 5.5	x̄ = 403

*) See Fig. 3B.

**) Ranges calculated according to the minimum homerange method: most peripheral radio fixes joined by straight lines, home range is considered to be the area contained within the polygon thus formed.

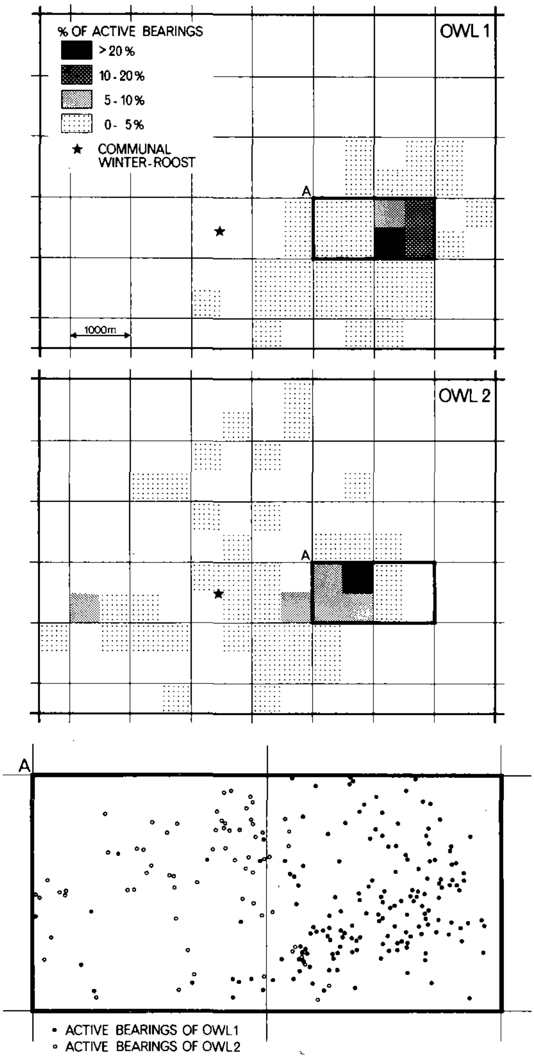


Fig. 8. Intensity of use of the home range for two individual Long-eared Owls using adjacent hunting areas (dates given in Table 1). Topography of the site is given in Fig. 7, where position of winter roost is plotted. The lower panel shows the actual bearings for the two owls in the area most intensively used, identified above (note letter A).

indeed "exclusive hunting areas" (Pitelka 1955) for an individual owl (or pair). Although individuals were not tracked simultaneously, owl I and owl II were followed shortly after one another, and in the period owl II was followed owl I was still using the same roosting tree, and likely hunted in the same area as the preceding month. Active bearings for these two owls (Fig. 8) show a high degree of segregation, and tend to support the idea of exclusive hunting areas.

If we wish to compare our data with that for other owl species, we must first consider the distortion caused by the communal roosting habits of the Long-eared Owl. A plot of all bearings includes the corridor of access to the intensive hunting area, and gives exaggeration of the area actually used for hunting. The figure most comparable to the homerange data of other owl species, where individual birds roost within their hunting area, is thus what we have called the intensive hunting area for the Long-eared Owl. Indeed, when making comparisons on this basis (Table 3) the hunting area of the owls using open field habitats (*Asio otus*, *A. flammeus* and *Nyctea*) in winter is closely similar.

2.3. BREEDING PHENOLOGY

If the weather is mild courtship activity may be observed early in the year (earliest calling female 1 January 1977, earliest male 7 January 1971). Phenology at the winter roost is depicted for one season in Fig. 9. Observations in late winter revealed that after leaving the winter roost (about 15 minutes after sunset) the pair sometimes flew directly to their breeding territory before going hunting. In late January and early February the pairs probably spend only a small fraction of their active period in the breeding territory, but by the end of February and

Table 2. Sizes of the most intensively used parts of the homeranges

	A	B	A	B	A	B	Total
	50%		75%		90%		home range
Owl I	65 ha	(5.7%)	185 ha	(16.3%)	350 ha	(30.8%)	1136 ha
Owl II	100 ha	(4.9%)	210 ha	(10.2%)	450 ha	(21.9%)	2059
Owl IV	150 ha	(7.8%)	370 ha	(19.2%)	700 ha	(36.4%)	1924 ha

A = area (ha) containing respectievely 50,75 and 90% of all active bearings, measured as 25 ha blocks and if necessary interpolated.
B = percentage of the total home range.

Table 3. Home ranges for several owl species. A = studies based on telemetry. B = studies based on visual observations; open field species, mostly day-hunters

	Owl species	Body weight (g)	Home range (ha)	Period of the year	Author
A)	Saw-whet Owl (*Aegolius acadicus*)	75	114	autumn	Forbes & Warner, 1974
	Little Owl (*Athena noctua*)	190	9	spring	Fuchs, unpublished
	Long-eared Owl (*Asio otus*)	260—320	1136—2560 (1) 185— 370 (2)	autumn, winter and spring	this study: 1) total range 2) intensively used range
	Tawny Owl (*Strix aluco*)	570	146 89	winter spring	Nilsson, 1978
	Barred Owl (*Strix varia*)	710	86— 369	whole year	Nicholls & Warner, 1972
	Morepork (*Ninox novaeseelandiae*)	150	35— 54	spring	Imboden, 1975
B)	Short-eared Owl (*Asio flammeus*)	340	23— 121	spring	Clark, 1975
	Snowy Owl ♂ ♀ (*Nyctea scandiaca*)	1700 2100	50— 260 150— 450	winter winter	Boxall & Lein, 1982

early March the female can usually be located on territory when the observer approaches and plays the hooting call of her male on a taperecorder (the female reacts by calling and wing-clapping). In a few cases the male approached from outside the territory, and we twice observed courtship feeding of the female, probably a very common event (Mannes & Bruin, cited in Glutz & Bauer 1980). The role of the male as the hunter for the family has already started. During this period the winter roost is gradually abandoned, and both sexes can be found by day on the breeding territory. This pattern of gradual territory occupation is in keeping with other observations in middle Europe (Glutz & Bauer 1980) but contrasts to the situation in England where the Long-eared Owl holds territory all year round (Scott, cited in Glue 1977).

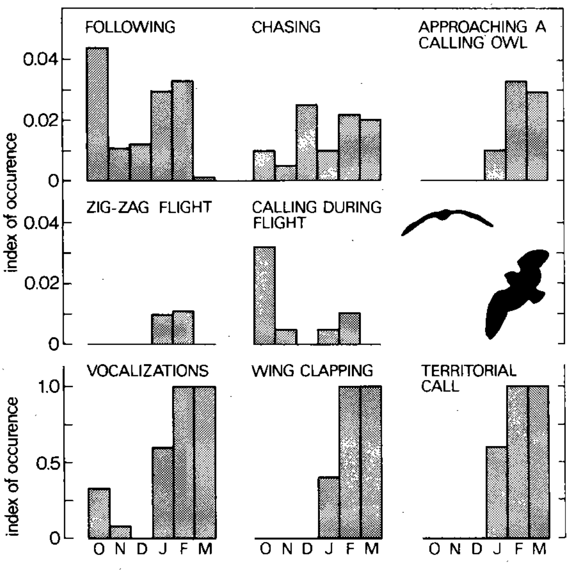


Fig. 9. Phenology of activities associated with territoriality and breeding (index of monthly occurence at the winter roost of the Vosbergen study site, winter 1970—71).

The female may be observed sitting in various nests in the territory, also by day, before she makes her final choice and starts laying, in our area almost always making use of old nests of the Carrion Crow or Magpie (see Table 4).

Fig. 10 shows the dates of clutch commencement and the distribution of clutch size for the study area 1974—1978. As has been shown for other vole specialists (Mebs 1964, Cavé 1968) mean laying date, and hence clutch size as well,

Table 4. Long-eared Owl nest situation

A. Treetype	Number	B. Height of the nest (in meters)	Number	C. Nesttype	Number
Evergreen		0	1	Carrion Crow	28
Spruce	14	1	—	Magpie with cap	7
Pine	13	2	3	Magpie without cap	10
Holly	2	3	9	Jay	1
Larch	1	4	11	Kestrel	1
Pinus sp.	1	5	12	Artificial nest	
Deciduous		6	13	(open platform)	2
Oak	24	7	7	Nestbox	1
Alder	4	8	4	Groundnest	1
Beech	4	9	6		
Birch	4	10	5		
Hawthorn	2	11	2		
Apple	2	12	4		
Cherry	2	13	1		
Willow	1	14	2		
Poplar	1	15	3		
Bramble	1	> 15	2		
Elder	1				
Total	77		85		51

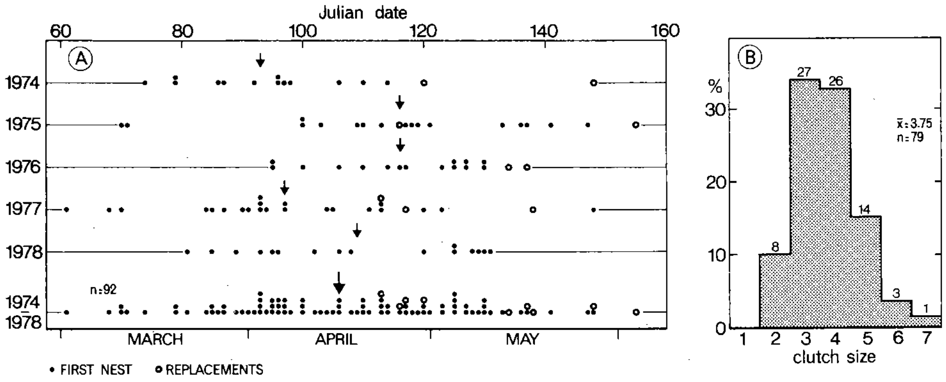


Fig. 10. (A) Laying dates in the study area (each dot represents initiation of one clutch, mean date for first clutches shown by arrows) (B) frequency distribution of clutch sizes (numerals give actual ample sizes).

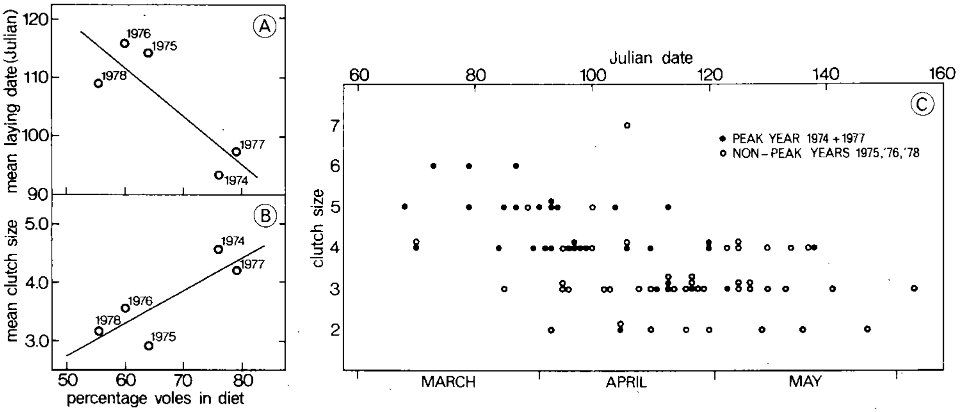


Fig. 11. Effect of vole cycle on reproduction in the Long-eared Owl. Mean laying date is advanced in years of high vole abundance (A), clutches are also larger then (B) and basic data are also given (C, note key showing vole abundance) showing the decline in clutch size with season.

is correlated with the occurrence of this prey in the diet (Fig. 11: laying is early in vole years). There is an indication in the data (Fig. 11C) that in vole peak years clutch size at a given laying date is larger (by about one egg) than in non-peak years, but the decline of clutch size in

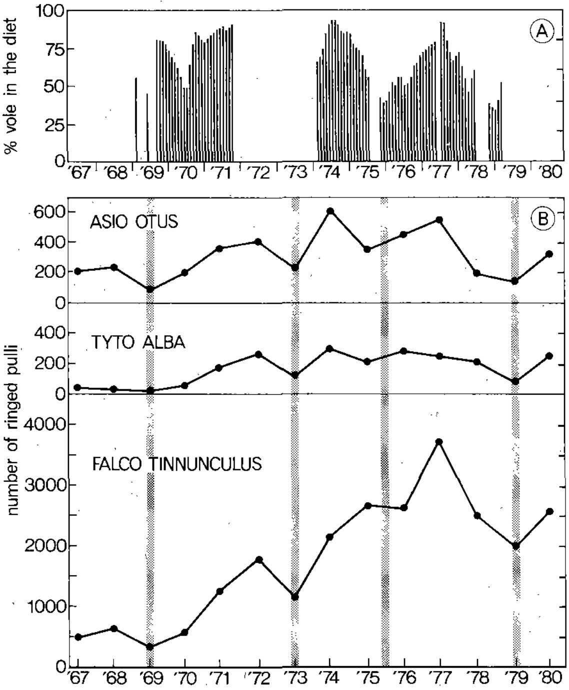


Fig. 12. Relationship between vole abundance (A, variation in incidence of voles in the diet of the Long-eared Owl in the study area, running average) and the reproductive output of vole specialists (B, estimated by the total number of pulli ringed in the Netherlands). Years of low vole numbers are shown by the stippled bars.

the course of the season follows the same slope. Differences in production (as estimated from the number of pulli ringed in the Netherlands) are also related to the vole cycle (Fig. 12). The laying period for the Long-eared Owl in the country as a whole (deduced by back-dating from ringing dates of the pulli) is intermediate compared to other owl species (Fig. 13). Back-dating was carried out by using a reliable mean time between hatching and ringing, in combination with a mean incubation period for each species.

2.4. BREEDING DENSITIES

For the province of Groningen a general survey is available, based on 5 × 5 km blocs surveyed by a network of observers (Fig. 3D). Densities were found to vary between 1 to 12 pairs per 25 km^2 bloc, and are in the range of observations elsewhere in western Europe if large scale surveys are considered (Table 5). As

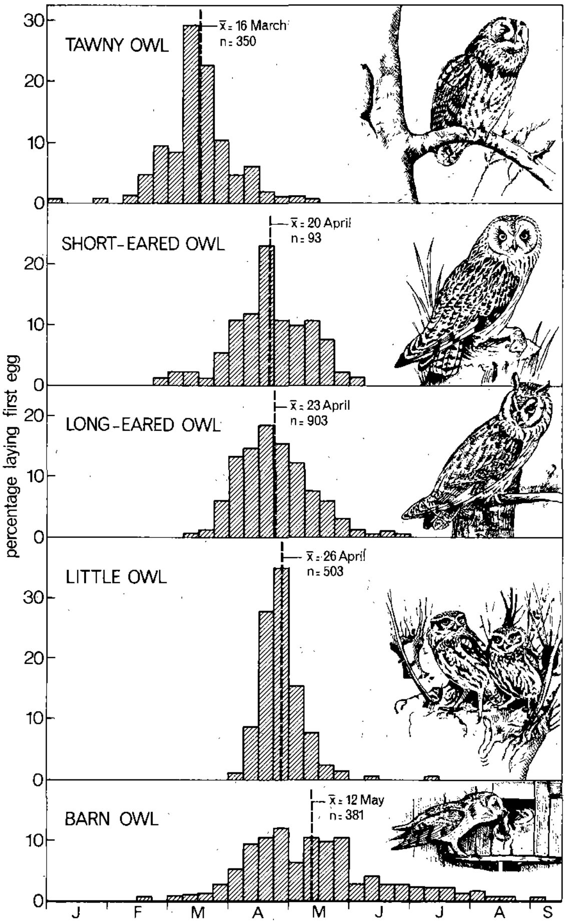


Fig. 13. Estimated laying dates in five owl species in the Netherlands (mean and sample size indicated; computed from ringing lists of the Vogeltrekstation, Arnhem). From top to bottom: *Strix aluco, Asio flammeus, Asio otus, Athene noctua, Tyto alba*. The owl vignettes are by E. Hazebroek.

occurred in 1978, in years with an inadequate food supply many pairs fail to breed, and in the Netherlands fluctuations in density can be expected (but the maximum-minimum ratio's do not in general exceed a factor of two).

2.5. RESUMÉ

The pattern and timing of moult will be described in chapter 10. Briefly, flight feather moult starts in late June when most juveniles, though still dependent on their parents, are already fully grown, and is finally completed in October. The main elements of the annual cycle

Table 5. Numbers of breeding pairs of the Long-eared Owl in selected study areas of at least 35 km^2

Locality	Country	Size of the area (km^2)	Number of breeding pairs/10 km^2	Author
Schleswig Holstein	Western Germany	200	0.3—1.4	Ziesemer, 1973
Hamburg area	Western Germany	230	0.2—2.3	Bruster, 1973
Elbe valley	Eastern Germany	870	1.1—1.5	Gleimich & Humitzsch, 1977
Southwestern Drente	The Netherlands	165	2.7—4.8	van Dijk a.o., 1972
Groningen	The Netherlands	2100	1.4	this study
Revinge	Sweden	43	2.0 (average)	Nilsson, 1981
Lorraine	France	148	0.3	Thiollay, 1967
Southern Michigan	USA	92	0.1	Craighead & Craighead, 1956
Wyoming	USA	36	1.0	Craighead & Craighead, 1956
Southern Idaho	USA	2315	0.07	Craig & Trost, 1979

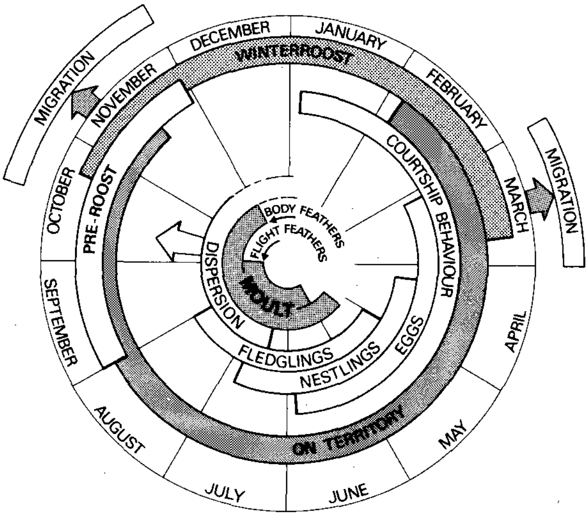


Fig. 14. Approximate chronology of the annual cycle in the Long-eared Owl.

are summarized for my study area in Fig. 14, which will serve as a frame of reference for the rest of the paper.

3. THE DIET

3.1. LITERATURE REVIEW

Due to the ease with which pellets of this species can be collected and analyzed, the food spectrum of the Long-eared Owl has been extensively reported from Europe. Uttendörfer's (1939, 1952) monumental analysis was based on more than 57.000 prey remains, and since then additional studies have become available (van Winkel 1964, Hagen 1965, Fairly 1967, Glue & Hammond 1974, Källander 1977; for a recent survey for the Netherlands see Smeenk 1972). In a review Marti (1976) presented a diet profile for this species and described the Long-eared Owl as mainly a mammal hunter in open areas. Mammals were found to constitute 98% of all prey in North America, and 89% in Europe, with species of voles (*Microtus*) being the most common prey. The average prey weight was estimated as 37.0 g in North America and 32.2 g in Europe. As Marti pointed out, however, there is a heavy bias towards winter samples in the material, and it will be my aim here to present the year-round diet, and comment on differences between years.

3.2. METHODS

Collecting pellets at the communal roosting sites used by day during the winter is an easy task, and was done at a number of localities (see Fig. 3B) at least monthly. By radio tracking owls we determined sites used for roosting by night, and these places were searched carefully during daytime to yield samples of the pellets produced during the night (the rhythm of pellet production is treated in chapter 4). In some cases the hunting area was searched carefully by several observers to locate night pellets, and all pellets found at sites where owls were never seen by day were considered as such. During breeding and especially in autumn it is much more difficult to find pellets, as they are not deposited in the nest or under the nesting tree (except during the first three weeks of the nestling period). Careful search of the nesting area was necessary, and usually the roost site was located within about 75 m of the nesting tree. At some nests fresh prey items was identified.

All pellets were dried at room temperature or in a stove kept at 40 °C, and if after inspection no fractures could be discerned the pellets were considered to be intact and the dry weight determined, and the material stored until analysis.

For analysis pellets were broken by hand, and skeletal fragments useful for identifying prey species cleaned with a little brush (for mammals the skull and mandibles, for birds the culmen and tarsometatarsus). Fur, feathers, bird stomachs and the sternum sometimes gave additional information. Mammalian prey were identified using Husson's (1962)

Table 6. Vertebrate prey of Long-eared Owl: results of pellet analysis and prey from nests during the period 1969—1979

	Total number of prey	Percentage based on number	Average body weight of prey	Percentage based on prey weight
Mammals				
Total	40 713	92.6	19.2	87.1
Common Vole (*Microtus arvalis*)	31 673	72.0	19	66.9
Wood Mouse (*Apodemus sylvaticus*)	3 713	8.4	21	8.6
Bank Vole (*Clethrionomys glareolus*)	1 710	3.9	18	3.5
Short-tailed Vole (*Microtus agrestis*)	1 570	3.6	22	3.8
Harvest Mouse (*Micromys minutus*)	963	2.2	6.5	0.7
Common Shrew (*Sorex araneus*)	371	0.8	9	0.7
House Mouse (*Mus musculus*)	252	0.6	20	0.5
White-toothed Shrew (*Crocidura russula*)	186	0.4	10	0.2
Water Vole, juv. (*Arvicola terrestris*)	84	0.2	50	0.4
Brown Rat, juv. (*Rattus norvegicus*)	50	0.1	100*	0.5
Mole (*Talpa europaea*)	48	0.1	75	0.4
Arvicola or *Rattus* juv.	33	0.1	85	0.3
Rabbit/Hare, juv. (*Oryctolagus cuniculus/Lepus timidus*)	25	0.1	100*	0.3
Pigmy Shrew (*Sorex minutus*)	23	0.1	5	0.0
Water Shrew (*Neomys fodiens*)	111	0.0	10	0.0
Bat sp.	1	0.0	—	0.0
Birds**				
Total	3 277	7.4	35.5	12.9
Body weight larger than 45 g	743	1.6	85	7.0
Body weight between 20—45 g	1 611	3.7	25	4.2
Body weight smaller than 20 g	923	2.1	15	1.7
Vertebrates				
Total	43 990		20.4	

*) 100 g was taken as the upper limit of prey weight actually eaten.
**) For specification of bird species see appendix 2.

key, with the simplification that in our study area the genus *Rattus* is represented only by the Brown Rat (*Rattus novegicus*) and *Crocidura* by the White-toothed Shrew, *Crocidura russula* (de Bruyn 1979). A minority of *Microtus* skull fragments could not be keyed to species, and were assigned to *M. agrestis* or *M. arvalis* according to the relative proportions found in intact skulls from that specific sample.

Bird remains were determined with the aid of the reference collection of the Zoological Laboratory, initiated by L. Tinbergen. Although insects occur in pellets from time to time their contribution to the diet is infinitesimal and they will be ignored here (remains identified include *Geotropus* spec., *Aphodius fimetrius*, *Hydrous piceus*, *Dytiscus* spec., *Melolontha* spec.).

The content of each intact pellet was noted separately, and the number of prey items concerned was taken to equal the greatest number of identified fragments of one species (greatest number of lower jaws etc.). Monthly totals comprise these data plus remains found in pellet fragments and debris.

In order to convert these data on prey frequency into biomass, the mean body weight for prey species in the study area was determined from the following sources: a) fresh, intact prey found during nest inspection, b) small mammals trapped locally, (own data and S. Daan, *pers. comm.*), c) birds caught locally during ringing programmes (P. Drent, *pers. comm.*). Seasonal and annual variation in weight has been ignored, but for some prey species only juvenile specimens were taken and this has been taken into account.

3.3. PREY SPECTRUM

Analyses of all pellets together with prey found at the nest gives an overall spectrum of prey composition in our study area (Table 6, Fig. 15). Mammals are the most important prey (92.6% based on number of prey items) and within this category the Common Vole, *Microtus arvalis*, dominates (72.0% of all prey). Passerine birds and the Wood Mouse, *Apodemus sylvaticus* add about 10% each. Calculations on the basis of prey weight do not change this pattern appreciably, although birds do increase somewhat in importance (12.9%). Among the birds, the weight category of 20—45 g dominates (largely *Passer*), and further *Turdus*, *Sturnus*, *Parus* and *Carduelis* are taken regularly (Appendix 2).

A modest number of night pellets were collected in two situations, and are compared with day-pellets from the same period and location in Table 7. In the open landscape of Zuidbroek the two do not differ, but in the Vosbergen where

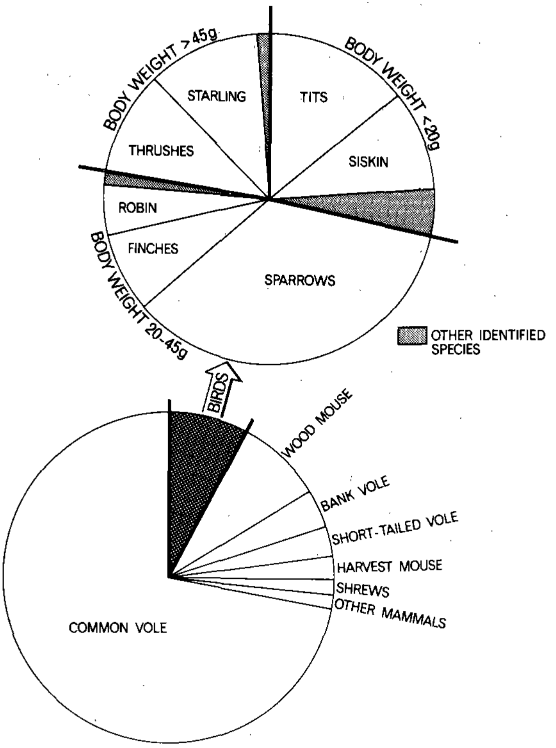


Fig. 15. Diet summary for the Long-eared Owl in the northern Netherlands, showing percentage incidence according to *number* of prey (see Table 6 and Appendix 2).

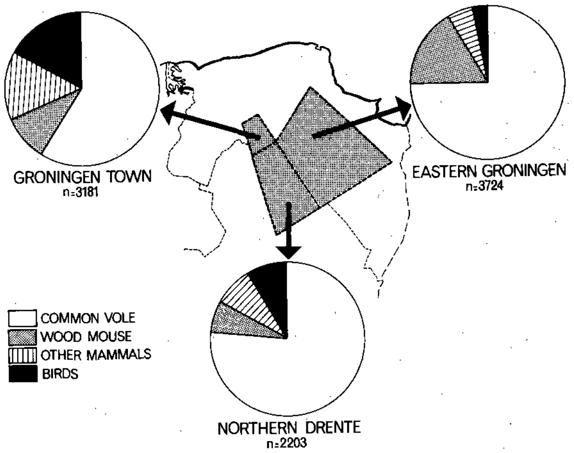


Fig. 16. Local variation in the diet of the Long-eared Owl: percentage incidence according to *number* of prey (sample size refers to number of prey items identified).

woodland adjoins meadow and cultivated fields the two differ markedly (χ^2 test, $p < .001$). The Vosbergen night pellets contain significantly more mammals and birds of the woodland habitat, whereas mammals typical of the open field habitat are underrepresented (Fisher exact test, $p < .05$). As we will see (section 4.2.) the night pellets comprise prey taken in the first half of the night, whereas the day pellets represent the yield of the second half of the hunting period. The Vosbergen data suggest a bias towards hunting in woodland during the first part of the night, perhaps triggered by the availability of birds searching for sleeping locations around sunset.

When the data for the 36 sites where pellets were analyzed are grouped by landscape categories (Fig. 16) the diet differs significantly (restricting the sample to the same months of collection yields $p < .001$ by the χ^2 test). It should be noted that in the suburbs of Groningen far more birds are captured than elsewhere.

3.4. REPERCUSSIONS OF THE VOLE CYCLE

The main prey item of the Long-eared Owl, the Common Vole, is known to experience a cyclic variation in numbers in the Netherlands and adjoining parts of the range, numbers reaching

Table 7. Prey composition based on number of prey items in night pellets compared to day pellets

	Open field species*	Woodland species**	Birds	Others	Total
Vosbergen, winter 1970—1971 (November—January)					
Night pellets	53 (55.8%)	29 (30.5%)	12 (12.6%)	1 (1.0%)	95
Day pellets	3988 (84.7%)	447 (9.5%)	251 (5.3%)	25 (0.5%)	4711
Zuidbroek, winter 1977 (January—March)					
Night pellets	54 (87.1%)	8 (12.9%)	— —	— —	62
Day pellets	310 (90.9%)	29 (8.5%)	2 (0.6%)	— —	341

*) *Microtus arvalis, Microtus agrestis, Micromys minutus, Arvicola terrestris, Talpa europaea.*
**) *Clethrionomys glareolus, Apodemus sylvaticus.*

peak values every 3 (or sometimes 4) years (Frank 1953, 1954, van Wijngaarden 1975, Becker 1958, de Bruijn 1979). Since 1968 voles experienced minima in the Netherlands in 1969, 1973, 1975—1976, and 1979 (de Bruijn 1979, van Dijk & van Os 1982), and this pattern of fluctuation is reflected in the proportion of voles in the diet of the Long-eared Owl (Fig. 12). In order to obtain a generalized picture of trends in the diet, the years of this study were classified as peak years (1971, 1974, 1977), years of increase (1970, 1976, 1979) and years of decrease (1969, 1975, 1978). When the data are averaged (Fig. 17) we see that in peak years the highest percentages of voles in the diet are reached in July and August (up to 95% of all prey), whereas in years of increase and years of decrease the peak is not reached until September—October, and does not exceed 80%. Years of decrease show an abrupt decline of the vole in the diet in early winter. The two other prey categories of course show an opposite trend. An unexpected result of this analysis is the consistently low contribution of the Wood Mouse to the summer diet.

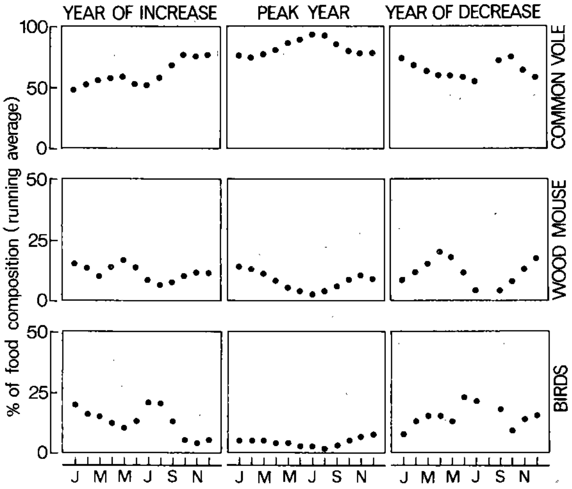


Fig. 17. Changes in the diet of the Long-eared Owl in the course of the vole cycle: running average of % prey number comprised by Common Vole, Wood Mouse, or birds (top to bottom) in years of increase, peak, or decrease in vole abundance (left to right). Note different scales.

During the winter, snow cover influences the diet (Table 8). In both snow periods considered the percentage of Wood Mouse (by number) increases, at the expense of the voles in the diet. In these samples there are no changes in the occurrence of birds in the diet, but as was noted above, Long-eared Owls may shift to suburban localities under conditions of heavy snow, where they exploit birds heavily.

3.5. COMPARISON WITH OTHER AREAS

Including the data of this study some 360.000 individual prey items have now been reported for the Long-eared Owl, and of course my own data do not change this general picture. At all seasons *Microtus* species are by far the most important prey, and the extent of variation in the course of the year is far less than in species such as Tawny Owl, *Strix aluco* (Southern 1954, Smeenk 1972, Koning *pers. comm.*), Little Owl, *Athene noctua* (Glutz & Bauer, 1980) and the Barn Owl, *Tyto alba* (Bohnsack 1966, de Bruijn 1979, de Jong *pers. comm.*).

The most comprehensive study elsewhere

Table 8. Prey composition (number of prey items) before, during and after a period with snow cover

	Before snow-period	Snow-period	After snow-period
Vosbergen 24-12-1969/11-1-1970			
Common Vole	519 (77.6%)	1154 (75.9%)	631 (82.3%)
Wood Mouse	44 (6.6%)	191 (12.6%)	36 (4.7%)
Birds	36 (5.4%)	76 (5.0%)	41 (5.3%)
Others	69 (10.3%)	99 (6.5%)	58 (7.6%)
Total	668	1520	766
Zuidbroek 17-12-1976/31-12-1976			
Common Vole	352 (72.9%)	43 (67.2%)	174 (69.9%)
Wood Mouse	110 (22.8%)	18 (28.1%)	60 (24.1%)
Birds	12 (2.5%)	2 (3.1%)	5 (2.0%)
Others	9 (1.9%)	1 (1.6%)	10 (4.0%)
Total	483	64	249

concerns a three-year diet analysis for the Long-eared Owl in southern Sweden (Nilsson 1981). The percentage of voles in the diet (*Microtus agrestis* in this case) was found to decrease from about 85% in midwinter to only 20% in June, followed by a quick recovery in autumn. Since vole populations in southern Sweden seem to show the same pattern of seasonal fluctuation as in the Netherlands (populations increasing 10—20 fold from spring to autumn as described by Nilsson for his area, and Cavé 1968 and Daan *pers. comm.* for the Netherlands) this radical difference in diet cannot be explained by differences simply in vole abundance. Rather the explanation must be sought (as was suggested by Nilsson) by changes in the availability of voles in relation to alternative prey (in southern Sweden *Arvicola terrestris* and birds are important prey in midsummer). Another way to compare the studies is to compute the niche breadth as measured by the diet (Nilsson followed the procedure of Levins 1968 in computing niche breadth and I have done the same). When the two areas are compared (Fig. 18) niche breadth is found to be greater in my study area than in southern Sweden with the exception of the summer months, *i.e.* in my area the Long-eared Owl generally has a more diverse diet and the mix of species is more stable.

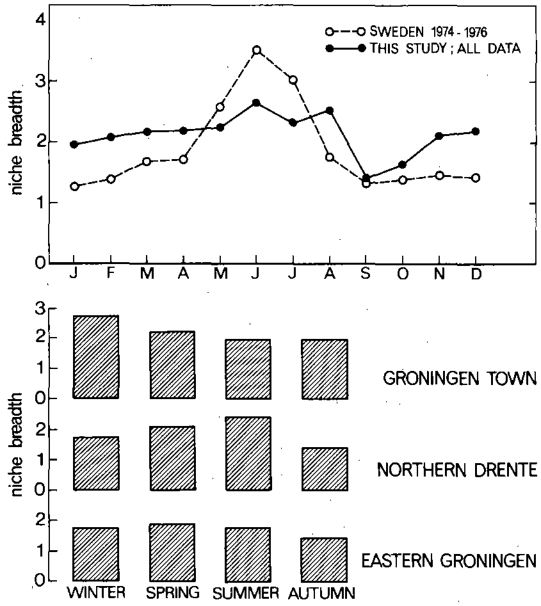


Fig. 18. Seasonal changes in niche breadth of the Long-eared Owl (defined as $(\Sigma_{Pi}{}^2)^{-1}$ where Pi is the proportion of the ith species in the diet, see Levins 1968) in my study area compared to southern Sweden (Nilsson 1981, upper panel) and in the three subdivisions shown in Fig. 16 (lower panel).

If we extend this analysis to the three sub-regions in my study, suburban Groningen is found to have the greatest niche breadth in winter (Fig. 18 lower panel). This is due to the relatively high number of birds in the diet, as has been found in other studies in urban or suburban habitats (thus Tinbergen (1933) recorded up to 80% of the diet as composed of birds in Rotterdam, and Johnson & Scharr (1970) give 24% birds for Lund and Hillarp (1971) 30% in Malmö, both in southern Sweden, where Nilsson recorded less than 10% in a nearby rural district). In summer niche breadth is greatest in northern Drente, again because of the bird component (juvenile birds become numerous in the woods at that time, and are easily caught by the Long-eared Owl). The third sub-region shows only minor variation in the course of the year.

Another point on which comparative data are available concerns the drop in the incidence of the Wood Mouse in the diet in the summer months, found also by Tinbergen (1933), van Winkel (1964), Wooler & Triggs (1968) and Glue & Hammond (1974). This May-July decrease has also been shown for the Barn Owl (Becker 1958, de Bruijn 1979) and the Tawny Owl (Southern 1954, Koning *pers. comm.*). Southern has suggested that this might be caused by an increase in the vegetation cover making the Wood Mouse more difficult to catch at that time of year. Nilsson (1981) has extended this argument to explain the opposite effect in his study area in southern Sweden: here the incidence of the Wood Mouse increased in the summer months. Nilsson noted that in Wood Mouse habitat vegetation growth in spring was slower than in the peat districts where alternative prey were taken, and hence he reasoned that the Wood Mouse became relatively *more* vulnerable as the season advanced. We obviously need far more data on habitat use and the rhythm of above-ground activity in small rodents before we can test these suggestions empirically. Despite its name we must not regard the Wood Mouse as being restricted to woods, as it in fact occurs widely in agricultural areas, especially along ditch margins and verges (von Knorre 1973) as witnessed by the high incidence in the diet of the Long-eared Owl in the eastern Groningen sub-region.

The opposite effect, the Wood Mouse becoming more vulnerable to owl predation, was noted in periods of snow cover. In my experience voles generally make tunnels under the snow layer, whereas I often found the Wood Mouse walking on the snow surface or climbing in bushes. We must not forget that this is only a minor effect, as voles remain the major prey item even during heavy snow cover (Uttendörfer 1952). I agree with Uttendörfer that at a given locality the incidence of birds in the diet does not change very much with the advent of snow, but sometimes Long-eared Owls may shift to urban sites at such times, where typically more birds occur in the diet, and in that sense one may speak of a diet shift (Czarnecki 1956).

4. METABOLIZED ENERGY THROUGHOUT THE YEAR

4.1. THE APPROACH

Two major hurdles stand in the way of making the step from the identifiable remains in an owl pellet to the food intake of the free-living owl. In the first place, Raczynsky and Ruprecht (1974) have demonstrated that there is a considerable loss of bony elements in the digestive process in owls. Their study showed that in captive Long-eared Owls fed small mammals and birds, the number of prey deduced from analysis of the pellets fell short of actual consumption by no less than 20.9%. This difficulty can be overcome if we make use of the relation between total pellet weight (dry weight) and weight of prey ingested (fresh weight), which has been found to be a reliable estimator, the conversion factor depending on type of prey. It will be convenient to present these data together with information on digestive efficiency, as the same trials provide both (4.3.).

The other problem concerns the number of pellets cast per 24 hr period by free-living owls. Although Guérin (1928) provided evidence that the Barn Owl in his study area generally produced two pellets per 24 hours, and had indications that the same obtained for the Long-eared Owl, other authors have been slow to consider this complication (thus Graber (1962) and Hagen (1965) both base their computations on the assumption of the invariate production of only one pellet per 24 hr). Extensive observations on birds in captivity, and confirmation of the applicability of this work to the free-living situation, seemed the only way to resolve this controversy (4.2.).

Once these matters have been resolved, energy intake, corrected for digestibility by presenting the data as metabolized energy, can be estimated for the greater part of the year (August through March) since a reliable sample of pellets of free-living birds was available. In the reproductive period a more direct method was followed, by installing weighing platforms at the nest, as will be described in section 9.4. The final part of the chapter provides an overview of the metabolized energy available to free-living owls through the period August through March.

4.2. DAILY PELLET PRODUCTION

Methods

Food consumption and pellet production was studied in a flight cage (floor area 40 m^2, height 3.5 m). This cage was situated outdoors in a quiet corner on the grounds of the Zoological Laboratory. Mice were offered to the owl on small boards (see Fig. 19). A microswitch under each board made registration on an event recorder (Esterline Angus) possible. In general dead laboratory mice in the weight range 15—20 g were offered. Mice were taken from deep-freeze storage and thawed before presentation. The cage had only one perch, under which a microswitch was fitted, registering time on or off the perch on the same recorder. Nearly all the time when the owl was at rest it was sitting on this perch. Sitting on the floor (except during a meal) and hanging from the cage walls was rare, and in fact more than 90% of the pellets were cast when the owl was on the perch, where they dropped through a funnel onto a moving sled, pulled with constant speed by a motordrive (see Fig. 19).

Measuring the location of the pellet on the sled provided the time of pellet production (accuracy ± 15 mins). Food was replenished at the end of each day (16.00—17.00) and the sled checked at this time as well as in the morning (09.00—10.00). In the rare cases that the pellet was found on the floor it was at least possible to determine if it had been produced during the night or during the day. Data were obtained throughout the year, with two individual owls. Pellets were dried (either at room temperature or in a stove at 40 °C) and weighed when dry to the nearest .01 g.

Supplementary data (number of day and night pellets, pellet weight) were obtained from owls lodged in outdoor cages without this equipment for measuring meal and pellet times. Techniques specific to the field experiments will be introduced later.

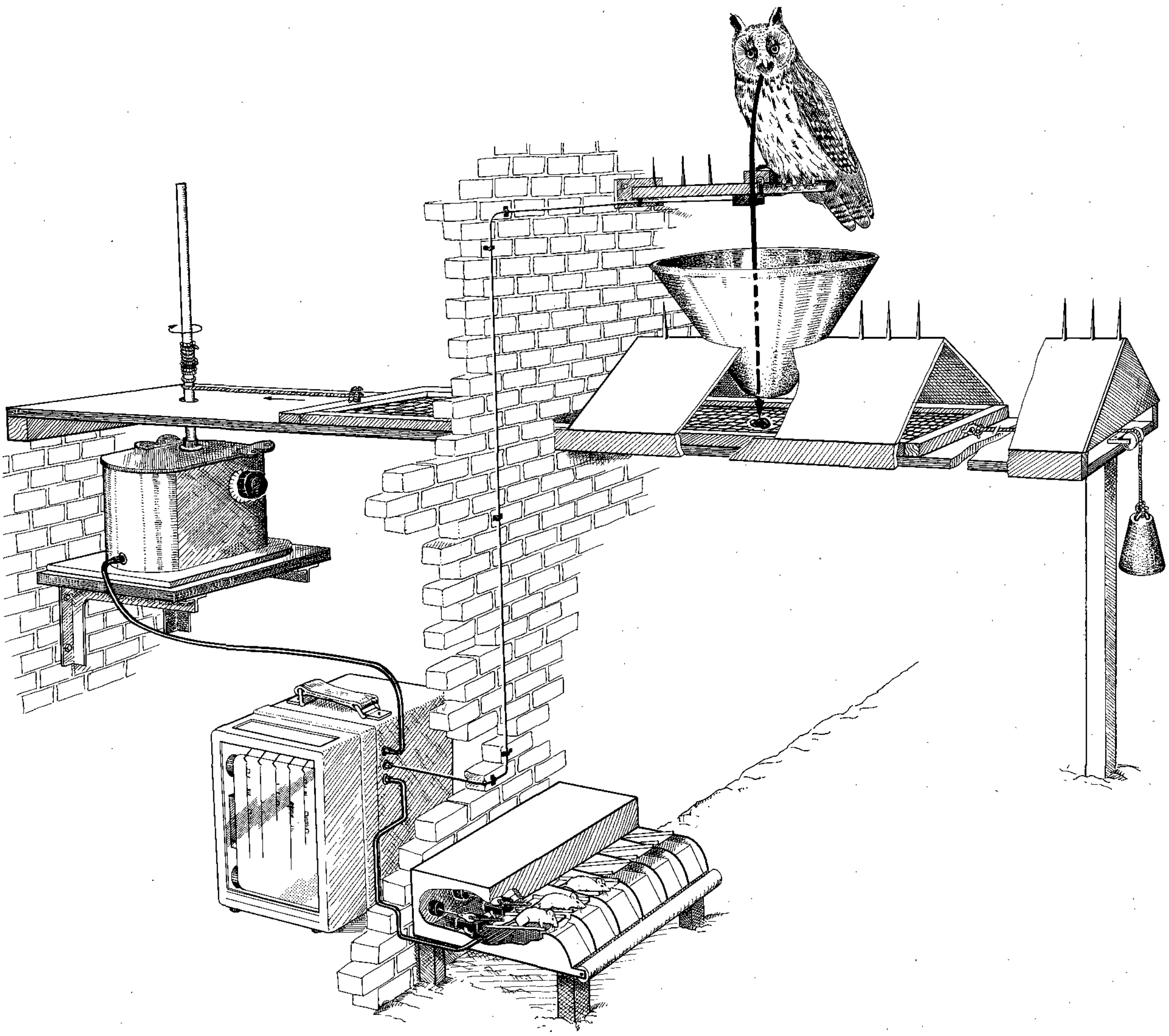


Fig. 19. Apparatus for registering meal times and pellet times in captivity (spikes prevent the owl from perching otherwise than above the funnel). For explanation see text.

Pellet production in captivity

The total weight of pellets produced during 24 hours does not show much variation between months. This suggests that total food intake in captivity is roughly the same throughout the year. However, the average weight of a single pellet and the average number of pellets produced during 24 hours periods show marked and opposite seasonal variation (Fig. 20). The heaviest pellets are produced in May (mean: 1.78 g) and the lowest weights are in November (mean: 0.85 g). In May—June the average number of pellets produced during 24 hours is about 1.2, increasing in autumn and reaching a peak in November—December of about 2.5 pellets.

The time of pellet production also shows seasonal differences. To illustrate this the time of pellet production for 45 periods of 24 hr are given for the winter and for the summer in Fig. 21. In the summer there is a relatively simple situation: more than 95% of all pellets are produced between 12.00—18.00 hr. In the winter the situation is somewhat more complex: a considerable part of the pellets are produced in

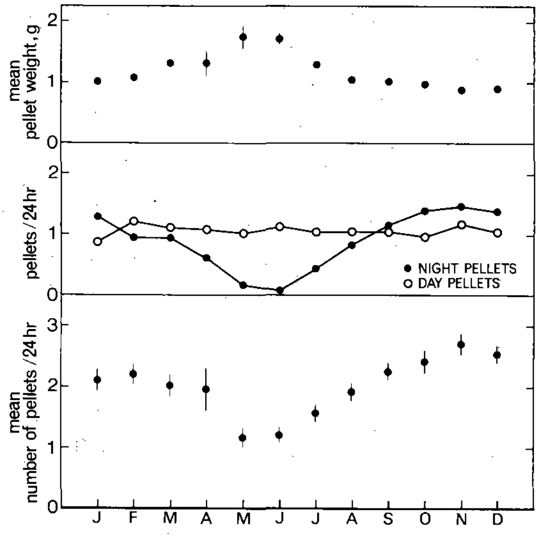


Fig. 20. Data on pellet production as measured in captivity (in the top panel vertical bars show 95 % confidence intervals of the mean, in the lower panel standard error; in all cases dots show the means) in the course of the year.

the same night as the meal was taken from which they originated. These pellets are here termed night pellets. Others are produced during daytime, mostly after 12.00 hr. A few are produced just after sunset of the day following the night where in the meal was taken. Pellets produced before sunset are classified as day pellets and the (small) fraction produced after sunset belong to the night pellets.

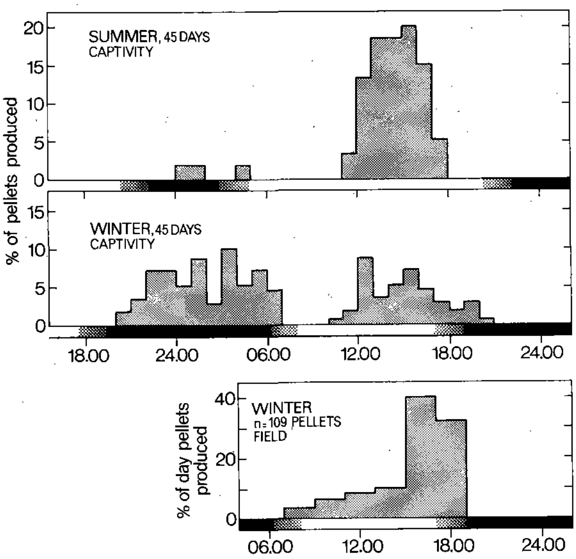


Fig. 21. Time of pellet production in captivity (upper two panels) and for the daylight hours in the field (lower panel). Seasonal variations in times of sunset and sunrise indicated by stippling.

In Fig. 20 data for all months are given for the mean numbers of day and night pellets produced during 24 hr. In all months daytime pellet production is very close to one, but night pellet numbers increase from virtually zero in June to 1.4 in November—December. Pellets produced during nighttime are in general somewhat lighter than the daytime pellets (Table 9). Although there is some variation between months, there is not a clear seasonal tendency. For all months (except April—June, excluded for reasons of a too small sample) the mean weight of the night pellets is 72.2% of the weight of the day pellets.

Field data

The monthly mean weight of all unbroken Long-eared Owl pellets found on various roosting places, in nestcups, under nest trees, etc. are given in Fig. 22. Not included here are pellets from juvenile owls upto a few weeks after hatching. Night pellets (see further) are likewise not included. Although the weights of the pellets found in the field are in general about twice as high as the weights of the pellets produced in captivity (yearly mean 2.37 g against 1.18 g) the seasonal tendency in pellet weight is similar. The highest mean pellet weight is found in July (3.11 g) and the lowest mean weight in December (1.79 g). Only the mean pellet weight for the month May does not fit very well in this graph. An explanation for this aberrant point is related to the pattern of meals that becomes established when the young are being raised in the nest.

As one approach towards obtaining information on the occurrence of night pellets, field experiments were carried out by offering recognizable prey at a set time, and searching the ground under the daytime roost subsequently for the corresponding pellets. One or two white mice were offered on a small pole at the roost close to sunset. After a few owls learned to take this prey the experiment was done with dead white mice marked with a little metal ring. In the days following the whole winterroost was carefully checked for white pellets. If Long-eared Owls in the long winter night in general

Table 9. Differences in weight (g) of day and night pellets produced in captivity

	Day pellets		Night pellets		$\frac{\text{weight night pellets}}{\text{weight day pellets}} \times 100\%$
	weight	(n)	weight	(n)	
January	1.24	(69)	.84	(102)	67.7%
February	1.44	(104)	.88	(135)	61.1%
March	1.57	(90)	1.07	(81)	68.2%
April	1.55	(13)	.76	(5)	(49.0%)
May	1.84	(26)	1.51	(6)	(82.0%)
June	1.62	(28)	.68	(3)	(42.0%)
July	1.25	(14)	.90	(15)	72.0%
August	1.24	(56)	.99	(44)	79.8%
September	1.03	(34)	.79	(41)	76.7%
October	1.19	(65)	.93	(91)	78.2%
November	1.04	(83)	.79	(144)	76.0%
December	1.07	(80)	.75	(105)	70.1%
					mean 72.2% (April—June excluded)

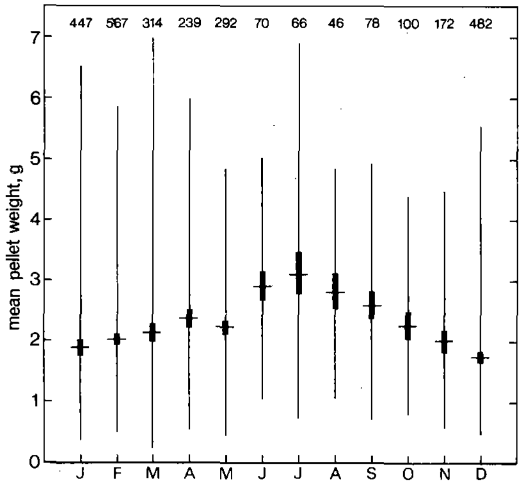


Fig. 22. Field data on pellet weight by month; shown are means ± 1 SD and the range; numerals indicate sample sizes (intact day pellets only).

Table 10. Results of the "white mouse" experiment (see text)

	Nov.	Dec.	Jan.	Feb.	March
Numbers of white mice eaten	18	22	28	21	29
Numbers of white mice remains recovered in day pellets	2	0	1	1	4
% recovered	11.1%	0%	3.6%	4.8%	13.8%

produce a pellet of their first meal(s) during that same night in their hunting area, white pellets on the winterroost (thus produced during daytime) should not occur too often. In that case there should be a tendency for more white pellets on the winterroost as the nights become shorter.

The results of the experiments with the white mice are given in Table 10. The numbers of white mice offered are relatively small and the data could be affected by (a) problems in finding all pellets (a part of the white mice remains could be produced in a day pellet on the roost, but was not found), (b) variation in hunting success, (c) weather conditions. Despite this restriction the overall conclusion of this experiment is that a considerable part of the remains of the first meal(s) of the Long-eared Owl in the winter could not be found under the dayroost. So it is very likely that these remains appear in the night pellets and are produced elsewhere in their hunting area. Moreover, the seasonal trend is confirmed: in the longest night (December) the occurrence of night pellets is more likely (and so the recovery frequency will be lower) than in March.

A direct proof for the existence of a night pellet was found in a telemetry experiment. On two occasions in the winter and one in the summer a small radio-transmitter (type SM1, manufactored by AVM Electronics) was inserted into the abdomen of a dead laboratory mouse. The transmitter (weight 1.5 g) was securely sewn on the backbone to prevent loss in the case the owl did not swallow the prey in one piece. The radio tagged mouse was offered to the owls and after ingestion it was possible to follow the owl during a part of the night and to estimate time and place of pellet production (see for telemetry equipment chapter 7).

A dead white mouse (16.1 g) with an implanted transmitter was taken on February 23, 1978 at 18.02 hr. At 18.08 hr the mouse was eaten completely, the transmitter signal was received very clearly. At 18.23 the owl flew away and the signal was not picked up again until 08.30 hr on the next day at a distance of ca. 1 km from the dayroost. After locating this site we found the transmitter in a pellet, together with the remains of the white mouse and a vole (Fig. 42). No roosting owls were found at that place and because the numbers of owls on the winterroost was unchanged we assumed that "our" owl had returned to the roost at the normal time, so the pellet must have been produced during that night.

On February 27, 1978, the experiment was repeated. The mouse was eaten at 18.14 and we could track the owl until 22.38 hr. After that time the signal was lost and was not picked up again. This owl also came back to his normal roost and because no transmitter was found, the location where the owl had perched the night before was examined. Unfortunately the perch was on a point overhanging a deep body of water, and the transmitter could not be recovered.

The third time the experiment was done on June 16, 1978. A previously "trained" male owl "caught" the mouse at 22.30 and flew with this prey to the breeding female. The time when the female ingested this prey could not be registered, but happened probably directly after the male brought it to the nest. The fluctuating signal of the transmitter (suggesting that the pellet was not yet produced) was received until 20.00 hr the next day, at that moment contact was lost probably due to pellet production and subsequently transmitter and pellet were found beneath the nest. In this case, with the short June night, they ended up in the day pellet.

From other telemetry experiments (see chapter 2) we collected data on roosting sites within the home range of the Long-eared Owls, where they sometimes stay during the night. Because it was likely that night pellets might be produced at these places, some of these sites were carefully searched during daylight. Because during regular controls by day roosting owls were never found there, pellets found at these places were regarded as night pellets (Table 11).

During the pilot study at the "Vosbergen" a few night pellets were also found. Unfortunately these pellets were not weighed, but information on the prey composition and the numbers of prey per pellet was available. Both the night pellets found in the "Zuidbroek" area as well as the "Vosbergen" night pellets are in general smaller than the day pellets of the same area and the same period. There is too little information to examine seasonal trends in the size of these night pellets. The mean weight for the night pellets (Zuidbroek sample) is 76% of the daytime pellet weight (December—March). This is very close to the relationship in captivity (72%).

A final source of field data concerns the time of pellet production at the dayroost. The evening before the observation day the ground beneath the roosting trees was carefully cleaned, and in some cases plastic sheets were spread to make pellets easier to find. During the "measuring day" the roost was visited once every 1—2 hours and all pellets were noted and collected.

The observations are presented in Fig. 21, and show that most pellets at the dayroost are produced after 12.00 hrs, with a clear peak just before sunset. Since the birds depart from the roost within a half hour of sunset, the sharp cutoff in pellet production apparent in the figure is perhaps an artefact. We suspect that some pel-

Table 11. Night pellets found in the Zuidbroek area in the winter of 1976—1977, compared with day pellets of that same area

	Night pellets			Day pellets		
	mean weight (g)	number of pellets	mean number of prey/pellet	mean weight (g)	number of pellets	mean number of prey/pellet
December/January	1.49 (± .62)	26	1.54	1.98 (± .75)	163	2.11
January	1.49 (± .62)	7	1.57	2.22 (± .85)	59	2.14
February/March	2.00 (± .33)	6	2.33	2.15 (± .86)	259	2.06

lets have in fact been deposited in the vicinity of the roost in the early evening, at sites not checked by us.

The overall pattern

Data given in Figs. 20, 21 and 22 suggest a relationship between pellet production (with respect to frequency and weight) and the length of the nocturnal period (the activity period of the Long-eared Owl). In the winter period with darkness lasting up to 16 hours, the frequency of pellet egestion is higher and pellet size is smaller than in the summer. In Fig. 23 these data are plotted against the length of the night (period of sunset to sunrise) and there is a significant correlation between mean pellet weight in captivity ($r = 0.712$, $p < 0.10$), mean pellet weight in the field ($r = -0.959$, $p < 0.01$), mean pellet frequency in captivity ($r = 0.911$, $p < 0.01$) and the length of that period. At the latitude of Groningen (53 °N) the locomotory activity is for nearly all months limited to the period just after sunset to just before sunrise, as can be seen in Fig. 24 for activity registrations under outdoor captivity conditions. The onset and the end of this activity period is the same as for free-living owls (chapter 7, and Glass 1969). This corroborates the statements of several authors that the Long-ear is one of the most strictly nocturnal owls (Bent 1938, Glutz & Bauer 1980). The seasonal change in the length of the activity period will induce differences in the time when the owls take their meals and so in the intervals between successive meals.

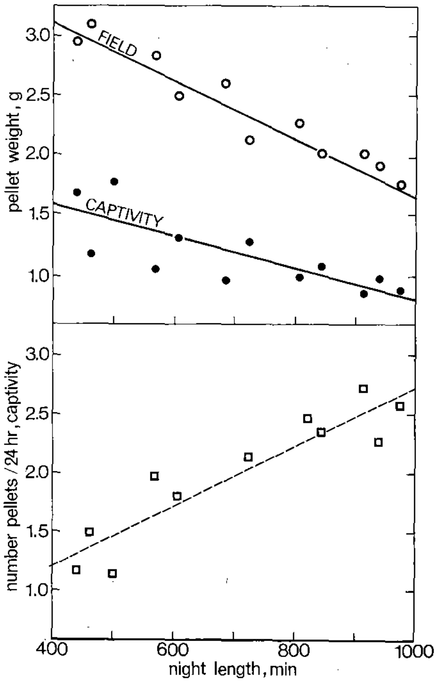


Fig. 23. Dependence of pellet weight (upper line field data, middle line in captivity) and pellet number (bottom panel, captivity) on night length (in minutes). Lines of regression respectively are $y = -.0023 x + 4.03$ ($r = -.96$), $y = -.0012 x + 2.03$ ($r = -.77$) and $y = -.0023 x + .329$ ($r = .91$).

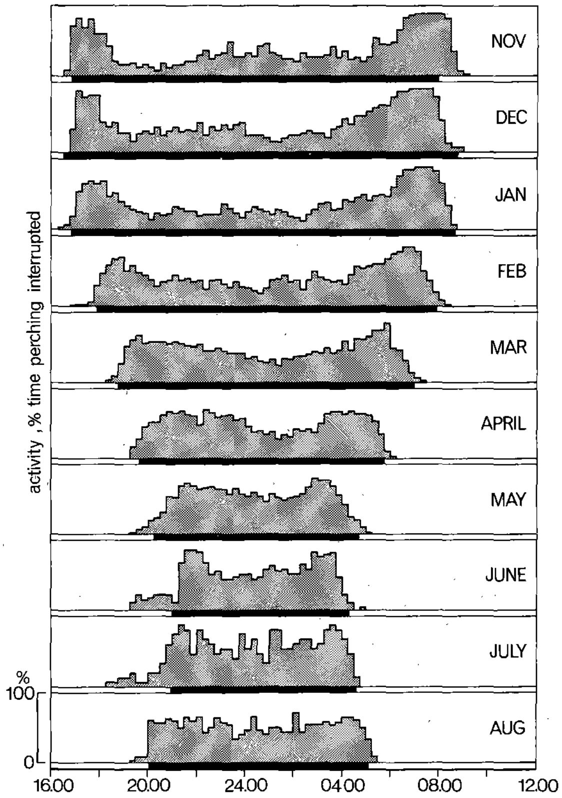


Fig. 24. Activity profiles for a captive Long-eared Owl kept in the aviary shown in Fig. 19; for each 15-minute period a microswitch at the perch recorded whether the bird was continuously perched (inactive) or had left the perch for a short flight (period then considered "active" regardless of the length of absence).

Experimental registrations of these meal-to-meal intervals under outdoor captivity conditions are given in Fig. 25 and monthly mean intervals show variation of 7.45 hr in January to 2.07 hr in May for situations of two meals a

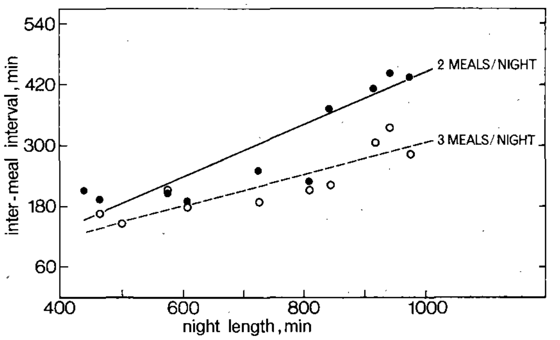


Fig. 25. Intervals between meals in relation to length of the night, captivity. Each point represents the mean for a month of observations.

night. It will be clear that a minimum amount of time will be necessary for digesting a prey and forming and casting the pellet. When the interval between two succeeding meals is too short the pellet of the first meal will not be cast before the second meal is taken. In that case one pellet will include remains of two (or even more) prey. Clearly in the summer, with shorter meal-to-meal intervals, the likelihood of pellets containing remains of several meals is greater than in the winter time.

Pellet formation in birds of prey and owls has been studied by several authors and has recently been reviewed by Duke *et al.* (1976). However, there is much variation in the results of these authors concerning meal-to-pellet intervals and pellet frequency. Most of this variation is due to the experimental conditions adopted. The study of Duke *et al.* (1976) shows an average meal-to-pellet interval (which was directly correlated with meal weight) of 10—13 hrs for the Great-horned Owl. However, the experimental conditions were such that the tested birds had to take their meal within a period of one hour during day-light. The data from Chitty (1938) show a much shorter meal-to-pellet interval for the Short-eared Owl (for mice fed during day-light) varying from 1.5—13 hrs with a mean of ca. 8.5 hrs. The data in the present study show a similar variation mainly depending on the season (length of the nocturnal period) and on whether the pellet is cast during the day or night. For the Long-eared Owl the total data give the following meal-to-pellet intervals: in summer, 16 hr (the very few night pellets are excluded from this calculation), and in winter, mean for night pellets 7 hr, for day pellets 13 hr. In this analysis the midpoint between two meals has been taken as the starting point for intervals where composite pellets are involved.

Very few authors give data on seasonal variations in pellet production. Marti's (1973) data on pellet production for the Long-eared Owl show some seasonal variations in number of pellets/day for birds kept in captivity outdoors, with lowest number of pellets produced in April—May (mean 1.0) and highest numbers in October—November (mean 1.7), thus showing the same trend in variation as the present study. Marti's study was carried out in Colorado (± 37 °N) and at this latitude there is less seasonal variation in photoperiod than in my area (53 °N). This could explain the smaller variation in the extreme values in Colorado (0.7) compared to Groningen (1.3).

Erkinaro (1973b) shows that caged specimens of the Tengmalm's Owl (*Aegolius funereus*) and the Short-eared Owl in Finland (65 °N) have a considerable seasonal variation in pellet size (the pellets being twice as large in spring and autumn as in summer and winter). In spring and autumn both species of owls maintain a long almost uninterrupted rest phase by day (Erkinaro 1973a) and in summer and winter their activity is spread evenly throughout the 24 hr period. The spring and autumn activity is comparable to the summer activity for the Long-eared Owl in my study, which causes shorter meal to meal intervals and thus larger pellets. Summer and winter activity is to some degree comparable to the winter activity (long active period) of the Long-

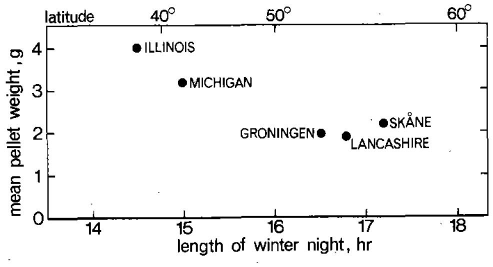


Fig. 26. Field data on pellet weight in the Long-eared Owl in relation to the length of the nocturnal period. Data from: Graber 1962 (Illinois), Armstrong 1958 (Michigan), South 1966 (Lancashire), this study (Groningen). Pellets from Skåne were kindly provided by I. N. Nilsson.

eared Owl in this study giving larger meal to meal intervals and thus smaller pellets.

The few field data on pellet weight for the Long-eared Owl during the winter are arranged according to the duration of the nocturnal period (or latitude) in Fig. 26. This again confirms the idea that the duration of the night period is an important parameter in determining the size of the pellets.

4.3. DETERMINATION OF THE METABOLIZABLE ENERGY COEFFICIENT AND THE RELATIONSHIP BETWEEN PELLET WEIGHT AND THE WEIGHT OF THE INGESTED PREY

Methods

The determination of the metabolizable energy coefficient (MEC) was carried out with Long-eared Owls kept in captivity for at least several months, but most animals were in captivity for more than one year. They were allowed to acclimate to the experimental conditions and diets for three to five days before the actual measurements were carried out. Each experimental trial lasted at least three days but in general five days.

The experiments were done in temperature controlled (± 1.5 °C) walk-in cabinets, in which the relative humidity varied between 70% and 80%. The photoperiod varied with season and simulated daylength. For practical reasons the time of "light out" was at 17.00 hr, so in general a few hours earlier than outdoors. The experiments for the determination of the MEC at low temperatures (−6.5 °C and −15 °C) were done in a freezer (temperature variation ± 1 °C).

In most cases the measurements were simultaneously carried out with two birds in the same cabinet. The owls were kept in individual small cages of 40 × 40 × 40 cm. In the cage was a perch. The floor was made from stainless steel wire and could be removed easily. Under this floor were two stainless steel plates, to collect the droppings and the pellets. Food was given always at the same time of the day, between 16.00 and 17.00 hr. At the same time the plates with the pellets and the droppings were collected and, if necessary, spilled food and droppings were scraped from floor and sides. Pellets and wasted food were carefully separated from the droppings and all these components were oven dried for 24 hrs, as recommended by Shannon and Brown (1969). In the morning excess food was taken away and weighed, and this figure subsequently corrected for desiccation. The owls were weighed daily between 16.00 and 17.00 hr. In this way accurate records of food intake, owl weight and weight of the produced excreta were collected for 24 hr periods.

Dried samples of the food, pellets and excreta were ground in an ultra-centrifugal mill (Rensch) and the caloric values of the samples were determined using a ballistic bomb calorimeter (Gallenkamp). In general a triplo determination of each sample was carried out. The bomb calorimeter was regularly calibrated with benzoïc acid according to specification of the manufacturer.

The weight of the food, waste material and the owls was determined on a Mettler balance accurate to .01 g. The samples for burning in the bomb calorimeter were weighed on a Mettler H20 analytic balance accurate to .0001 g.

In some cases the nitrogen, fat and ash content was determined for dried samples of the food and/or the waste. For the nitrogen determinations the Kjeldahl procedure was used. Fat extraction was done with petroleum-ether. Ash percentages were calculated by weighing the ash-residues after burning in the bomb calorimeter.

A survey of experimental conditions with respect to season and temperatures is given in Table 12. In addition to the temperature controlled experiments, some experiments were carried out under outdoor conditions with fluctuating temperatures. However, the technical procedure was the same as in the other experiments.

In all these experiments the standard food was the freshly frozen laboratory mouse (race CBA). All mice offered were in the weight class between 14 and 18 gram. Before presentation the food was thawed. In the experiments below zero, thawed food was offered at least three times during the nocturnal periods.

MEC of different food types was studied in winter and in spring at a temperature of 9.5 °C. Besides the laboratory mouse ("*Mus musculus*") the following species were studied: Wood Mouse (*Apodemus sylvaticus*), Harvest Mouse (*Micromys minutus*), Common Vole (*Microtus arvalis*), Shrews (*Soricidae*) and House Sparrow (*Passer domesticus*). All mice were trapped in the field, mostly in autumn.

Data obtained in these experiments were also used to establish the relationship between the weight of the ingested prey and the weight of the pellets. More information was collected in experiments where only the weight of the food eaten and the weight of the pellets was determined.

Results

The determination of the caloric value and the water content of the six types of food used for the experiments are given in Table 13. Data on the food intake necessary for maintaining constant body weight in the different experimental situations will be given in chapter 6.

Metabolizable energy coefficient (MEC) was calculated as:

Table 12. Metabolizable Energy Coefficient (MEC) for laboratory mouse (mean and range)

Temperature	Winter	Spring	Summer	Late Autumn
−15 °C	.740 (.721-.758)	—	—	—
− 6.5 °C	.750 (.749-.752)	—	—	—
1.5 °C	.741 (.740-.742)	.777 (.748-.809)	.799 (1 exp.)	.744 (.738-.750)
9.5 °C	.752 (.748-.756)	.774 (.768-.780)	—	.750 (.745-.754)
16.5 °C	—	.771 (.769-.772)	.782 (mean of 4 exp.)	.756 (.753-.759)
22 °C	—	—	.750 (1 exp.)	—

Table 13. Water, fat, ash, nitrogen content and caloric value of the various diets (mean and range)

	Number of samples	% water	% fat	kJ/g fresh weight	kJ/g dry weight	% ash	% nitrogen
Laboratory mouse (*"Mus musculus"*) weight: 15—30 g	18	66.9 (63.5—69.4)	9.6 (6.1—14.3)	8.29 (7.03— 8.83)	25.07 (23.99—27.33)	3.9 (3.2—4.8)	2.89 (2.76—3.04)
Common Vole (*Microtus arvalis*) weight: 15.0—21.6 g	5	67.0 (62.8—69.3)	—	7.74	23.48	4.1 (3.9—4.4)	—
Wood Mouse (*Apodemus sylvaticus*) weight: 17—29 g	6	63.1 (52.1—71.3)	2.8 (0.2—6.3)	8.00 (6.28—10.30)	21.68 (20.80—22.69)	3.6 (3.4—3.9)	—
Harvest Mouse (*Micromys minutus*) weight: 5.0—6.4 g	7	67.0 (62.5—70.8)	—	7.58 (6.95— 8.16)	23.78	3.0	—
Shrews (*Soricidae*) weight: 6.2—9.7 g	6	68.8 (66.4—73.0)	—	7.12 (6.15— 7.58)	22.73 (22.48—23.61)	4.1 (3.9—4.3)	—
House Sparrow (*Passer domesticus*) weight: 26—33 g	3	65.6 (64.3—66.3)	—	7.79	21.81	5.6	—

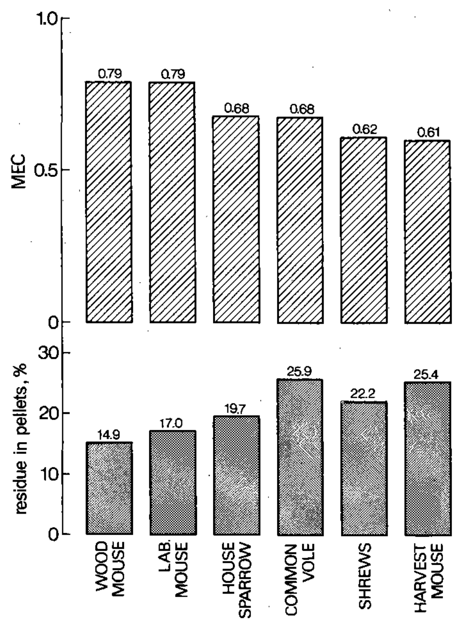


Fig. 27. Metabolizable Energy Coefficients (MEC) i.e. caloric retention of various prey types according to laboratory trials (above) and weight percentages rejected ("residue", bottom) in the pellets.

(kJ. food intake - kJ. rejecta)/kJ. food intake. For food intake and rejecta, values of the whole test period were used (in general 5 days).

As can be seen in Fig. 27 MEC varies from .790 for the Wood Mouse to .611 for the Harvest Mouse. Because the Common Vole is the most important prey item for the Long-eared Owls tests on this prey were carried out 4 times. The average MEC was .682 (single values: .655; .674; .683; .715).

From the same experiments together with additional measurements data on the relationship between weight of the ingested prey and the weight of the pellets were obtained. In agreement with the data on the MEC, Wood Mouse and laboratory mouse show the lowest fraction recovered in the pellets and for Harvest Mouse and Common Vole this fraction is highest (Fig. 27). Shrews and birds are in this aspect intermediate. The outdoor experiments in the period May—November did not differ significantly from experiments in the same period under constant temperature conditions (15 °C) with respect to the MEC. For this reason these data are taken together. Fig. 28 shows the seasonal fluctuation of the MEC for laboratory mouse in this period. During the period of the moult with rapid feather growth (chapter 10) this efficiency is highest (.790-.794), and before and after the moult this efficiency is lower (.750 and .758). Especially in May and No-

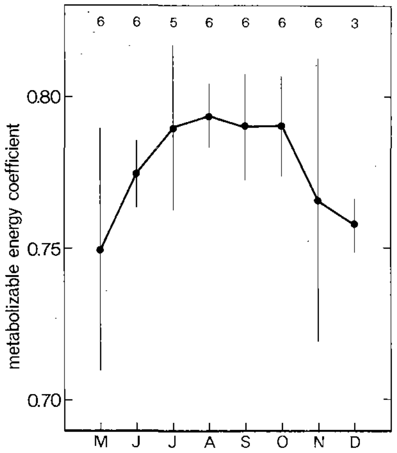


Fig. 28. Variation in the MEC for the laboratory mouse (number of 5-day trials indicated at top) in the course of the year (means ± 1 SD).

vember there is a considerable individual variation in the MEC which might be due to differences in chronology of the moult.

Effects of ambient temperature on the MEC are indicated in Table 12. As can be seen, differences due to temperature are small and do not reflect a consistent trend. Seasonal fluctuations seem to be more important.

Discussion

The correlation between food consumption and pellet weight for various kinds of prey makes this relationship useable for the estimation of consumption under field conditions. In general food simulations made on the basis of this relationship will be more reliable than using data on the numbers of determinable skulls or other bony elements in the pellets.

Goszczynski's (1976) experiments on food digestion in the Barn Owl (*Tyto alba*) indicated a relation of the weight of the pellets to the weight of the food eaten of 23% for small rodents and *Soricidae*. For small birds this value was about 30%. These values are somewhat higher than for the present study of the Long-eared Owl, which could be due to the lesser degree of digestion of bones in the Barn Owl (Raczynski & Ruprecht 1974). Duke *et al.* (1975, 1976) who studied food consumption and pellet formation in several raptors found somewhat lower values for the proportion of a meal appearing in the pellets. For the Snowy Owl (*Nyctea scandiaca*) and the Great-horned Owl (*Bubo virginianus*) these values were about 12%, for the Barred Owl (*Strix varia*) 13%, for the Short-eared Owl (*Asio flammeus*) and the Screech Owl (*Otus asio*) 16% and for the Saw-whet Owl (*Aegolius acadicus*) 17.5%. In all these experiments laboratory mouse was the standard diet. The fraction of the closely related Short-eared Owl is nearly the same as for the Long-eared Owl in the present study fed on laboratory mouse (16% versus 17%). Duke *et al.* (1976) suggested that the difference in the proportion of a meal appearing in the pellets between the larger owls and the smaller owls is probably due to the fact that larger owls crush skulls and bones more than smaller owls do and hence expose the bony material to a greater influence of the gastric juice.

Several authors have commented on the difference in digestion between hawks and owls (Errington 1930, Craighead & Craighead 1956, Clark 1972, Duke *et al.* 1975, 1976). Hawks digest bones more thoroughly due to a greater acidity of the gastric juice (Duke *et al.* 1975). Proportions of the meals appearing in the pellets vary between 3.3% for the Kestrel (*Falco sparverius*) and 6.9% for the Rough-legged Buzzard (*Buteo lagopus*) (Duke *et al.* 1976).

The increasing emphasis of research on bioenergetics of birds especially for passerines has led to the recent compilation by Kendeigh, Dolnik and Gavrilov (1977). By contrast there are only few studies on the MEC for Falconiformes and Strigiformes. The first published data are from Graber (1962) for the Longeared Owl fed on the laboratory mouse. His data show a MEC of 0.87 on the average. However, as was pointed out earlier by Kirkwood (1979) his data for the caloric content of the food (laboratory mouse) is aberrant (16.3 kJ/gram fresh weight) when compared with other data in the literature (8.9 kJ/gram (Brisbin 1970), 8.6 (Bird & Ho 1976), 9.9 (Duke *et al.* 1973), 9.4 (Myrcha & Walkowa 1968) and my own determinations (8.0 kJ/gram fresh weight)). Substituting a value of 8.4 kJ/gram fresh weight in Graber's result yields a MEC of 0.75 for winter measurements at 18.5 °C. This value is the same as the one presented in this study for laboratory mouse (for winter at 9.5 °C). Ceska (1980) obtained .76 for this species, .75 for the Barn Owl and .80 for the Tawny Owl on a laboratory mouse diet. For the Snowy Owl at temperatures between −20 °C and 5 °C Gessaman (1972) gives a MEC of 0.70. For animals kept outdoors (average temperature −21 °C) in Alaska these values are higher: 0.74—0.80. Duke *et al.* (1973) presented values of 0.69 and 0.65 for a Great-horned Owl on a diet of the laboratory mouse and one-day-old turkey poults. Unpublished data of my own give values of 0.77 for the Barn Owl, 0.78 for the Tawny Owl (*Strix aluco*) and 0.74 for the Little Owl (*Athena noctua*). All animals were fed on the laboratory mouse. For the Kestrel (*Falco tinnunculus*) on a laboratory mouse diet the MEC was 0.80, and on a diet of Common Voles (*Microtus arvalis*) it was 0.66 to 0.72.

Published data from West (1968) for the Willow Ptarmigan (*Lagopus lagopus*) and Owen (1970) for the Blue-winged Teal (*Anas discors*) shows that these animals have a higher MEC during the moult period reflecting the trend shown in this study.

Literature data confirms that assimilation efficiency is not only dependent on the species studied and the kind of the food offered but also will be influenced by the stage of the annual cycle (Owen 1970, Moss 1973, West 1968, El-Wailly 1966), temperature (El-Wailly 1966, Brooks 1968, Cain 1973), photoperiodism (West 1960), amount of food eaten (Moss & Parkinson 1972), amount of water available (Moldenhauer & Talor 1973). However, these studies fail to reveal consistent patterns so far. Some authors also found changes in digestion related to the age of growing birds; this point will be taken up with my own data on digestion in young owls in chapter 8.

4.4. GEI AND ME OUTSIDE THE BREEDING PERIOD

I will here assemble the data needed to estimate total energy intake (GEI) by combining pellet production and pellet composition. Of course I cannot achieve the precision of obtaining year to year comparisons, but must be content with a generalized picture taking all years together. The main objective must be to delimit the fluctuation in intake through the season.

The calculation starts with the mean weight of the pellets produced during the daytime in the field (Fig. 22), corrected to "absolute dry weight" by subtracting 10% (= mean water content of stove-dried pellets) from the "air-dry" weights recorded. These weight figures are next multiplied by the mean number of pellets found to be produced during the daytime (data from captive owls, Fig. 20) thus giving the total weight of day pellet material. The next task is to find out how much must be added to this for the night. The data on this point are limited, and we must assume that the Zuidbroek weights are representative, allowing the generalization that a night pellet is 76% of the weight of the day pellet. Since from captive data we are informed on the frequency of night pellet formation (Fig. 20) we can now arrive at monthly estimates and indeed now have the total pellet residue in hand. There does seem to be an anomaly in the pellet production data for January (day pellets, see Table 14) which, however, remains unexplained. To avoid bias we have also inserted the value extrapolated from December and January as an alternative estimate for day pellet production in January (this figure has of course a bearing for the night pellet weights as well since they are derived from the day pellet weight total).

Our next step in the reconstruction is to translate the figures on "total dry weight pellets" into residues of recognizable prey categories, since we do know how to work back from residue weights to dry weight of biomass eaten. It was found expedient to divide all prey into four categories:

"voles" = *Microtus arvalis*, *M. agrestis* and *Clethrionomys glareolus*
"mice" = *Apodemus sylvaticus* and *Mus musculus*
"birds"
"others" = mainly shrews and *Micromys minutus*

From the generalized diet statistics given in Table 14 (occurrence of prey by month in terms of numbers) as a first step the percent of each prey category in the prey *biomass* eaten has been calculated. For the dominant prey (voles) the mean prey dry weight for each month was

Table 14. Calculation of the GEI and ME (per bird per day) outside the breeding period by the "pellet-method"

	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Jan.*	Febr.	March
Prey composition (% of total number)									
Voles 1)	83	86	79	68	66	77		80	75
Mice 2)	4	4	11	11	17	9		8	11
Birds	9	4	2	13	8	9		6	8
Others 3)	4	6	8	8	9	5		6	6
Prey composition (% of dry weight)									
Voles	78	80	73	52	53	66		72	63
Mice	4	5	14	13	20	10		9	14
Birds	15	9	5	27	18	19		13	18
Others	3	6	8	8	9	5		6	6
Prey composition (% of pellet weight)									
Voles	83	85	79	59	62	73		76	69
Mice	2	3	9	9	13	6		6	9
Birds	12	7	4	24	16	16		11	16
Others	3	5	8	8	9	5		6	6
Total weight of day and night pellets (g dry)	4.23	4.45	4.14	4.15	3.43	3.18	3.56*	3.65	4.26
Residue in pellets (g dry)									
Voles	3.51	3.78	3.28	2.45	2.13	2.32	2.60	2.81	2.94
Mice	.08	.13	.37	.37	.45	.19	.21	.22	.38
Birds	.51	.31	.16	1.00	.55	.51	.57	.40	.68
Others	.13	.22	.33	.33	.31	.16	.18	.22	.26
Biomass eaten (g dry)									
Voles	13.50	14.53	12.61	9.42	8.19	8.92	10.00	10.81	11.31
Mice	.53	.87	2.47	2.47	3.00	1.27	1.40	1.47	2.53
Birds	2.55	1.55	.80	5.00	2.75	2.55	2.85	2.00	3.40
Others	.57	.96	1.43	1.43	1.35	.70	.78	.96	1.13
Total	17.15	17.91	17.31	18.32	15.29	13.44	15.03	15.24	18.37
Gross Energy Intake (kJ)									
Voles	311.18	340.15	287.63	217.70	192.79	192.58	215.90	233.39	244.52
Mice	11.47	18.83	53.46	53.46	64.93	27.49	30.30	31.81	54.75
Birds	55.64	33.82	17.45	109.09	60.00	55.64	62.18	43.64	74.18
Others	13.26	22.34	33.28	33.28	31.41	16.29	18.15	22.34	26.29
Total	391.55	415.14	391.82	413.53	349.13	292.00	326.53	331.18	399.74
Metabolized Energy (kJ)									
Voles	213.16	231.98	196.16	143.90	126.08	123.06	137.96	155.90	163.34
Mice	9.11	14.88	42.23	40.95	49.22	20.37	22.45	24.62	42.38
Birds	38.17	23.10	11.92	72.22	39.30	35.67	39.86	29.20	49.63
Others	8.17	13.69	20.40	19.77	18.47	9.37	10.44	13.43	15.80
Total	268.61	283.65	270.71	276.77	233.07	188.47	210.71	223.15	271.15

1) *Microtus arvalis*, *Microtus agrestis*, *Clethrionomys glareolus*.

2) *Apodemus sylvaticus*, *Mus musculus*.

3) mainly shrews and *Micromys minutus*.
* = extrapolated for pellet frequency (see text).

known, and for the other prey an average value was taken from my own observations supplemented by Blem (1975) for the House Sparrow and Gorecki (1967) for small rodents. Next, the contribution of each category to the residue in the pellets has been derived from this, by cor-

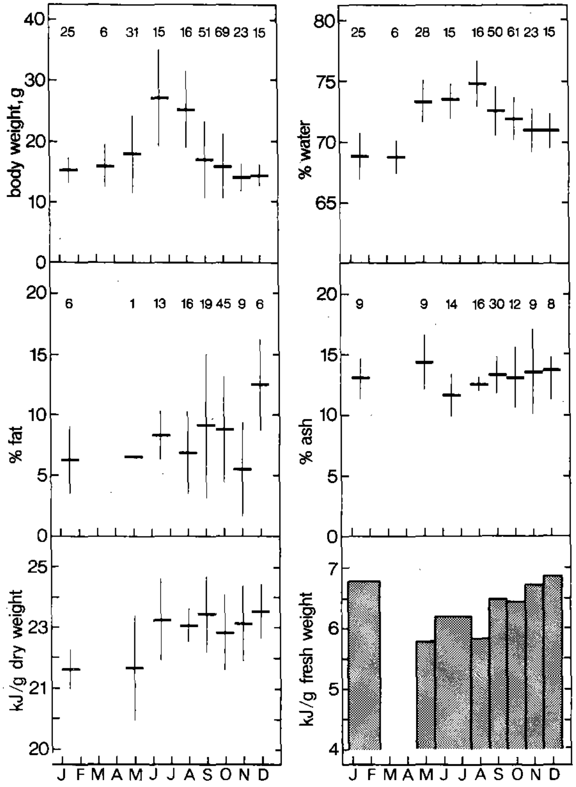


Fig. 29. Seasonal variation in body weight, constituents and energy content of the Common Vole, *Microtus arvalis*. Sample sizes are indicated at top (the lower panels have the same sample sizes as the ash content) and means are shown ± 1 SD as appropriate.

recting the biomass percent figures for the residue rates given in Fig. 27. For each month we can now reconstruct what proportion of the total pellet remains was likely to have originated from a given prey category, and hence the actual dry weight represented.

As shown in the calculation in Table 14, we are now in a position to reconstruct the daily ration of the free-living owl, in terms of dry weight prey biomass eaten. These biomass figures can be converted to energy values by using the monthly determination for voles (Fig. 29) and the average determinations for other prey, given in Table 13. We now have the gross energy intake (GEI) for the months August through March, during which this procedure can be applied (as was pointed out earlier, it is not possible to recover pellets quantitatively in the breeding period, hence the more direct weighing approach with the nest platforms was used).

The energy actually available to the owl, i.e. the metabolized energy or $\mathrm{ME}_{\mathrm{field}}$, can be derived from the GEI data by applying the conversion rates measured in our laboratory trials. Seasonal changes in the conversion rate were measured only for the laboratory mouse, so we have assumed that the slight seasonal trend towards peak digestibility in the autumn (Fig. 28) obtains for the other prey too, and have extrapolated the measured MEC for the other prey accordingly (see Table 14). When multiplied with the GEI, we obtain the $\mathrm{ME}_{\mathrm{field}}$ values, and these have been presented in Fig. 30. The values for August through November on the one hand and March on the other are surprisingly uniform (mean 275 kJ) while the winter period (December through February) is characterized by a $\mathrm{ME}_{\mathrm{field}}$ level about 19% lower than this.

The reliability of this indirect method of ascertaining the daily ration of free-living owls can be checked when we have quantified the various avenues of energy expenditure, the task of the coming chapters.

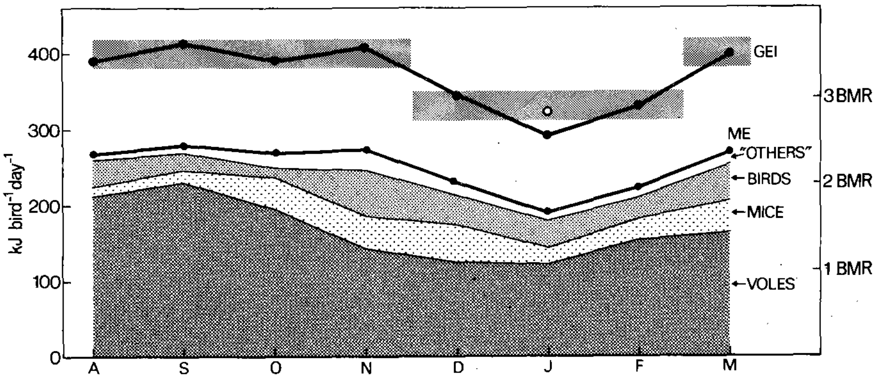


Fig. 30. Reconstruction of the Gross Energy Intake (GEI) and Metabolized Energy (ME) of the free-living Long-eared Owl on the basis of the pellet method throughout the non-reproductive period. The main components of the diet are shown (see text and table 14); the right-hand scale shows units of Basal Metabolic Rate (BMR) as measured in this species. The open circle for GEI in January is an extrapolation from data in December and February (see text).

5. SEASONAL VARIATION IN METABOLIC RATE

5.1 INTRODUCTION

This chapter will take us a first step towards quantifying the energy *expenditure* of the animal, by considering the energy loss of the quiescent post-absorptive individual. By measuring the gaseous exchange (oxygen uptake and carbon dioxide output) it is possible to calculate the energy expenditure of the individual with considerable accuracy, and this technique has become widely known as "indirect calorimetry". One of the advantages of this procedure is that it makes it possible to determine the basal metabolic rate, the basic building block of the energy budget and a parameter of supreme comparative significance. Basal metabolic rate (BMR) is defined as the rate of energy utilization of fasting, inactive birds in the zone of thermoneutrality (Kendeigh 1972) and in the inactive phase of their diurnal cycle (Aschoff & Pohl 1970). BMR thus provides the lowest and most consistent measure of metabolism. What makes it so interesting is its close relationship to body weight. Our first problem will be to examine how BMR varies with body weight within the species (the older literature on this topic is covered by Brody 1945, see also Kleiber 1961, Hayward 1965a, Heusner & Jameson 1981). Secondly BMR varies with body weight in a characteristic manner when interspecific comparisons are drawn, and as we shall see the owls as a group are consistent in this regard, but differ as a group quite distinctly from other non-passerine birds.

Below a certain temperature homeotherms must use extra energy in order to maintain their body temperature. This point is called the lower critical temperature (LCT), and can be recognized in indirect calorimetry trials because this is the point at which metabolic rate increases for the first time as ambient temperature is lowered. The level to which metabolic rate climbs is an expression of the cost of temperature regulation (TR), and these are clearly measurements of great ecological relevance. Data will be given to define the lower critical temperature at different seasons of the year, and below this point metabolism will be composed of BMR plus the temperature regulation component, or taken together, quite simply standard metabolic rate (SMR). The slope with which SMR increases with decreasing ambient temperature is another key parameter, and is a measure of the quality of the insulation.

In practice I measured BMR and SMR for the same bird on the same day by exposing it to different ambient temperatures. By repeating these measurements monthly for a group of birds information on seasonal fluctuations of SMR was obtained. Although temperature as basically the most important factor affecting metabolic rate is given the main emphasis, effects of time of day, wind and radiation were also investigated.

5.2. METHODS

The experimental birds were kept in a large outdoor aviary and subject to natural temperatures and photoperiods (see chapter 1). The general procedure for measuring BMR and SMR was that an owl was removed from this outside aviary between 16.00 and 17.00 hr. The bird was weighed and placed in a plexiglass respiration chamber of 18 l. The chamber was provided with a perch and in the bottom and the top wall was a hole (diameter 0.5 cm) respectively for air inflow and air outflow. The respiration chamber was then placed in a temperature controlled cabinet (a modified freezer with a window) situated in a larger walk-in cabinet maintained at room temperature. Temperature in the respiration chamber and in the cabinet was measured by thermocouples. During the oxygen measurements nobody was inside this large cabinet as in some cases an elevation of oxygen uptake was registered when somebody went inside even without making "noise". During the night prior to the day of measurements the temperature was adjusted to the mean outside temperature for that particular month. Lights off and on was synchronous with natural sunset and sunrise. Air flow through the respiration chamber was controlled at the same speed as during the actual measurements (roughly 2 $\mathrm{l.min^{-1}}$). No food was given to the owl. The next day the bird was weighed again. In some cases body temperature was measured with an implanted copper-constantan thermocouple. Implantation was carried out by making a small incision just below the lowest rib. The thermocouple, which was coated with a thin plastic film, was then inserted and pushed downwards for about two cm under the skin. It was fixed in that position by a suture on the lowest rib. The wire was then brought out to the tail where it was fixed with a suture on the base and the end of the tail with tape. The whole procedure took only a few minutes and was done under a local anesthetic. The output of all thermocouples was recorded (Kipp micrograph, model BD5). For the detection of activity a radar system was used, mounted outside the cabinet at a distance of about 75 cm from the owl's position. This system was connected with a recorder. Details are given by Westerterp (1977). Moreover the owl could be kept under observation in most cases by a TV-camera connected to a monitor. During daytime (the condition under which most runs were made) illumination was by means of fluorescent lighting outside the temperature cabinet and a spotlight directed on the owl. In normal test runs the first step was to increase the temperature to about 25—30 °C, which was in all cases within the zone of thermoneutrality. The bird was maintained for at least one hour at that temperature before starting measurements. If activity registrations and direct TV-observations indicated that the bird was at rest and the metabolic rate was at a constant level for at least 15 minutes the temperature was lowered in steps of 5—10 °C. Again one hour was given to the bird to adjust at the new temperature and the same procedure was followed for the next step. For successive tests temperature was always lowered. In general the range from 30 to −20 °C was carried out in the course of one test day.

Oxygen consumption (continuously) and carbon dioxide production (occasionally) was measured in an open flow system. The rate of the air flow through the respiration box was ± 2 $1.min^{-1}$ and was measured with a calibrated oil gasmeter. For oxygen concentration a paramagnetic analyser (Taylor Servomex type OA 184) and for the carbon dioxide concentration an infrared analyser (Grubb Parsons, model SB2) was used. The output voltages of both analysers were recorded continuously by means of a multipoint recorder (Philips, PP 3500). The whole system was designed and described by Westerterp (1977). Both analysers were calibrated regularly and adjusted daily before each test run in which the barometric pressure was taken into account, so recalculation to standard pressure was unnecessary. Both analysers were always used at the same temperature (20 °C; fluctuations less than 1 °C). So all data were recalculated for STP by using one standard correction for temperature. At the end of the test period the bird was weighed again. When metabolic calculations on a mass specific basis were made this final weight was used.

In addition to this general program oxygen consumption was measured over longer periods of time, at least 24 hrs, in order to obtain data on daily variation in SMR. During these measurements temperature was kept constant. Lights on and off corresponded with sunset and sunrise.

Effects of wind speed on SMR were determined in a small windtunnel. The windtunnel was placed in the temperature cabinet, so measurements could be done at different ambient temperatures. Three different wind speeds were created by using different wheel-drives. In order to test the wind profile on the surface of the feathers a stuffed owl was placed in the windtunnel. Wind speed at various places was then measured with the aid of Pitot-tubes. Mean values of the three different settings are: 0.9, 1.2 and 1.8 $msec^{-1}$.

Effects of artificial radiation on SMR was tested in the same way as Lustick (1969). A somewhat modified respiration chamber was used. All the walls were painted black in order to prevent refections. On the cover was a layer of water of one cm, which absorbs all radiation above 1400 nm. According to Gates (1966) this simulates the atmospheric vapour layer at sea level. Special lamps of 60 and 100 Watt (Philips E 27, colour temperature 3150—3200°K) were used. By varying the heights of the lamps the intensity of radiation could be changed. Radiation at the level of the owls was measured with a radiometer (Lambda). Mean radiation, at the level of the owl's head, was respectively 8, 28 and 61 $Jsec^{-1}m^{-2}$ in the three different test runs. During the test day only one radiation intensity at three different temperatures (1, 10 and 25 °C) was used. Oxygen consumption was measured in the same way as in the normal runs.

5.3 RESULTS

Basal metabolic rate

Basal metabolic rate, expressed on a per bird basis, for females is in all months higher than for males, except for January—February (Table 15; Figure 31). The mean difference in BMR be-

Table 15. Long-eared Owl; seasonal variation in Basal Metabolic Rate. Mean values ± standard deviation are given. Body weight is determined immediately after measurements

	Number of tested birds	Oxygen consumption (ccO_2 $bird^{-1}$ min^{-1})	Body weight (g)
Males			
January—February	6	4.31 ± .37	229 ± 14
March—April	5	3.97 ± .28	247 ± 7
May—June	5	3.73 ± .23	238 ± 20
July—August	5	3.61 ± .36	228 ± 9
September—October	6	3.63 ± .34	230 ± 15
November—December	4	3.70 ± .15	227 ± 15
Females			
January—February	8	4.13 ± .27	256 ± 12
March—April	11	4.45 ± .63	311 ± 41
May—June	16	4.42 ± .56	305 ± 39
July—August	14	4.04 ± .43	253 ± 14
September—October	12	4.16 ± .61	258 ± 19
November—December	10	4.07 ± .34	252 ± 19

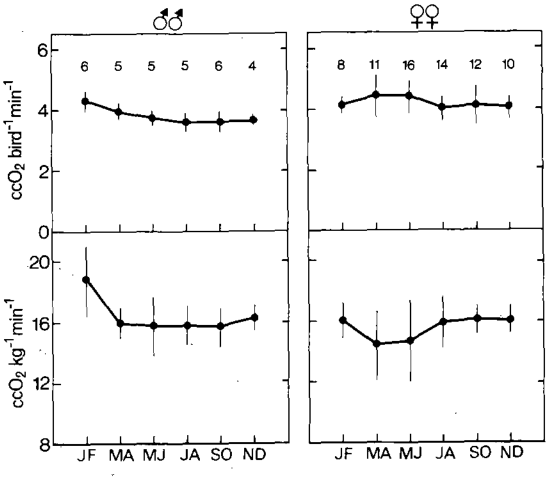


Fig. 31. Seasonal variation in Basal Metabolic Rate, expressed per bird (above) and on a weight specific basis (below) for each sex (number of individuals tested shown at top). Means and ± 1 SD are shown for bimonthly periods.

tween the sexes is about 10%. However, when BMR is expressed in a mass dependent way mean BMR for males is somewhat higher (5%). These differences between males and females are only significant in May—June and July—August (calculated for bird^{-1}) and in January—February (calculated for kg $^{-1}$) ($p < .05$, t-test). Seasonal variation in BMR for males is small in most months; only the January—February values deviate from this pattern only when expressed on weight specific basis. These months differ significantly by 16% from the preceding 2-month period.

For females BMR is 8% higher in the reproduction period (May to July). This difference is however, not significant. Calculated on a mass specific basis (kg^{-1}) BMR in these months is actually 10% lower (difference significant $p < .05$) than in the other months, suggesting a change in body composition. As can be seen in Table 15 mean female body weight shows an important increase in March—July, a point we will take up in detail later.

Combined measurements of oxygen consumption and the carbon-dioxide production indicate that the RQ-value was about 0.72 (± .03). Data were, however, insufficient to test for any seasonal fluctuations in RQ. Because all measurements were carried out under identical conditions (birds post-absorptive for at least 20 hrs) this RQ-value and the corresponding caloric equivalent for 1 liter oxygen of 19.69 kJ (Selkurt 1966) was used for calculating heat production from the oxygen measurements.

Temperature regulation and body temperature

As an example of the SMR measurements the results for a winter period (January—February) and for a summer period (July—August) are given in Fig. 32.

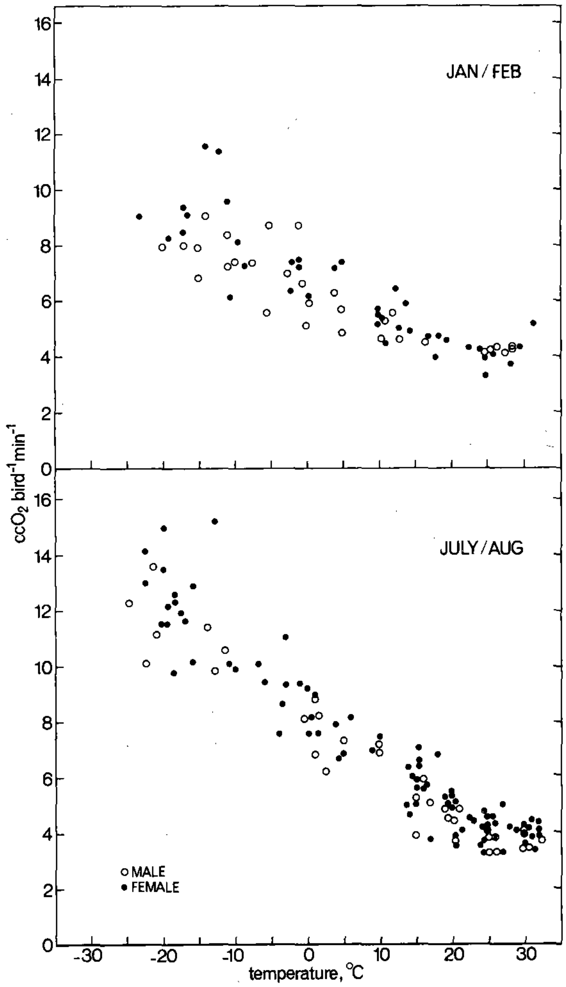


Fig. 32. Oxygen consumption (cc O_2 at STP per bird per minute) in relation to ambient temperature in winter (above, pooled data for 14 individuals) and summer (below, pooled data for 19 individuals). For analysis see Fig. 33.

A zone of thermoneutrality is in winter more clearly developed than in summer. Determination of the lower critical temperature is a somewhat arbitrary procedure since the underlying model is not strictly adhered to. According to the Newtonian model of cooling (Scholander *et al.* 1950a, b, c) metabolic rate below the lower critical temperature (LCT) should increase in linear fashion, and if this linear dependence on ambient temperature is extrapolated to zero metabolism one should obtain the body temperature of the animal. In most of the owl data, however (Table 16) this extrapolated temperature was far in excess of the real mean body temperature (compare T_{b1} and T_{b2} and Table 16). This contradiction has frequently been reported by others working with the larger non-passerines (Calder & Schmidt-Nielsen 1967, Calder & King 1974). Under these conditions two methods of determining LCT are open. In method one, the LCT is determined roughly by visual inspection and the metabolic data for all temperatures below this used to calculate a linear regression (i.e., the dependence of metabo-

Table 16. Values for Standard Metabolic Rate, SMR (mean ± SD)

	n	BW	LCT_1	LCT_2	TC_1	TC_2	T_{b1}	T_{b2}
Males								
January—February	6	231	16.9 ± 4.1	11.4 ± 2.7	.122 ± .038	.153 ± .014	51.9	39.2
March—April	7	247	17.7 ± 2.1	16.4 ± 1.4	.161 ± .034	.169 ± .016	46.0	39.2
May—June	7	235	16.7 ± 3.5	16.7 ± 3.1	.162 ± .037	.164 ± .017	40.0	39.2
July-August	6	230	22.6 ± 2.7	22.2 ± 2.0	.162 ± .024	.202 ± .022	46.3	39.9
September—October	6	231	21.4 ± 2.4	20.9 ± 2.2	.163 ± .062	.190 ± .027	47.6	39.9
November—December	5	227	15.5 ± 2.2	14.7 ± 2.2	.140 ± .042	.154 ± .015	47.3	39.2
Females								
January—February	9	256	17.9 ± 2.8	14.9 ± 3.0	.176 ± .066	.173 ± .031	50.2	39.9
March—April	13	311	18.9 ± 3.1	17.9 ± 2.5	.154 ± .042	.204 ± .027	49.9	39.9
May—June	18	296	19.7 ± 4.4	18.7 ± 3.0	.164 ± .034	.209 ± .030	49.9	39.9
July—August	15	254	21.7 ± 2.3	22.4 ± 2.0	.195 ± .055	.217 ± .022	45.7	40.4
September—October	12	255	20.2 ± 3.7	19.6 ± 3.0	.186 ± .067	.203 ± .025	41.4	40.4
November—December	11	252	15.8 ± 4.6	17.1 ± 3.9	.202 ± .065	.179 ± .029	39.3	39.9

n = number of tested birds
BW = mean body weight, g
LCT_1 = Lower Critical Temperature, calculated by method 1 (see text), °C
LCT_2 = Lower Critical Temperature, calculated by method 2 (see text), °C
TC_1 = Temperature Coefficient, calculated by method 1, ccO_2 $bird^{-1}$ min^{-1} $°C^{-1}$
TC_2 = Temperature Coefficient, calculated by method 2, ccO_2 $bird^{-1}$ min^{-1} $°C^{-1}$
T_{b1} = Body temperature, extrapolated for metabolic rate = O (method 1), °C
T_{b2} = Body temperature, measured by thermocouples, °C (basis for method 2)

lism on ambient temperature). Once this equation has been obtained, the exact LCT can be found by determining at which temperature the previously determined basal metabolic rate intersects this. From the linear regression equation the "aparent body temperature" can also be calculated, and as we have already commented turns out to be generally unrealistically high.

In method two, following West 1968, actually measured body temperatures are taken as point of departure (when not taken during the runs, obtained from Fig. 35). Using the known body temperature as the point of origin, it is then possible to find the line of best fit through the data points relating metabolism to temperature. Again, the intersection of this line with the previously found basal metabolism will provide the LCT.

The two methods yield slightly different slopes for the temperature effect on metabolism (the temperature coefficient, TC in Table 16) with West's method of forcing the line through actually measured body temperature yielding a higher value. A seasonal trend for both the LCT and the temperature coefficient appears to hold for both sexes (fig. 33), both showing peak values in summer. We will take up the problem of explaining these changes when the moulting process is dealt with.

Long-eared Owls managed to keep their body temperatures highly constant despite the often rather low temperatures to which they were exposed. (Fig. 34). There seems to be a small seasonal and sexual difference in body temperature. Mean body temperature for females in the non-moulting period (November-May) is 39.9 °C (± .34) and 40.4 °C (± .46) during the moult period (June-October). The values for males are 39.2 °C (± .34) and 39.9 °C (± .26) respectively (Fig. 35).

Daily variation in SMR and body temperature

A daily rhythm in metabolic rate for owls with a peak in the nocturnal period has been demonstrated by Graber (1962) and Gatehouse & Markham (1970).

I do not have data on daily rhythm in BMR as such. Fig. 36 gives, however, values of daily variation in SMR during the 24 hr measurements at constant (mean monthly) temperatures. Daily rhythm is modified by the fact that during longer periods of food deprivation metabolic rate shows a decrease. So oxygen consumption on day II is on the average 21.6% lower than on day I. If we compare metabolic rate

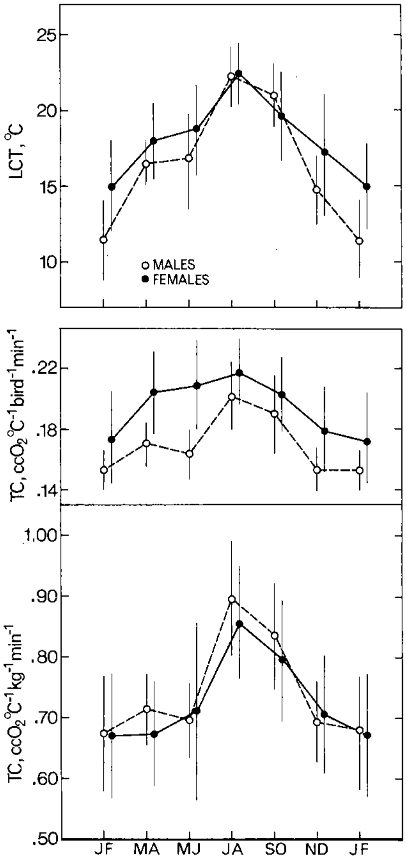


Fig. 33. Lower Critical Temperature (LCT in °C, top) and Temperature Coefficient (TC, slope of the metabolic response, in ccO_2 bird^{-1} min^{-1}, centre, and in ccO_2 on a weight basis, bottom) in relation to season (bimonthly means ± 1 SD). All computations according to method 2 (West 1968).

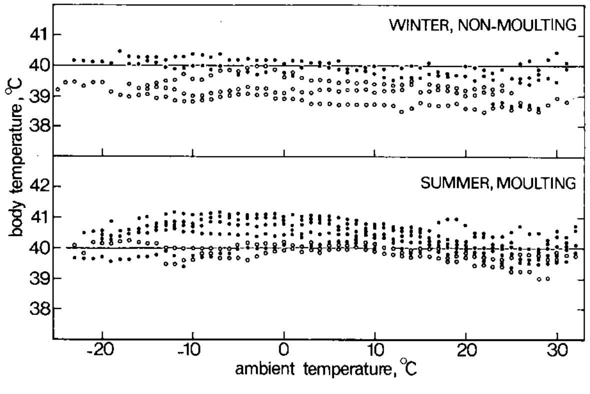


Fig. 34. Body temperature in relation to ambient temperature. Plotted are 5-minute means for males (circles) and females (dots) held in a temperature cabinet.

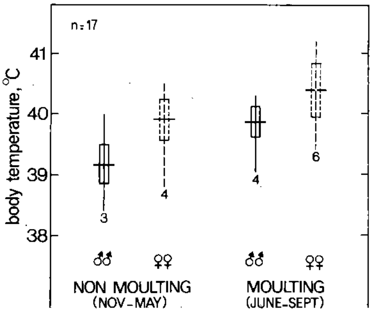


Fig. 35. Body temperature at normal air temperatures (means ± 1 SD, range and number of birds indicated) for non-moulting and moulting periods.

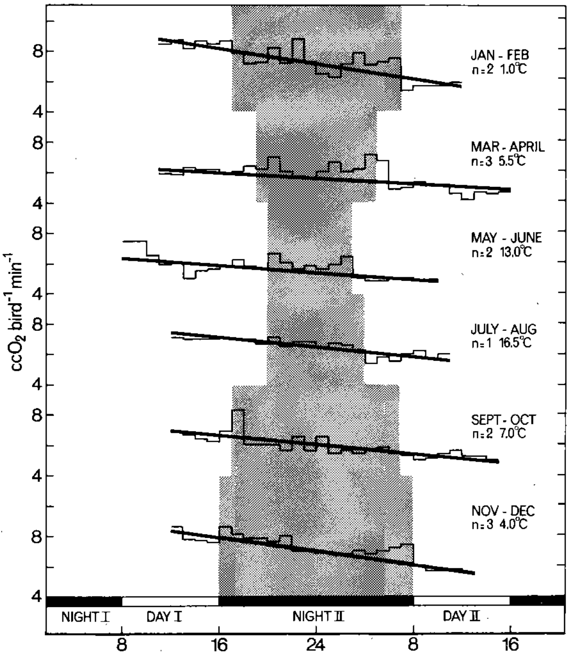


Fig. 36. Oxygen consumption during long-term trials throughout the year when the birds were held without food at an air temperature typical for that time of the year (light cycle as outdoors). The bars show one-hour means for oxygen uptake when at complete rest in the metabolism chamber (for methods see text). A trendline has been drawn, connecting the means on day I and day II, and confirms to the decline documented for the Kestrel during starvation (Shapiro & Weathers, 1981).

at night II with the mean values of day I and day II oxygen consumption seems te be on the average 8.2% higher during the normal active period of the Long-eared Owl. Daily variation in body temperature (Fig. 37) shows the same reversed rhythms compared to normally day-ac-

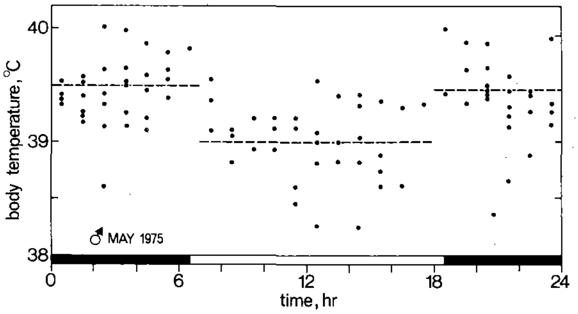


Fig. 37. Body temperature of an individual owl in relation to time of day, showing differences between day and night (light cycle indicated at bottom).

tive birds. Night values average 0.5 °C higher than daytime values.

Effects of wind and radiation on SMR

Increase in wind speed at the three measured temperatures (−5 °C, 10 °C and 25 °C) seems to give an elevation in metabolic rate with about the same percentage. So at temperatures within the zone of thermoneutrality (25 °C) this rise is the same as at the other temperatures. Mean values for the different wind speeds are 18.9%, 25.3% and 35.7% increase in oxygen consumption for wind speeds of 0.9, 1.2 and 1.8 msec^{-1} respectively (Fig. 38). In contrast to this finding the reduction in metabolic rate brought about by artificial radiation seems to depend on the ambient temperature: in the thermoneutral zone this reduction is only 1.6—4.4% for the range of intensities employed, whereas at an ambient temperature of 1 °C these values were 8.6—20.9% (Fig. 38).

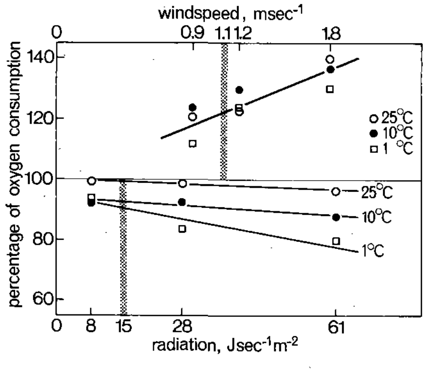


Fig. 38. Effect of wind (above) and radiation (below) on metabolic rate at various temperatures, as determined in a modified respiration chamber (see text). Normal environment levels at the roost are shown by stippled bars.

5.4 DISCUSSION

Seasonal changes in BMR

Elevation of BMR sets in for the Long-eared Owl male towards the end of the winter while this event happens later for the female. Courtship behaviour in this species starts very early in spring and in fact territories will be occupied at least during part of the night by early February. Male courtship feeding will start now while the female spends a lot of time in the breeding territory. This means that the male will increase his hunting activity while the female will reduce her hunting activity. It is possible that this fundamental difference in the roles between the sexes is reflected in their basal metabolic rates, higher activity levels leading to a higher BMR for the males.

Although female BMR increases in April there is a sharp decline in BMR when this is calculated on a mass-specific basis. As will be discussed in chapter 10 it is likely that this increase in weight is caused by fat deposition in that period. Changes in body composition, in this case a higher fat content, might cause a lower weight specific metabolic rate as was earlier suggested by Hayward (1965a, b) for *Peromyscus*. Calculating the weight coefficient for linear regression for log BMR and log body weight might illustrate this. This coefficient is for females in the reproductive period .25. For females outside the reproduction period combined with males throughout the year (this group shows only moderate weight variation) this coefficient is .67.

Although seasonal changes in BMR between "winter" and "summer" birds have been found for passerines (winter birds having a higher BMR) non-passerines did not exhibit this seasonal difference (for review see Kendeigh *et al.* 1977 and Weathers 1980). This conclusion can also be stated for the Long-eared Owl. In general it can be said that no correlation exists between BMR and outside temperature but variation in BMR is probably more influenced by events in the annual cycle, like reproduction and moult.

Table 17. Basal Metabolic Rates for *Strigiformes*

If available, day-time measurements taken in winter are presented in the table. Some authors give data for both sexes; in that case the mean value is given. Linear regression was calculated for log body weight (g) on log BMR (kJ bird^{-1} day^{-1}) using a single mean value for each species. This mean is also given in the table. Formula for *Strigiformes* (13 species): BMR = $1.435W^{.759}$ (r = .973) (BMR in kJ; W in grams). General formula for non-passerines of Kendeigh *et. al.*, (1977) is: BMR = $2.187\ W^{.735}$.

Species	Weight (grams)	Season	Time of measurement	BMR (kJday^{-1})	Authority
Micrathene whitneyi	46	?	day	22	Ligon, 1968, 1969
Glaucidium gnoma	54	?	—	39	Ligon, 1969
Aegolius acadicus	124	?	—	57	Ligon, 1969
Aegolius acadicus	83	winter	—	44	Gatehouse & Markham, 1970
Aegolius acadicus	85	winter	—	61	Graber, 1962
	97			54	species mean
Otus trichopsis	120	?	—	38	Ligon, 1969
Speotypo cunicularia	143	winter	—	59	Coulombe, 1970
Otus asio	166	?	—	51	Ligon, 1969
Otus asio	151	winter	—	61	Gatehouse & Markham, 1970
	159			56	species mean
Glaucidium cuculoides	163	summer	?	75	Johnson & Collins, 1975
Asio otus	252	winter	day	83	Graber, 1962
Asio otus	241	—	—	114	this study
Asio otus	236	summer	night	113	Gavrilov & Dolnik (in: Kendeigh *et al.* 1977)
	243			106	species mean
Surnua ulula	333	winter	?	147	Johnson & Collins, 1975
Asio flammeus	406	—	day	117	Graber, 1962
Strix aluco	520	?	?	180	Herzog, 1930
Bubo virginianus	1450	?	?	452	Benedict & Fox, 1927
Nyctea scandiaca	2026	winter	day/night	364	Gessaman, 1972 (revised)

BMR of Strigiformes

For comparing BMR values with data on other birds it is best to use data outside the reproduction and moult period. Mean BMR for the male Long-eared Owl is then 4.25(± .122) for a mean body weight of 229 (± 15)(n = 9). For females these values are respectively 4.39 (± .330) and 254 (± 16)(n = 18). (BMR is given here in ccO_2bird^{-1}min^{-1} and body weight in grams). If we multiply this with the caloric equivalent for oxygen these values are 112.1 kJbird^{-1}day^{-1} for the males and 115.7 kJbird^{-1}day^{-1} for the females.

Graber (1962) reports a value of 82.5 kJbird^{-1}day^{-1} for a Long-eared Owl with a body weight of 252 g and of unknown sex. Gavrilov and Dolnik (in: Kendeigh *et al.* 1977) give a value of 113.0 kJbird^{-1}day^{-1} for a Long-eared Owl with a body weight of 236 g, which is nearly identical with our value. However, this bird was measured in the summer and during daytime.

Zar (1968) and Ligon (1968, 1969) give regressions for the logarithmic relationship for BMR to weight for *Strigiformes*. *Strigiformes* appear to have a lower elevation than the classic data for non-passerines given by Lasiewski and Dawson (1967). Since that time new data have become available. For owls these data are given in Table 17 and are plotted in Fig. 39, including data from this study. Compared with the regression equation for non-passerines, $2.187W^{.735}$ (n = 77 species) (Kendeigh *et al.* 1977) the elevation for *Strigiformes*, $1.435W^{.759}$ (n = 13 species), is considerably lower (± 75% of the general non-passerine level).

Among the non-passerines, owls are not the only order with low BMR's. Especially *Caprimulgiformes*, which order includes nightjars, goatsuckers and frogmouths, are characterized by a particulary low BMR (Bartholomew *et al.* 1962, Lasiewski & Dawson 1964, Dawson & Fisher 1969, Lasiewski 1969, Lasiewski *et al.* 1970). It is of interest that systematically *Caprimulgiformes* seem to be the nearest relatives to the owls (Everett 1977). With this group owls have their nocturnal way of life in common. It might be possible that a lower metabolic rate is an adaptation to their nocturnal life. A nocturnally active bird may face less uncertainty by day, and can choose a favourable microclimate

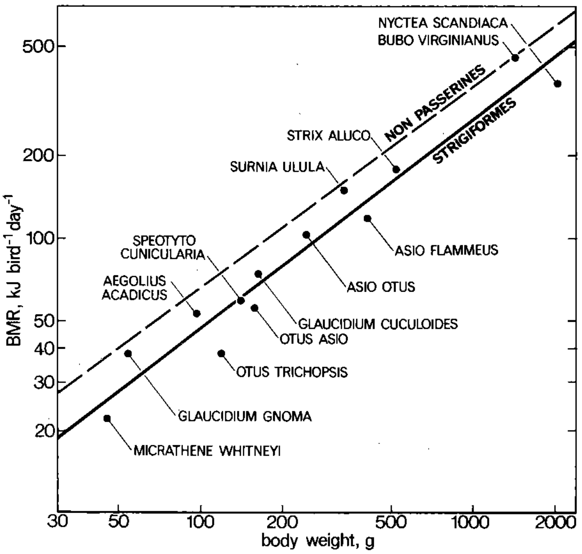


Fig. 39. Basal Metabolic Rate (BMR) in kJ per bird per day for the *Strigiformes* in relation to body weight (data sources are given in Table 17). The regressionline calculated for these data is compared with the general prediction for BMR-body weight relationship in non passerine birds (Kendeigh *et al.* 1977, for equations see Table 17).

for the resting phase, and can afford to allow its metabolic processes to proceed slowly at this time. We will return to this problem in the final discussion.

Explanations for deviating BMR's in certain bird species or group of birds are given as an adaptation to local climates. Thus Dawson & Bennett (1973) were able to show in *Columbiformes* that pigeons closely associated with hot and arid situations have lower BMR values while non-desert pigeons have BMR values comparable with those predicted from the Lasiewski and Dawson equation for non-passerines. Weathers (1980) showed increased BMR's for species in cold climate with on the average 47%. If we arrange the owl data of Table 17 in order of more northern ("polar") and southern ("tropical" or "desert") species (see Table 18) there might be a tendency of southern owls to have lower BMR values than northern owls. The most polar owl of all (Snowy Owl) makes an exception difficult to explain.

Many theoretical attempts have been made to explain the coefficient for metabolic power to weight. McMahon (1973) predicted that metabolic power output should be proportional to $W^{.75}$ for reasons of elastic stability and flexure that will set limits on body size and the dimensions on body-supporting members. However Kendeigh *et al.* (1977) predicted for quite different reasons that BMR will vary with weight according to $W^{.67}$ (which is in conformity with

Table 18. BMR values of Strigiformes arranged according to distribution

Distribution	Species	BMR kJbird^{-1} day^{-1}				
		obs.	pred*	%Δ	pred**	%Δ
Northern	*Nyctea scandiaca*	364	589	62	464	78
	Surnia ulula	147	156	94	118	125
	Glaucidium gnoma	39	41	95	30	131
Temperate	*Aegolius acadicus*	54	63	86	46	117
	Asio flammeus	117	181	65	137	85
	Asio otus	106	124	85	93	114
	Strix aluco	180	217	83	165	109
	Bubo virginianus	452	461	98	360	126
	Otus asio	56	91	62	67	83
Southern	*Speotyto cunicularia*	59	84	70	62	95
	Glaucidium cuculoides	75	92	82	68	110
	Micrathene whitneyi	22	36	61	26	84
	Otus trichopsis	38	74	51	54	70

Mean deviation of the 3 northern species: 11% higher than expected for owls**
Mean deviation of the 6 temperate species: 6% higher than expected for owls**
Mean deviation of the 4 southern species: 10% lower than expected for owls**
* By the equation for non-passerines of Kendeigh *et al.* 1977
** By the equation for *Strigiformes*, this study
%Δ = (observed — predicted) × 100%

the surface law as developed by Rubner (1883)). Kendeigh *et al.* suggest that $W^{.67}$ should be a compromise through natural selection between temperature regulation ($W^{.50}$) and power for flight ($W^{.83}$) (Dolnik 1969). Segregation of the data from Kendeigh *et al.* according to time of the day and season indeed lowers the coefficient of weight more towards $W^{.67}$.

Although data for only one species gives in general a small variation for weight, it is interesting to find a coefficient of $W^{.662}$ for the Long-eared Owl (females in the reproduction period excluded; weight variation from 220 to 315 g). Heusner & Jameson (1981) reported a mass exponent of .67 for the lizard *Sceloporus* which differs significantly from Kleiber's weight exponent of .75 (Kleiber 1961). In this species a weight range of 1—25 g was considered.

Information from future research on one species with enough variation in body size, but not in fat content, will probably give us more insight in this question.

Temperature regulation

Recently Gavrilov (1982) provided a compilation of seasonal differences in the temperature coefficient and the lower critical temperature for non-passerines. Substituting in his equations for my captive Long-eared Owls (average body weight 240 g) it turns out that the LCT is within 0.2 °C of the predicted value for both summer and winter. Secondly, the increase in the temperature coefficient in summer as compared to the winter is also very close to prediction (13% as compared to 14%) despite the fact that my summer birds have already started the moult. In the absolute level of the temperature coefficient, however, the Long-eared Owl is nowhere near the prediction. In fact, the slope of metabolism against temperature is 21% less than expected for a bird its size, i.e. the owl seems to be getting something for nothing. As will be taken up again in the chapter of moult, the insulative properties of the feather coat of the Long-eared Owl are undoubtedly superior to other birds of that weight range on account of the far higher density of feathers and consequent higher plumage weight per surface area. In the final discussion we will return to the magnitude of the savings entailed throughout the year due to the superior insulation of the plumage.

Wind and radiation

Birkebak (1966) calculated from theoretical assumptions that the rate of increase in heat loss due to wind velocity would be about 10% per $m^{-1}sec^{-1}$, but the only data available for owls is about double this rate (20% in my data, and 19% in Gessaman's 1972 low temperature data on the Snowy Owl). Because effects of wind speed are roughly the same at 25 °C as at other temperatures it is likely that increasing wind velocity foreshortens the zone of thermoneutrality and hence elevates the lower critical temperature. There are no critical data, however, to show this effect.

Turning now to radiation, the savings accrueing to the roosting owl from solar radiation at lower temperatures are quite comparable to the data presented by Lustick (1969), Hamilton and Heppner (1967) and de Jong (1976) for small passerines saving from 5% to 36% of their expected metabolic cost. They were in general however, exposed to higher levels of radiation. It might be possible that larger birds have more profit from radiation than smaller birds. However, in the Long-eared Owl effect of microclimate really needs more research.

6. METABOLIZED ENERGY UNDER CAGED CONDITIONS

6.1. INTRODUCTION

Metabolized energy (ME) is the net amount of energy obtained from the food eaten, thus after subtraction of the gastro-intestinal and urinary wastes. Kendeigh (1949) championed the importance of this parameter in the ecological energetics of birds, and pioneered a method of measurement that has been widely adopted since. In the Kendeigh method birds are held individually in very small cages, and under circumstances when not undergoing reproduction, moult, migratory unrest, growth or fat deposition the ME so determined he termed the *existence metabolism* (EM). Determinations of EM are now available for a considerable number of bird species at various temperatures and photoperiods (reviewed by Kendeigh *et al.* 1977). Although a polynomial regression sometimes best describes the negative relationship between EM and ambient temperature (Davis 1955, Owen 1970) in most cases a simple linear fit is sufficient, in general with a lower temperature coefficient than for standard metabolic rate (Kendeigh *et al.* 1977).

Existence metabolism should theoretically at least differ from free-living existence only by the cost of locomotion (principally for foraging). Hence EM values have often been used as the starting point in arriving at estimates of the cost of free-living (West 1960, 1968, Kahl 1964, Kale 1965, Helms 1968, Owen 1969, Schartz & Zimmerman 1971, Kendeigh 1973). This extrapolation to complex natural situations involves simplifications of the microclimate actually experienced (King 1974) and the small-cage conditions of the measurements may interfere with normal behavioural thermoregulation (Weiner 1970). A major drawback is the variability in locomotor activity shown by different species when caged (West 1960, Zimmerman 1965) making comparison difficult and extrapolation to free-living tenuous.

Despite these limitations the Kendeigh approach offers several distinct advantages. I will employ the term ME_{cage} as a general term for the technique (only a few qualify in retrospect for EM)and will here employ it to cover the following points:

1) Me_{cage} is an integration of BMR, temperature regulation, heat increment of feeding (SDA) and cage locomotory activity. Because BMR and temperature regulation was measured in other ways (chapter 5) ME_{cage} values offer the opportunity to estimate the latter often elusive components.
2) ME_{cage} in relation to changes in body-weight during the period of measurement allows estimation of the cost of weight gain or loss (Owen 1969).
3) ME_{cage} is more often reported than any other metabolic measure and provides an additional comparative perspective.

6.2. METHODS

Experimental conditions and techniques for measuring gross energy intake and the energy lost in pellets and droppings have already been described in chapter 4. Gross energy intake minus the rejecta provides ME_{cage}, and in general data were obtained in trials of five consecutive days. Each day the owls were weighed at the end of the light period. Each trial thus provides 5 ME_{cage} values for a 24 hr period, as well as the weight change of the owl in that period, if any. For each trial the five ME_{cage} values were plotted in relation to weight change (g per 24 hr) and a linear regression of the data performed. If the correlation coefficient was 0.75 or better the relationship was accepted as adequately established and the ME_{cage} corresponding to a weight change of 0 g read from the regression equation and entered as the outcome of the trial (ME_{cage}, no change in body weight). In a very few cases the plot yielded a low correlation coefficient, and the ME_{cage} for no change in body weight was derived by substituting the overall mean of 13.5 kJ per g weight change (see on).

The caloric equivalent of weight change was determined in the total material by considering only those 24 hr periods in which body weight changed by less than 5 g. It was found that changes beyond this were caused by extreme food intakes, and as it was by no means sure that the alimentary tract was empty by the end of the day, a prerequisite to keep the readings comparable, it was deemed advisable to delete these data.

6.3 RESULTS

ME_{cage} during winter and summer, corrected to represent conditions of constant weight, is given in Fig. 40. For comparison, energy expenditure of the post-absorptive quiescent owl, obtained by the oxygen consumption method with fasting birds maintained at the same temperatures as the ME_{cage} determinations, is included in the figure. There is sufficient spread in experimental temperatures in the winter ME_{cage} data set to allow analysis. The effect of temperature on ME_{cage} calculated by linear regression shows a shallower slope than the data on SMR obtained earlier, which means that the absolute difference in level of these two measures diminishes with decreasing temperature. All we can say for the summer ME_{cage} is that the difference with the SMR data is still more extreme (at 15 °C the ME_{cage} exceeds the SMR by 26 kJ in winter, but by 50 kJ in summer).

A possible difference between the sexes can only be examined in the summer data, as there is a shortage of male values in winter. For the summer 15 °C subset ME_{cage} for female owls is about 14% higher than for the males, a difference reminiscent of the overall difference in BMR between the two sexes we earlier found (10% higher in the females when expressed per bird). When expressed per kg weight, males

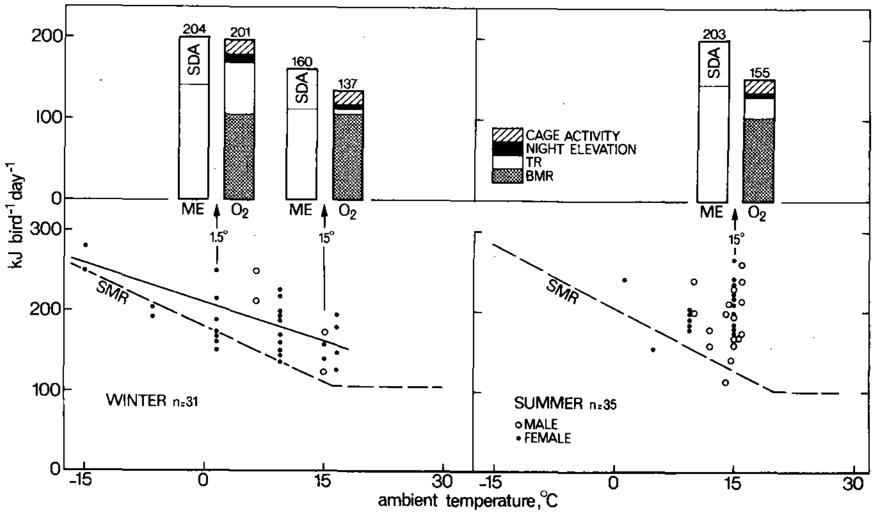


Fig. 40. Metabolized Energy (ME) in small cages extrapolated to zero weight change, at different ambient temperatures in winter and summer. Each point is the mean of a 5-day trial. For comparison SMR data have been entered, and along top a reconstruction of components of energy expenditure is given for three temperatures. For the winter data a line of regression of ME on ambient temperature has been calculated (see text).

have a somewhat higher ME_{cage} (6% higher) as we found for the BMR.

The caloric equivalent of weight change gave an overall mean of 13.47 kJ for one g change in weight. Females in the reproductive phase show the highest equivalent (15.02 kJ) suggesting deposition of fat. Data for other conditions and periods cluster around 12—13 kJ. None of these differences are however significant (Student t-test; $p > .05$). For this reason throughout this study the mean value of 13.5 kJ was used.

6.4. DISCUSSION

There are a number of published data with which my findings can be compared. Taking the caloric equivalent of weight change first, my overall mean of 13.5 kJ per g weight change falls within the range of the more extensive data amassed for *Anas discors* by Owen 1970 (12—29 kJ per g) and for various passerines by Dolnik 1968 (8—38 kJ per g). Given my method it was not possible to distinguish between the cost of synthesis on the one hand and the energy regained when body weight is later sacrificed. To achieve this distinction it will be necessary to devise means of assaying which body components (protein, fat, water to name the most critical) in fact change when the total body weight of the intact animal is observed to vary. A first step might be to measure specific gravity of the experimental birds each time the body weight is taken. We will return to this problem when discussing the caloric cost of growth (chapter 8).

More specific to my study, Gavrilov and Dolnik (in Kendeigh *et al.* 1977) summarize their study of existence metabolism in the Long-eared Owl by presenting an equation expressing EM as a function of ambient temperature (for long photoperiods). Substituting for an ambient temperature of 15 °C, their ME value works out at 286 kJ, which exceeds my own summer maximum somewhat (one of my females reached 275 kJ). The reason for the discrepancy may be that Gavrilov and Dolnik's birds lived in larger cages, where they conceivably incurred higher costs in locomotion. Turning now to the year-round average ME_{cage} for the Long-eared Owl recently presented by Ceska (1980), I must admit that I regard his figure of 345 kJ with considerable suspicion; not only it is far above anything I have measured in my caged birds, but it exceeds by far my estimates for the ME of free-living owls as well (see Table 14). Since Ceska does not present his data in detail I am unable to offer any explanation. Finally Marti (1973) presents data for food intake (laboratory mice) of captive Long-eared Owls in terms of g mouse per bird per day, and if I apply the caloric value of the food and the digestibility as determined in this study, the ME_{cage} works out to range from 166—280 kJ. Better agreement with the data presented in Fig. 40 could scarcely be asked for.

In Fig. 40 it can be seen that for the winter periods the difference between ME_{cage} and the energy expenditure of the quiescent owl (SMR) is less at 1.5 °C than at 15 °C. This suggests a

Table 19. Metabolized Energy (cage) for *Strigiformes* and *Falconiformes*. In most cases metabolized energy was calculated from given data on food intake in captivity, using a caloric value of 8.4 kJ/gram fresh weight for mice or rats and a metabolizable efficiency coefficient of .76. Measurements at extreme temperatures were ignored. If there was a possibility for a choice, temperatures of ± 15 °C were used. In general only small cages were used, so the possibility of (flight) activity was limited. However, this is, together with temperature, a point which might cause variation. Some authors give data for both sexes; in that case a mean value is given in this table. Linear regression was calculated for log body weight (g) on log ME (kJ) for *Strigiformes* as well as *Falconiformes*. A single mean value for each species was used in the case the particular species was studied by more authors. For the linear regression for *Falconiformes* birds weighing more than 2100 grams were not used because no equivalent owl data for these weights exist. Linear regression for *Falconiformes*: $ME = 9.772W^{.577}$ ($r = .918$; $n = 21$) and for *Strigiformes* $ME = 8.630W^{.578}$ ($r = .958$; $n = 13$) where: ME in kJ $bird^{-1}$ day^{-1} and W in grams. The numbers in the *Falconiformes* refer to Fig. 41.

	Body weight (g)	ME cage ($kJday^{-1}$)	Authority
Strigiformes			
Aegolius acadicus	96	111	Graber, 1962 (revised)
Aegolius acadicus	94	178	Collins, 1963
Aegolius acadicus	96	92	Duke *et al.*, 1976
	95	127	species mean
Aegolius funereus	138	184	Gavrilov & Dolnik, in: Kendeigh *et al.* 1977
Otus asio	149	124	Duke *et al.*, 1976
Otus asio	149	165	Craighead *et al.*, 1956
	149	144	species mean
Speotyto cunicularia	166	169	Marti, 1973
Athena noctua	199	130	Wijnandts, unpublished
Asio otus	305	201	Graber, 1962 (revised)
Asio otus	230	345	Ceska, 1980
Asio otus	283	285	Gavrilov *et al.*, 1977
Asio otus	275	200	this study
Asio otus	295	239	Marti, 1973
	298	254	species mean
Tyto alba	262	190	Kirkwood, 1979
Tyto alba	515	359	Wallick *et al.*, 1975
Tyto alba	333	292	Wijnandts, unpublished
Tyto alba	280	358	Ceska, 1980
Tyto alba	246	255	Gavrilov *et al.*, 1977
Tyto alba	599	385	Marti, 1973
	373	306	species mean
Asio flammeus	406	261	Graber, 1962 (revised)
Asio flammeus	385	248	Page *et al.*, 1975
Asio flammeus	455	325	Chitty, 1938
Asio flammeus	432	363	Duke *et al.*, 1976
	420	299	species mean
Strix aluco	572	227	Wijnandts, unpublished
Strix aluco	420	410	Ceska, 1980
	496	318	species mean
Strix varia	741	309	Duke *et al.*, 1976
Strix varia	625	340	Craighead *et al.*, 1956
	683	324	species mean
Strix nebulosa	1045	391	Craighead *et al.*, 1956
Bubo virginianus	1615	960	Duke *et al.*, 1973
Bubo virginianus	1660	465	Duke *et al.*, 1975
Bubo virginianus	1215	738	Howard, 1958
Bubo virginianus	1332	401	Marti, 1973
Bubo virginianus	1770	512	Duke *et al.*, 1976
Bubo virginianus	1159	423	Craighead *et al.*, 1956
	1459	583	species mean
Nyctea scandiaca	1318	1450	Ceska, 1980
Nyctea scandiaca	1970	444	Gessaman, 1972
Nyctea scandiaca	1900	690	Duke *et al.*, 1975
Nyctea scandiaca	1700	585	Duke *et al.*, 1976
	1722	792	species mean
Falconiformes			
Accipiter striatus (1)	106	158	Koplin *et al.*, 1980
Accipiter striatus (1)	107	95	Craighead *et al.*, 1956
	107	127	species mean

	Body weight (g)	ME cage (kJday^{-1})	Authority
Falco sparverius (2)	126	171	Koplin *et al.*, 1980
Falco sparverius (2)	120	102	Gessaman, 1980
Falco sparverius (2)	101	134	Barrett *et al.*, 1975
Falco sparverius (2)	105	105	Duke *et al.*, 1976
Falco sparverius (2)	99	99	Craighead *et al.*, 1956
	110	122	species mean
Accipiter nisus (3)	149	188	Gavrilov in: Kendeigh *et al.* 1977
Falco columbarius (4)	173	230	Koplin *et al.*, 1980
Falco tinnunculus (5)	204	160	Kirkwood, 1979
Falco tinnunculus (5)	195	235	Koplin *et al.*, 1980
	200	198	species mean
Elaneus caeruleus (6)	238	264	Tarboton, 1978
Accipiter cooperii (7)	375	331	Craighead *et al.*, 1956
Circus cyaneus (8)	435	361	Craighead *et al.*, 1956
Buteo platypterus (9)	416	342	Mosher *et al.*, 1974
Buteo platypterus (9)	470	194	Duke *et al.*, 1976
	443	268	species mean
Pernis apivorus (10)	649	456	Gavrilov in: Kendeigh *et al.* 1977
Falco mexicanus (11)	497	352	Koplin *et al.*, 1980
Falco mexicanus (11)	806	573	Craighead *et al.*, 1956
	652	463	species mean
Falco peregrinus (12)	702	477	Craighead *et al.*, 1956
Falco peregrinus (12)	680	458	Duke *et al.*, 1975
	691	468	species mean
Falco rusticolus (13)	880	531	Duke *et al.*, 1975
Polyborus plancus (14)	975	375	Gavrilov in: Kendeigh *et al.* 1977
Buteo buteo (15)	983	527	Gavrilov in: Kendeigh *et al.* 1977
Accipiter gentilis (16)	880	789	Fevold, 1958
Accipiter gentilis (16)	1100	611	Duke *et al.*, 1976
	990	700	species mean
Buteo lagopus (17)	1020	347	Duke *et al.*, 1976
Falco cherrug (18)	1036	770	Koplin *et al.*, 1980
Buteo swainsoni (19)	1160	372	Duke *et al.*, 1975
Buteo jamaicensis (20)	1389	680	Koplin *et al.*, 1980
Buteo jamaicensis (20)	1210	490	Duke *et al.*, 1975
Buteo jamaicensis (20)	1320	420	Duke *et al.*, 1976
Buteo jamaicensis (20)	1110	589	Craighead *et al.*, 1956
	1257	545	species mean
Neophron perenopterus (21)	2063	942	Gavrilov in: Kendeigh *et al.* 1977
Heliaeetus leucocephalus	3300	1635	Duke *et al.*, 1975
Heliaeetus leucocephalus	3870	1578	Duke *et al.*, 1976
	3585	1607	species mean
Sarcoramphus papa	3650	1256	Gavrilov in: Kendeigh *et al.* 1977
Sarcoramphus papa	3730	722	Duke *et al.*, 1976
	3690	989	species mean
Gyps africanus	3700	1273	Houston, 1976
Harpia harpyja	4300	1524	Gavrilov & Dolnik in: Kendeigh *et al.*, 1977
Aquila chrysaetos	4740	1820	Fevold *et al.*, 1958
Gyps rueppelli	4900	1432	Houston, 1976

compensatory effect of the heat increment of feeding (SDA) contributing towards the cost of temperature regulation (see discussion in Kendeigh *et al.* 1977). To come closer to understanding what is going on, I have attempted to compartmentize the SMR data. BMR and the temperature regulation component have already been discussed at length in the preceding chapter, and I have chosen to call the higher SMR measured during the nocturnal period "night elevation" (8.2% higher than during daytime, cf. chapter 5; of course the duration of the night enters into the calculation). The final component, cage activity, was calculated from the 24-hr measurements as the difference between *total* oxygen intake and the *minimum* intake during rest. This difference averaged 20 kJ per 24 hr and is assumed to apply equally at all temperatures and seasons.

Looking again at the winter data, there seems a convincing case for the substitution of the heat increment of feeding for energy expenditure specifically for temperature regulation, the more so since at the LCT, 15 °C, this appears to be disippated. But how large is the SDA component actually? From data in Brody (1945) and Ricklefs (1974) the SDA for a mouse diet can be estimated at 22% of the gross energy intake, and the blocs in the diagram have been filled in accordingly. If I were to estimate SDA empirically from my winter data, it can be argued that the difference between ME_{cage} and SMR at 15 °C can give a first approximation. This figure (160—137 = 23 kJ or 14% of ME_{cage}) is close to the empirical estimates provided by Kendeigh *et al.* (1977) for a number of passerines, varying from 11—14% of ME_{cage}. There are two immediate difficulties however. First, a SDA of only 14% of the ME would not provide a sufficient source of compensation for the 1.5 °C conditions (where temperature regulation costs some 60 kJ). Secondly, the level of dissipation in the summer data set, albeit their more heterogeneous nature, reaches 24% of ME_{cage} (fig. 40, right panel). Given the variability of my data I can go no further than to conclude that SDA for the Long-eared Owl on a mouse diet lies somewhere in the range 14—24% of the ME. Probably by coincidence there is some justification for both extremes in the literature.

Turning now to the comparative aspect, I have combed the literature for data on the food consumption of hawks and owls in captivity, and have converted these where necessary to obtain ME_{cage} values at approximately 15 °C (see Table 19, providing data on 21 species of *Falconiformes* and 13 species of *Strigiformes*). Recently Kendeigh *et al.* 1977, have provided a general compilation of ME_{cage} data for non-passerines, and I have plotted my figures in relation to their general equation for comparison (Fig. 41). The data for each group are reasonably consistent, and justify providing an equation for each separately. It is striking that the slope of the three lines (respectively non-passerines in general, *Falconiformes* and *Strigiformes*) is virtually identical (the exponent is .59 for the Kendeigh *et al.* equation and .58 for the other two). Secondly, it appears that *Falconiformes* and *Strigiformes* get by with less food per day than many other non-passerines of comparable body weight. For a bird in the weight range 250—350 g, an owl needs 30% less every day than the "generalized non-passerine" represented in the Kendeigh *et al.* compilation. This calls to mind the similar economy in the BMR we noted in the previous chapter, and may indeed be related to it.

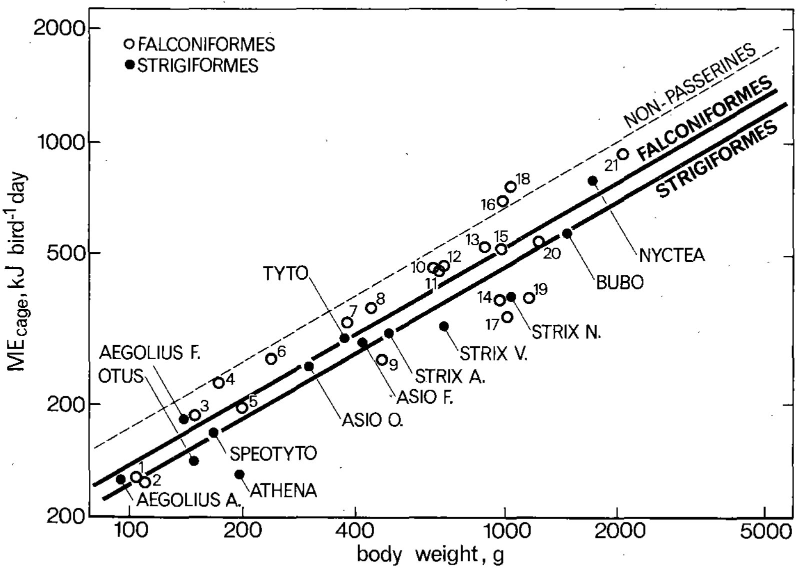


Fig. 41. Metabolized Energy (ME) as determined for birds kept in small cages in relation to body weight for *Strigiformes* (black dots, data source see Table 19) and *Falconiformes* (species numbered, see Table 19). The lines of regression are shown and for comparison the general prediction for non-passerine birds of Kendeigh *et al.* (1977) is also entered ($ME = 11.41W^{.592}$; mean for 0 ° and 30 °C) for the 15 °C target temperature of the compilation.

The Long-eared Owl, though nothing exceptional when compared to other *Strigiformes*, is thus one of the most economical birds in existence. Nevertheless it must obtain all its prey by hunting flight, and avian flight we know to be an extremeley expensive activity. How to balance the budget of the free-living owl will thus be our next concern.

7. BALANCING THE ENERGY BUDGET FOR FREE-LIVING OWLS IN WINTER

7.1 INTRODUCTION

In my attempt to quantify the components of energy expenditure of the Long-eared Owl I have now reached the point that flight must be considered. It has been beyond the scope of this study to quantify flight cost, but what I hope to show in this chapter is that in winter at least the budget can be balanced by accepting the cost factor predicted by Pennycuick's (1972, 1975) aerodynamic flight model. We already have an estimate of the energy available to the free living owl in winter (by the pellet method, chapter 4) and we have dealt with the other components of expenditure (chapters 5 and 6). Our task here will be to present the radiotelemetry data on duration of flight, once this is known, a calculation can show how much energy the owl most likely expended during the winter.

The Long-eared Owl is generally considered to be a typical hunter on the wing, beating back and forth across his homerange in long glides interspersed with brief bouts of deepish wing beats (Davis & Prytherch 1976) staying low to the ground. This flight style has been described as comparable to that of the diurnal raptor *Circus cyaneus* (Illner in Glutz & Bauer 1980). Hovering has been observed, but the bouts are much shorter than in the Short-eared Owl (pers.obs.). I have also observed hunting from a perch, but this is not common. The rather long wings suggest adaptation to the open field habitat (Lack 1966) and Poole (1938) has pointed out that compared to many other owls the Long-ear has a relatively light wing-loading factor.

7.2 TELEMETRY TECHNIQUES

Table 1 and 20 provides information on the five owls that received radio transmitters. The mean duration of the tracking period was 17 days, but in two cases observations were terminated by death of the experimental birds. Owl II was struck by a Peregrine Falcon (*Falco peregrinus*) at sunrise on the way back to the roost. We were making bearings at the time and quickly arrived at the scene whereupon the Peregrine flew up; upon inspection of the partially eaten owl the stomach proved to contain two voles (Peregrine predation on Long-eared Owls has previously been noted by both Uttendörfer 1952 and Rockenbauch 1971). Owl V was killed by traffic when hunting along a highway, a common mortality cause in my study area (his body weight had increased by 30 g during the observation period). Owl I was still carrying the transmitter 60 days after trapping, and as far as could be observed her condition did not seem to be adversely affected. Owl III was not found again when after 8 days of tracking the transmitter failed. Owl IV finally was retrapped after 36 days; her body weight was down slightly (by 15 g) but she seemed in perfect condition, was freed of the transmitter and released.

The transmitter used was of the SM-2 type (150 MHz) manufactured by AVM-Instrument Company, Illinois,

Table 20. Time spent in flight activity as observed by telemetry

Owl no.	Sex	Body weight (g)*	Period	Duration of the active period (min.)**	Recorded activity, (min.)***	Estimated duration of flight time (min.)	Flight time as % of active period
IV	♀	315	Nov./Dec.	895 ± 22 (n = 4)	195 ± 53; 98—217 (n = 11)	156	17.4
I	♀	320	Dec./Jan.	895 ± 10 (n = 6)	275 ± 57; 225—363 (n = 7)	220	24.6
II	♂	260	Feb.	747 ± 13 (n = 6)	152 ± 39; 92—185 (n = 6)	122	16.3
III	♂	260	Oct.	693 ± 16 (n = 5)	204 ± 71; 66—235 (n = 5)	163	23.5
Winter average				807	206	165	20.4
Winter median					198	158	19.6
V	♀	268	May****	± 450	131 (n = 9)	105	23.3

* when first trapped
** mean ± SD
*** mean ± SD, range, number of observation nights
**** solitary male, after the nest was abandoned by the female

Fig. 42. Radiotelemetry equipment: (A) Long-eared Owl equipped with harness. The antenna can be seen protruding from the package on the back. (B) Miniaturized radio-transmitter which has been fed to an owl and subsequently recovered in a pellet. (C) Directional antenna for taking bearings and needle output as seen by the observer when equipment is mounted on the vehicle as shown in (D).

USA, and equipped with two 1.35 V mercury cells as power source (Mallory or Duracel PX625) and a stiff 25 cm wire antenna. The ground-wire was incorporated in the harnass by which the transmitter was attached to the back of the owl (for method see Amlaner *et al.* 1978 and Fig. 42). Total weight of transmitter plus harnass was 16—18 g (5—7% of the body weight of the owl). The attachment procedure took about 15 minutes after which the owls were released. The owls were always trapped in the morning to allow us to check everything over during daylight to make sure the transmitter was working properly, and allow the owl a recovery period before going off to hunt again. In no case could we observe a handicap in flight.

Tracking was carried out with two receivers (LA12, AVM) mounted each on the roof of a motor car in combination with a directional 3-element turnable antenna (Yagi, Fig. 42). The bearing of the antenna could be read off on a compass rosette. The position of the car was fixed by taking three bearings on prominent features in the surroundings (generally the flickering glare of the natural gas towers in my area). Where possible simultaneous bearings of the owl were taken every ten minutes from each car (synchronized by walkie-talkie contact) and all cross-bearings were plotted on a detailed map the next day (for examples see chapter 2).

Whether or not the owl was actually in flight could usually be inferred from the pattern of the signal. When perched the owl gave a fairly steady signal, while in flight large fluctuations in signal amplitude were typical. In some cases preening activities could mimic the flight signal pattern, however this was not a serious problem since the bearing did not change and provides a means of discrimination. During the observation period each observer kept his eye on the needle output of the signal and kept a continuous log of activity; in most cases only minor differences in interpretation occurred. Activities were registered using stopwatches (total duration per hour). Moreover each minute the activity was recorded as either present or absent (by noting a + or − on the logsheet) hence we have two measures for activity: the total duration and its distribution over the minutes of the hour.

To determine the potential error involved in assigning the designation "flight" on the basis of the signal pattern, a number of tests were run with a caged owl equipped with a transmitter, and later simultaneous visual and telemetry observations were run on free-living owls. Flight bouts tended to be overestimated in the telemetry data, apparently not so much because the signal did not revert at once to the "perch" type when flight ceased, but rather because vigorous head or body movements during preening regularly misled the observer into concluding that a short flight had taken place. A more frequent routine of taking bearings than the 10-minute interval adopted might well have reduced these errors in interpretation. The over-estimation of flight was found to comprise 20%, and this figure has been applied as a correction factor.

7.3 DURATION AND DISTRIBUTION OF HUNTING FLIGHTS

In all cases start and end of hunting activities agreed closely with that of control owls in the vicinity; mean departure time was 20.4 (± 8.2, n = 28) minutes after sunset and arrival time was 41.7 (± 12.5, n = 24) minutes before sunrise. The telemetry records showed considerable variation in the patterning of flight activity (examples are presented in Fig. 43). An overall influence of weather conditions is suggested by the figure, and when the data are segregated (Fig. 44) it will be seen that flight is inhibited during precipitation, and during periods of sleet in particular the Long-eared Owl avoids flight almost completely.

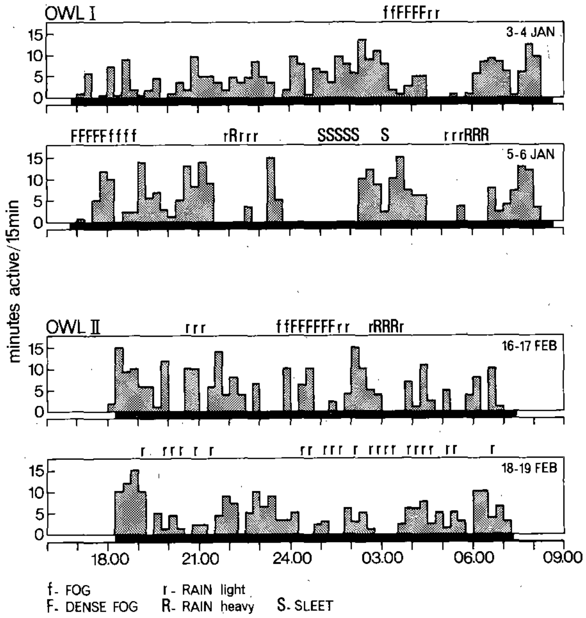


Fig. 43 Nocturnal activity (mainly flight; see text) as determined by radio-telemetry in four sample nights. Prevailing weather conditions indicated by key.

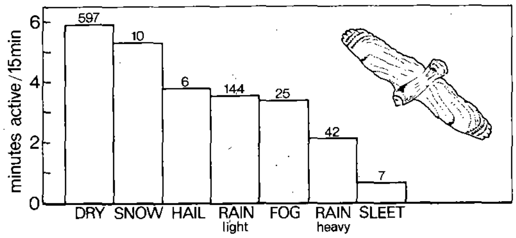


Fig. 44. Nocturnal activity of the Long-eared Owl in relation to prevailing weather conditions (radio-telemetry data, number of 15-minute periods shown) arranged in the sequence of increasing flight inhibition.

Due to their nocturnal way of life little is known of the activity pattern of owls. Glutz & Bauer (1980) assume that the Long-eared Owl shows two main periods of activity: about 3 hours during the first part of the night, and 2½ hours in the second part following upon a phase of inactivity of about 3 hours intercalated around midnight. If we combine our separate activity records as three-point running averages, this pattern fails to emerge in any of our individuals (Fig. 45). The only obvious activity peaks have to do with roost departure just after sunset, and return to the roost before sunrise. Ac-

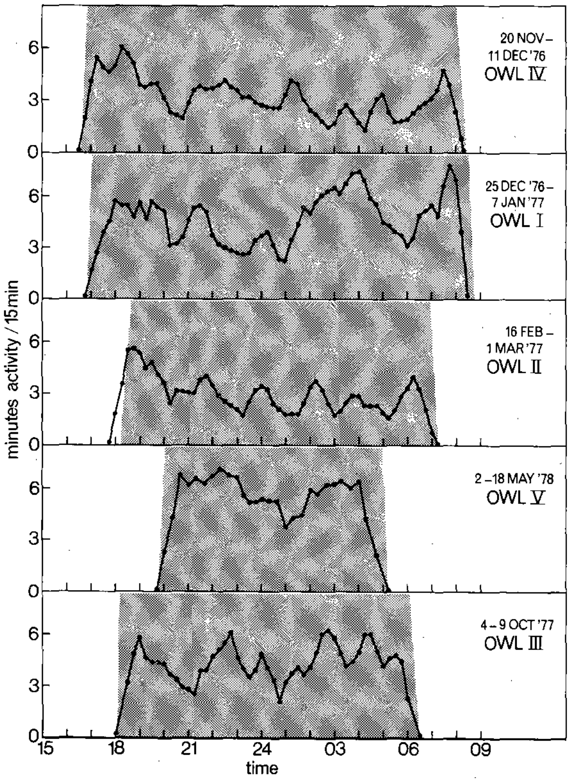


Fig. 45. Nocturnal activity profiles (running means) for the five owls tracked by radio-telemetry (for derivation see text).

tivity is not evenly spread over the night, however, and at least for owl II a shortterm periodicity seems indicated. The interval between peaks in these data is 2.3 hours, a value closely similar to the short-term rhythm of aboveground activity in voles (slightly more than 2 hrs, Daan & Slopsema 1978, Raptor Group RUG/RIJP 1982). Although this vole rhythm was originally discovered during daytime, winter observations indicate a 2 hr periodicity at night also (Hoogeboom *et al. in prep*). During daytime, vole hunters such as Hen Harrier, Kestrel and Buzzard learn to exploit these short-term peaks in vole activity (Raptor Group RUG/RIJP 1982) and the Long-eared Owl may well be doing the same by night.

The distribution of flight bouts is shown in Fig. 46A. The pattern seems uniform: 50% of all flight bouts are less than five minutes in duration, while only 10% are longer than 10 minutes. There did not seem to be a trend during the night, but on the other hand, in keeping with the suggestion put forward by Glutz & Bauer (1980) the rest periods tend to be more prolonged around midnight (Fig. 46B).

The total amount of time spent in flight during the night period is given in Table 20 for the five individuals followed. Extremes vary from one to five hours per night, but for the whole winter period (October through February) the median flight time is 158 minutes (thus about 20% of the active period is spent in flight, if we define the active period as time elapsing between departure from the roost until return the next morning).

Published data for daily flight time for raptors hunting small mammals in the winter vary from as low as 34 minutes (only 6% of the active period) for the Common Buzzard in southern Sweden (Sylvén 1982) to as high as 344 minutes (43% of the active period) for the Saw-whet Owl in Minnesota (Forbes & Warner 1974). Tawny Owls in the relatively open habitat of Revinge (southern Sweden), in contrast to observations elsewhere (Smeenk 1972, Southern 1970) hunted on the wing for about 282 minutes per 24 hr (34% of their active period in late winter when the observations were made, Nilsson 1978). The closest correspondence with my data is to be found in observations on raptors in the same landscape. A Hen Harrier was found to devote 184 minutes per day to flight (32% of the active period in winter, Raptor Group RUG/RIJP 1982) and in late winter Kestrels average about 170 minutes in flight per day (Masman *pers. comm.*).

The differences in flight times between the individuals I followed are hard to account for, and in particular owl I and II show consistent differences that have puzzled me. Weather conditions were in both periods about the same, and the owls hunted in adjacent areas even showing some overlap (Fig. 8). The observation periods differ by only five weeks and a dramatic change in prey density sufficient to explain the observed "easier hunting" of owl II seems unlikely, since the upswing in vole reproduction takes place much later in the season. A contributory factor may be the difference in requirement between the individuals: owl I was a female with body weight 23% higher than the male owl II. Clearly

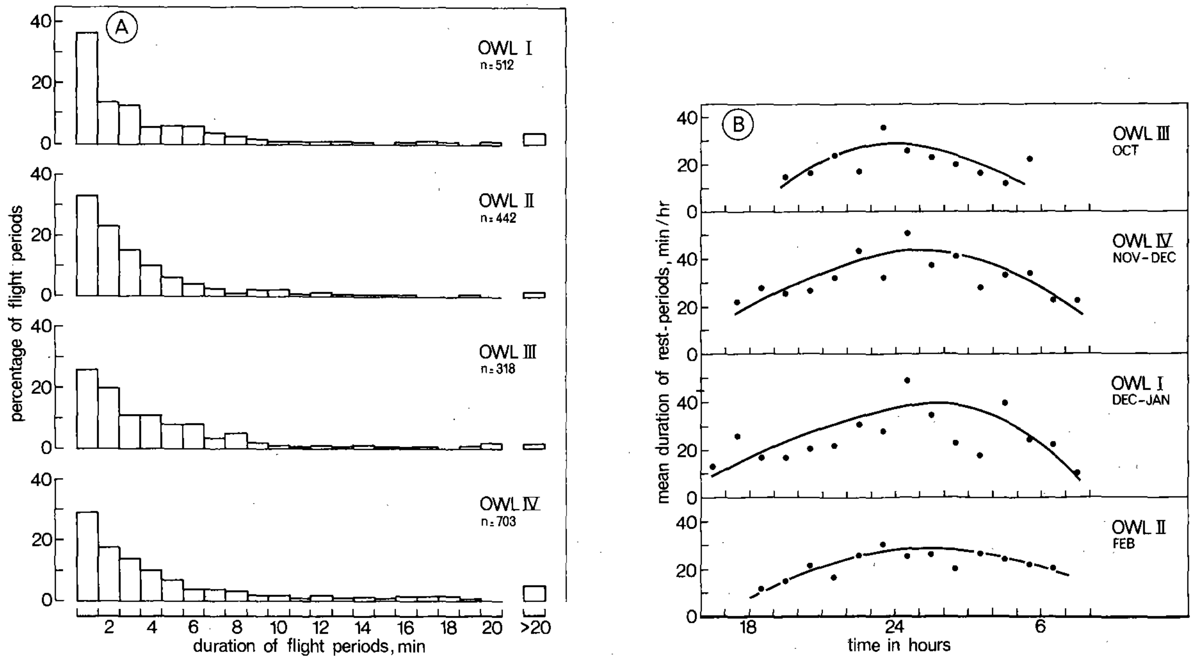


Fig. 46. Frequency distribution of flight bouts (A) and trend in the duration of the resting periods in the course of the night (B) based on radio telemetry data.

this is not the whole answer, and it remains possible that a difference in hunting success is really involved, as individual variation in hunting time and hunting success with about a factor two has been reported in male Kestrels with adjacent hunting grounds (Drent & Daan 1980).

7.4 POWER REQUIREMENT FOR FLIGHT

Calculation of the minimum power required to fly, according to the model proposed by Pennycuick (1972, 1975) requires information on body weight and wing span. The mean body weight for the Long-eared Owl for the period October through March was found to be 290 g (data in chapter 10) as a mean for both sexes. Wing span was taken as 0.95 m (Mebs 1971 and my own measurements). Substituting these values in Pennycuick's equation yields a value of 2.8 W as the minimum power for flight, and on the assumption that avian muscles achieve a mechanical efficiency of 23% (the mean of determinations by Bernstein *et al.* 1973 and Tucker 1972) this minimum power entails an energy expenditure of 39.7 kJ/hr. When expressed in multiples of BMR, this figure works out to 8.3 times BMR for the Long-eared Owl, a relatively low figure when compared to several generalizations (12.1 BMR, Kendeigh *et al.* 1977, 14.9 BMR, Berger & Hart 1974, 17 BMR, Tucker 1974) but it is close to the value determined for the Fish Crow, *Corvus ossifragus*, where flight cost was determined by Bernstein *et al.* (1973) at 8—9 BMR. Recently Dolnik (1982) has presented data on metabolic cost of flight in relation to the mean duration of flight activity per 24 hr. He found species with prolonged flight activity to experience lower costs for flight per hour, and argued against accepting set ratio's of BMR as estimates of flight cost. For the Long-eared Owl, with a mean flight duration of 2.5 hr/24 hr, Dolnik's curve would predict 9.5 BMR as the metabolic cost factor for flight, so we can accept Pennycuick's estimate as being of the right order.

7.5. BALANCING THE BUDGET

Accepting 39.7 kJ/hr as the cost factor for flight in the Long-eared Owl, the median flight cost for the period October—March would be 104 kJ for the 158 flight minutes/24 hr and would comprise 42% of the ME available to the free-living owl according to Table 14. Can we balance the budget on this basis? The simplest way to show this is to calculate how much energy is available for flight. We start with the assumption that our cage trials with captive owls provide a reasonable starting point for metabolic cost by day when the birds are roosting. The ME_{cage} value for 4.1 °C, the mean air temperature of October—March ("winter") was 195.3 kJ per bird per 24 hr. But at night, with many short bursts of flight, and the SDA effect of the meals, there is unlikely to be a separate cost factor for temperature regulation, and I will assume that aside from flight the owl at this time will metabolize at the resting level typical for night (chapter 5). The cost factor for the total 24 hr period, exclusive of the 158 minute flight period, then works out to 148.4 kJ (195.3 kJ total — 34.1 kJ for temperature regulation cost saved by night — 12.8 kJ resting metabolism during the 158 flight minutes). The ME for free-living birds in winter is 252 kJ (Table 14) so 103.6 kJ are available to cover costs in the 158 minute flight period, which results in a value of 39.3 kJ/hr, virtually the same figure as the requirement according to Pennycuick.

A difficulty in accepting the ME_{cage} determination as the empirical basis for assembling the energy expenditure of free-living owls in winter is the question of the comparability of the microclimate experienced by the roosting owls in the field with the cage situation. According to our measurements in the day roosts in the field, wind speed is considerably damped in the roosts, and in general does not surpass 25% of the windspeed measured simultaneously in the open fields nearby. On the other hand solar radiation is also less (59% of the open field values). Hence in winter mean solar radiation in the roosting trees is about 42 J $m^{-2}sec^{-1}$. The two effects, energy loss through the cooling effect of the wind, and energy gain through solar radiation, seem to about balance one another at the roost (Fig. 42: an elevation of SMR by 10% counteracted by a reduction of SMR between 10—17%).

8. REPRODUCTION

8.1 INTRODUCTION

As was already pointed out in the overview in chapter 2, reproduction in the Long-eared Owl is a lengthy process spanning five months (from the courtship phase until the offspring become independent). Classically this period is considered a time of stress for the parents, and indeed there is some evidence that the metabolic working level of the parents while tending nestlings is elevated to some 33—50% above the non-reproductive level (Drent & Daan 1980). It will be my aim here to estimate the costs of three aspects of breeding, namely egg formation, incubation and juvenile growth. The impact these processes have on the energy budget of the parents will be considered in chapter 9.

8.2 METHODS

Nests were inspected once a week, when the eggs were weighed with a spring balance to 0.1 g, and linear dimensions obtained with a caliper to 0.1 mm. Time budget data on incubation was assessed during 63 complete nights of observation; in addition nest-air temperatures were registered during four nights. Thermisters were fixed in position at both the top level of the eggs and at the bottom of the nest-cup, and thus allowed assessment of the gradient of nest air temperature. Extension leads allowed the recorder (Esterline Angus) to be placed up to 40 m from the nest-tree. Internal egg temperature was measured by inserting a small flexible thermister through a small hole drilled through the egg at the air cell and subsequently sealed using dentist's cement. Two Long-eared Owl eggs were prepared in this fashion; additional measurements were taken by substituting Bankiva eggs in the nest, as they are closely similar in dimensions and weight.

The proportion of the egg actually covered by the brood-patch of the female was estimated by introducing a fixed wooden egg into the nest (similar in size and shape to the natural egg) whose surface was completely covered by temperature-sensitive stickers. These stickers were irreversibly altered from white to black when the temperature exceeded 37 °C, and hence the egg when retrieved gave a sector of black corresponding to the part actually covered by the brood-patch (the egg was left in the nest about twenty minutes on three occasions).

Cooling rates were determined by inserting eggs fitted with thermisters in a natural nest of the Long-eared Owl, and effects of clutch size were simulated by adding various numbers of Bankiva eggs. The nest and eggs were placed in a temperature cabinet (maintained at 21 °C) and each cooling trial commenced by warming the eggs to the natural egg temperature (34 °C) by means of a dummy owl with artificial brood-patch through which water could be circulated (surface temperature of the brood-patch 39 °C). When egg temperature had stabilized the dummy owl was removed and cooling of the eggs measured during the subsequent 1.5 hours.

Information on metabolized energy was obtained for five hand-reared owlets following the same procedures employed with the adults (chapter 5). Temperature conditions were held as much as possible in agreement with the natural situation, which meant that the birds experienced outside temperatures from three weeks of age onwards. For measurements of oxygen consumption young of various ages were temporarily brought into the laboratory (generally for the whole day). Body temperature of the owlets was monitored by attaching a thermocouple to the skin under the wing and fixing this in position with tape.

8.3 GONADAL GROWTH AND EGG PRODUCTION

Information on gonadal weight was obtained by dissecting a carcass collection from the Institute for Nature Research (R.I.N.) Arnhem, originating mainly from taxidermists and in most cases killed by traffic. Mean testes weight (combined left and right testis) was outside the reproductive period .013 g (± .006, n = 18) for the Long-eared Owl. Although weight increase started at the close of January — early February no individuals with fully developed testes were represented in the collection. Ricklefs (1974) showed that mature testes weight comprises 1.8% of adult body weight in eight avian species, and taking this value we obtain a figure of 4.7 g for the Long-eared Owl. If gonadal recrudescence comprises 1.5 months and total cost 4.7 × 13.5 = 63.5 kJ, the daily rate would be 1.41 kJ, or only 1.3% of the male BMR. In this calculation the cost factor of 13.5 kJ per gram is chosen in accordance with the equivalent determined empirically (cost per g body weight change) in the ME trials.

Resting ovary weight for the Long-eared Owl averaged .053 g (± .026, n = 25). The highest ovary weight recorded in my material was 5.71 g, and this probably represents the fully developed condition. The most closely comparable data concern the California Quail *Lophortyx californianus* with a resting ovary weight of .06 g and a fully developed ovary of 6 g (Lewin 1963). Oviduct weight was not obtained in my study, but we can estimate it by adopting the value of 5.5 g found for the Quail (Lewin 1963). Mature gonadal tissue in the female Long-eared Owl will thus approximate 11.2 g (5.7 + 5.5). Our data indicate that the weight increase takes place over two months (from early February to mid-April) and will comprise roughly 11.1 g (11.2 g − resting level value). Assuming a cost factor of 13.5 kJ per g growth will require 149.5 kJ or a daily increment of 2.49 kJ, equivalent to 2.1% of the female BMR. If growth is not linear, as assumed in these approximate calculations, but sigmoid, peak values will be higher but of course the total cost does not change.

The energy requirement for egg formation can be deduced from the energy content of the fully formed egg, and the daily requirement depends on the rate of egg growth (Ricklefs 1974). In birds the explosive period of egg growth is relatively short, setting in 3—10 days prior to ovulation depending on egg weight. For two species with egg weight closely similar to the Long-eared Owl, Ricklefs (1974) gives this major growth period as 5 days (Jackdaws) and 7 days (Pigeons). The shortest replacement intervals observed in the Long-eared Owl (loss of clutch until appearance of first egg of replacement) were 8 and 9 days. For the purpose of our computation we will therefore assume a rapid follicular growth phase of 6 days. If we now follow King (1973) in dividing this growth over the six days according to a sigmoidal curve, it can be calculated that the amount of growth per day will proceed according to the following schedule: 2.8%, 16.7%, 30.5%, 30.5%, 16.7% and 2.8%. Growth of the clutch can be assigned a time course by adding the growth increments of individual eggs that are staggered one to another with an inter-egg interval of 1.93 days (± 1.00, n = 61).

Our next problem is to determine fresh egg weight in the species. For 19 eggs volume was determined by water displacement, and was found to depend on linear dimensions by the following formula. Volume (cc) = $1.46 \sqrt{(\text{length} \times \text{breadth})} - 31.10$ where length and breadth are measured in mm (r = .97, n = 19). In eight cases fresh eggs were weighed; in combination with the calculated volume the specific gravity of the fresh Long-eared Owl egg was found to be 1.096 (± .014, n = 8). The volume formula and value for specific gravity allow reconstruction of the fresh egg weight where dimensions are known. This method was preferred to extrapolation based on the daily weight loss of the eggs (.170 g ± .053, n = 26) because only rarely was the age of the egg known accurately enough which is a prerequisite for the method.

Fresh egg weight as calculated for the different years is given in Table 21 and averaged 24.5 g (± 1.86, n = 196). No consistent pattern in relation to the vole cycle could be discerned. Table 22 gives the composition of three Long-eared Owl eggs (determinations in the Ecophysiological Laboratory, Institute of Ecological Research, Arnhem, by courtesy of Dr. J. A. L. Mertens). The standard Long-eared Owl egg of 24.5 g contains 99.7 kJ. The efficiency of energy conversion in egg production is estimated to be 70% (King 1973), hence a single egg will cost in all 142.5 kJ to be produced (to obtain the daily cost this total amount can be divided over the time according to the % schedule presented above). For the most frequently occurring clutches (3 and 4) a peak value for synthesis occurs of 73.3 kJ per day (for 2 and 4 days respectively). This would represent an increment of 63% of female BMR. Employing the growth model of Ricklefs (1974) with a steeply ascending growth rate (the so-called J-curve) the peak value would be 15% higher (for an indentical total clutch cost). The cost of producing the clutch will clearly have repercussions for the energy budget of the free-living pair, whereas the costs of gonadal recrudescence can be classified as minor.

Table 21. Mean fresh weight (8) of the eggs of the Long-eared Owl in the years 1974—1978

	All clutches		4-egg clutches	
	mean ± SD	(n)	mean ± SD	(n)
1974	25.1 ± 2.16	(31)	25.6 ± 1.49	(26)
1975	25.7 ± 1.37	(32)	24.9 ± 0.96	(8)
1976	24.6 ± 1.48	(39)	26.0 ± 1.13	(15)
1977	24.1 ± 1.50	(59)	23.4 ± 0.92	(20)
1978	23.4 ± 2.11	(35)	24.1 ± 0.65	(8)
Combined years	24.5 ± 1.86	(196)	24.9 ± 1.52	(77)

Mean fresh weight in "peak"-years (1974, 1977): 24.4 (n = 90). In other years (1975, 1976, 1978): 24.5 (n = 106).

Table 22. Composition and energy content of the egg of the Long-eared Owl (means for 3 eggs)

Fresh weight	26.5 g =	100%
Shell weight	1.7 g =	6.4%
Water content	20.9 g =	78.9%
Dry matter	3.9 g =	14.7%
fat	1.46 g =	5.5%
protein	2.11 g =	8.0%
carbohydrate	0.10 g =	0.4%
inorganic	0.21 g =	0.8%
Energy content	107.8 kJ entire egg	

8.4. ENERGY COST OF INCUBATION AND BROODING

Heat loss from the eggs in the nest during steady incubation can be estimated by using a modification of Kendeigh's (1963) formula: heat loss (kJ hour^{-1}) = $w_c \times c \times b\,(T_e—T_{na}) \times (1—s)$

where w_c = weight of the clutch (calculated from the fresh egg weight of 24.5 g and the observed rate of weight loss (.17 g day^{-1})

c = specific heat of egg material (3.35 J g^{-1} °C^{-1}, Romanoff & Romanoff 1949, Kashkin 1961)

b = cooling rate of the eggs (for an isolated egg of 25 g determined at 1.57 °C per hour per °C, slightly lower than the 1.73 predicted by Kendeigh *et al.* 1977; for the entire clutch in a natural nest cooling rate varies with clutch size and is 1.06 °C per hour per °C for the modal clutch of four but goes up to 1.27 °C in a clutch of three)

T_e = internal egg temperature (measured at two nests at 35.6 °C (± 1.38, n = 159 readings at 15 min intervals) and 34.1 °C (± 0.70, n = 146). The mean of 34.9 °C will be used in the formula, and is close to previous readings for *Strigiformes* given by Howell 1964 (34.2 °C and 35.5 °C for *Tyto alba* and *Speotyto cunicularia* respectively)

T_{na} = nest-air temperature (independent of ambient temperature at least in the range 8°—20 °C, with a mean value of 27.5 °C which will be used here)

s = surface of the egg covered by the brood-patch and hence not exposed to cooling (readings with the temperature-sensitive strips gave a mean brood-patch coverage of 18.5%, virtually identical to the estimates arrived at by other means for the Herring Gull and Great Tit by Drent (1970) and Mertens (in Kendeigh *et al.* 1977).

Calculations for the heat loss of the Long-eared Owl clutch are collected in Table 23 for the different phases of incubation. Cost for incubation can be arrived at if we include cost of rewarming the clutch following absence from the nest. Observations indicated continuous incubation by day, but during the night the female interrupted incubation on the average 2.8 times (± 2.19, n = 63 nights) for an average absence

Table 23. Estimation of incubation energy (for clutch size 4) according to the method of Kendeigh (1963)

Incubation week	Mean clutch weight (g)	Average heat loss during steady incubation (kJh^{-1})	Additional heat for rewarming the eggs ($kJday^{-1}$)	Total ($kJday^{-1}$)	Heat production embryo's ($kJday^{-1}$)	Metabolic contribution of female ($kJday^{-1}$)
1	55.2	1.18	2.59	27.69 + 2.59 = 30.28	.07	30.21
2	93.6	2.01	4.39	47.14 + 4.39 = 51.56	1.40	50.16
3	88.9	1.90	4.17	44.58 + 4.18 = 48.75	7.20	41.55
4	84.1	1.80	3.95	42.24 + 3.95 = 46.19	21.71	24.48
5	40.5	.87	1.90	20.42 + 1.90 = 22.32	17.40	4.92

of 11.5 minutes (± 10.99, n = 126) as can be seen from Fig. 47. This will mean that the female is away 31.9 minutes per 24 hrs (resulting in an attentiveness figure of 97.7% for the entire 24-hr period). During these absences internal egg temperature will fall by about 5 °C (ambient temperature 6.5 °C and a cooling rate of 1.06 °C per hour per °C gradient) and this heat must be replaced before steady incubation conditions as given in the formula will apply (Kendeigh *et al.* 1977). As can be seen in the Table, rewarming comprises about 10% of total heat requirement for incubation. Only a part of the total needs be provided by the female owl, as the growing embryos will contribute heat as well. The embryonic contribution was estimated by combining the formula of Vleck *et al.* (1979) predicting oxygen consumption of avian embryos on the basis of the yolk-free mass, with a formula developed by Mertens (pers. comm.) giving yolk-free mass at specific ages for avian embryos in general. On the basis of this computation (Table 23) the female owl faces the heaviest energy drain in the second week when incubation demands an increment of 43% of BMR; the mean value is 26% of female BMR (close to the few empirical estimates available for cost of incubation, Biebach, Drent & Haftorn, in press).

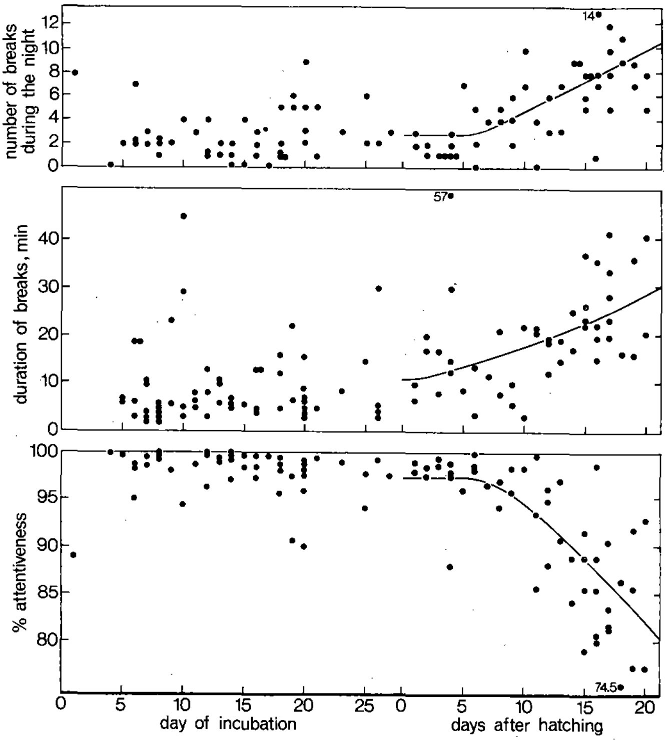


Fig. 47. Activity records at the nest of the Long-eared Owl during incubation (28 days) and the subsequent nestling period (21 days) showing (top to bottom) number of breaks (= absence of the female), their duration, and % attentiveness (= % of total time female on nest per 24 hr). Each dot represents a night of observation at one nest.

After hatching the female has to brood the young for at least 14 days before the owlets are able to maintain body temperature on their own. Kendeigh *et al.* (1977) developed a predictive formula for brooding cost, adapting Mertens (1972) model of heat loss of the avian brood, as follows:

M (brooding cost, kJ day^{-1}) = $.301\,W^{.613}\,(T_b—T_a)$

where W = weight of brood in g
T_b = body temperature of young
T_a = ambient temperature

For a brood of three, values for the first week will be 91.2 brood weight in g (W) maintained at a temperature gradient of 26 °C ($T_b = 39°$, $T_a = 13$ °C). The second week, with the same temperature gradient, the brood weight has increased to 271 g. The total cost works out at 124.5 kJ per day for the first week and 242.7 kJ for the second, and by subtracting the heat production of the owlets (35.5 kJ per day in the first week and 165.4 kJ in the second) we then obtain an estimate for the cost that must be borne by the female, of 89 kJ per day in the first week and 77 kJ per day in the second. Couched in terms of BMR, these values represent increments of the female BMR of 76% and 66% respectively.

8.5. GROWTH OF THE OWLETS

Hatchlings of the Long-eared Owl are covered with a white protoptile down, the skin a pink shimmer through the down. The closed eyelids are opened on about day 5, and the egg-tooth disappears in the period 5—7 days. During the second week the mesoptile down begins to develop, starting on the back and upper surface of the wings, and ending on the head; in the same week the remiges start to develop. By the third week the mesoptile down has completely replaced the protoptile predecesser, and the vanes of the remiges start to appear. The remiges and greater primary coverts that also make an appearance will not be replaced until a year later.

In general nestlings leave the nest at an age of 21—23 days, long before they are able to fly. Mostly they remain perched high up in the canopy, and if disturbed climb with the aid of the bill, legs and wings. During the fourth week the mesoptile down starts to disappear, and rapid growth of wing and tail feathers sets in. A brownish white margin appears on the facial disk. The owlets engage in short descending flights at an age of 30—35 days.

During the fifth and sixth weeks replacement of the mesoptile down continues but it is still clearly visible on head, neck, belly and legs and on the ventral wing surface. The facial disk undergoes change and the ear plumets are replaced (fully grown by 2½ months). By the end of week 8 mesoptile down can only be found on head and legs, and all flight feathers are fully grown. It is not known when the young become completely independent of the parents, but I have observed food begging up to 2 months after hatching.

Mean weight of the hatchlings is 17.4 g (Appendix 2), and by day 20—21 when the owlets leave the nest body weight is about 219 g, after which it increases slowly to an asymptote of 248 g (Fig. 48). Beyond day 35 I was unable to obtain body weights, and when the gap to adult weight (males 270 g, females 310 g as weighed in early winter) is bridged is uncertain. Sutter (in Glutz & Bauer 1980) has indicated that there still may be a weight differential between juveniles and adults in early winter.

Employing the graphical method of Ricklefs (1967a) a general equation was fitted to my Longeared Owl growth curve. Growth was adequately described by the logistic equation where body mass at age t in g is given by:

$$BW(g) = \frac{A}{1+e^{-k(t-t_i)}}$$

where A = asymptotic weight (248 g)
K = growth constant (.225)
t = age in days for which the body mass is sought
t_i = inflection point of the growth curve (11.0 days)

The time required to grow from 10% to 90% of asymptotic weight ($t_{10—90}$ in Ricklefs' notation) was 19.5 days. The fitted curve is depicted in Fig. 48, and fits the observed course of body weight closely. This fitted curve will allow us to make comparisons with other *Strigiformes* (see discussion).

For a number of linear dimensions (tarsus

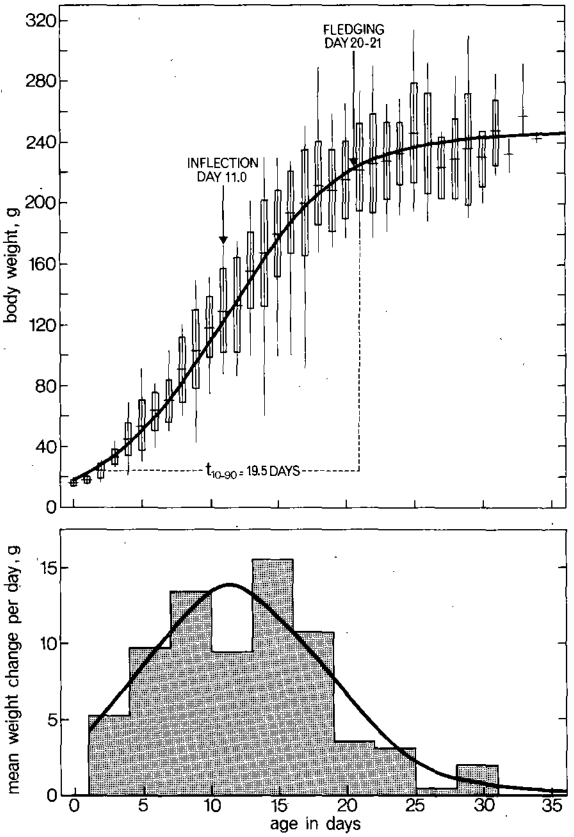


Fig. 48. Growth of young in the Long-eared Owl. Top graph: field data (means ± 1 SD and range) on body weight in relation to age (top) including the smoothed logistic curve, and the time period required to achieve the central 80 % of growth ($t_{10\text{-}90}$). Bottom graph: mean weight increments in g (3-day means and smoothed curve).

length, wing chord, length of primary IX, primary X, secondary X and the middle rectrix) fitted curves (in this case the Gompertz equation, see Ricklefs 1967a) are presented in Fig. 49. Another measure of feather growth is total feather weight, and data on this point are assembled in Fig. 50: the body feathers commence growth sooner, but are outstripped by the flight feathers that reach 75% of final weight by 32 days.

8.6. CHANGES IN BODY COMPOSITION WITH AGE

Changes in body composition and energy content of the growing Long-eared Owl are depicted in Fig. 51 and Fig. 52. Water content drops from 85% of body weight at hatching to 68% on day 30—32. Mean adult water content

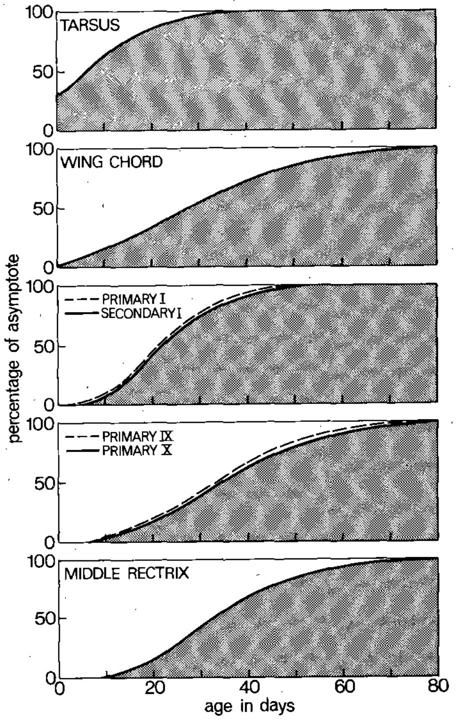


Fig. 49. Linear growth of tarsus wing chord and various feathers expressed as percentage of asymptote achieved at a given age (smoothed curves see text).

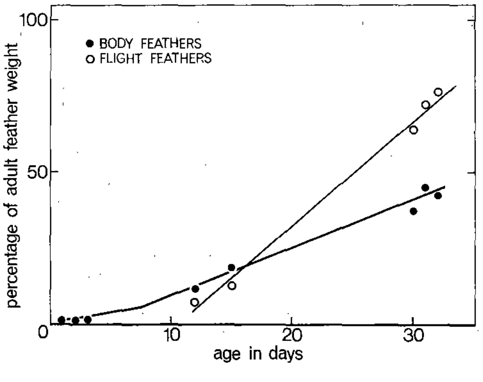


Fig. 50. Plumage growth as measured by total weight of body feathers and flight feathers, expressed as percentage of adult weight achieved at a given age.

is about 61%. This range and rate of change with growth is similar to that in other altricial birds (Ricklefs 1967, 1974, Brisbin 1969, Westerterp 1973, Dunn 1975a). Change in energy content with age (Fig. 51) is largely due to decreasing water content, resulting in a linear increase in energy content with age (reaching

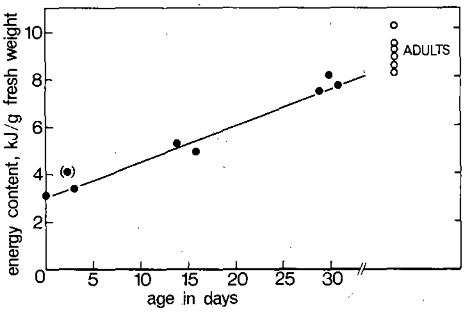


Fig. 51. Energy content of the growing Long-eared Owl (open circles show adult values) in relation to age. The line has been used to estimate values at intermediate ages (formula: y = .151 x + 2.97). Point between brackets includes yolk-sac.

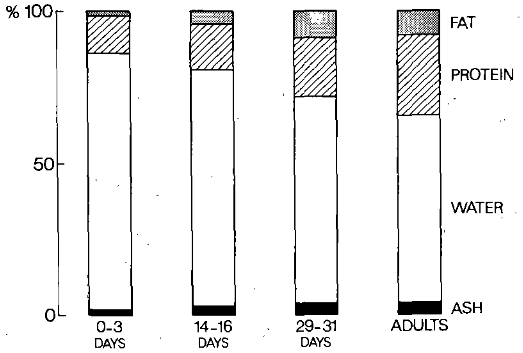


Fig. 52. Changes in body composition (% of fresh weight) with age in the Long-eared Owl.

85% of the adult mean value of 9.13 kJ by day 30—32).

If the assumption is made that ash-free dry matter is composed solely of fat and protein, then the proportion of these components in the total can be reconstructed (the total weight is known, and the caloric value of fat can be taken as 37.68 kJ per g, that for protein as 23.02 kJ per g). These figures are given in Fig. 52, and show that by about day 30 fat content has reached the adult value, as has the mean energy content per g lean dry weight (19.8 kJ). These values are close to those given for other altricial birds (Myrcha & Pinowski 1970, Dunn 1975b).

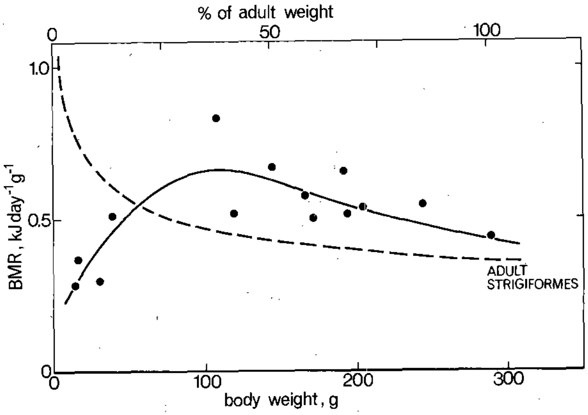


Fig. 53. Basal Metabolic Rate (BMR) in 8 nestling Long-eared Owls in relation to body weight. For comparison the expectation for adult *Strigiformes* is entered (see chapter 9).

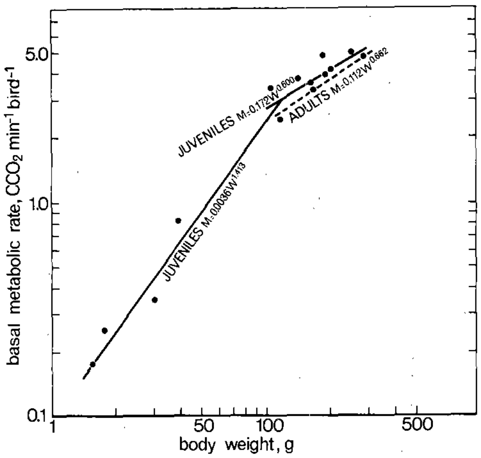


Fig. 54. BMR in relation to body weight in growing Long-eared Owls (double logaritmic plot) described by two equations (transition at aproximately 120 g body weight). The prediction for adult Long-eared Owls is also shown (note congruence in weight exponent when compared to older juveniles).

8.7. BASAL METABOLIC RATE AND TEMPERATURE REGULATION IN THE OWLETS

Measurements of oxygen consumption of young owls at 30—35 °C (within the thermoneutral zone) are given in Fig. 53, converted to energy consumption per unit body weight assuming 1 l O_2 = 19.7 kJ (RQ = 0.72). Compared to BMR levels typical for adult *Strigiformes* (broken line in Fig. 52) it will be seen that at a body weight of 120 g the rate of metabolism per g body weight peaks about 55% above the adult level, to decline slowly towards the expected value after that. Body temperature in nestlings ranges from 39.6 to 42.0 °C (mean 40.6, n = 6) and is also slightly higher than adult levels. The

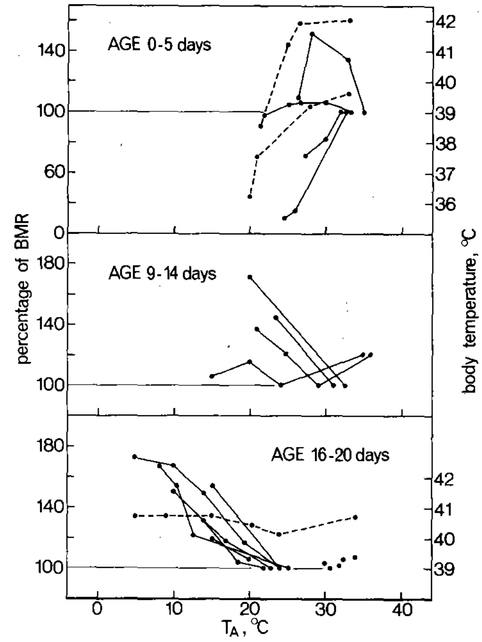


Fig. 55. Development of temperature regulation in the Long-eared Owl. Metabolic response to declining ambient temperature is shown in relation to BMR (percentage ordinate). In some cases registrations of body temperature are included (dotted lines, scale at right). A consistent thermogenic response is not shown in the first five days of nestling life. (BMR dots on bottom panel for temperature > 30 °C are not connected by lines for clarity).

pattern of change of BMR with age is closely similar to the pattern sketched as intermediate between altricial and precocial birds by Ricklefs (1974), in that the peak occurs relatively earlier than in typical altricial species. Another way of looking at these rate changes is to present overall metabolism in a double logarithmic plot (Fig. 54), and here the discontinuity apparent at the metabolic peak (approximately 120 g body weight) shows up clearly as a point where the exponent relating metabolism to body weight changes.

Progressive improvement in thermoregulation is indicated by the few trials conducted (Fig. 55) with rapid improvement especially in the period 9—14 days. From about 16 days the LCT lies at about 23 °C and juveniles show a somewhat steeper slope of metabolic response to declining temperature when compared to adult owls.

8.8. EFFICIENCY OF DIGESTION AND METABOLIZED ENERGY IN THE OWLETS

Metabolizable energy coefficient (MEC) is highest during the first few days after hatching and decreases gradually until it stabilizes around 78.5% by about week four (Fig. 56), the same

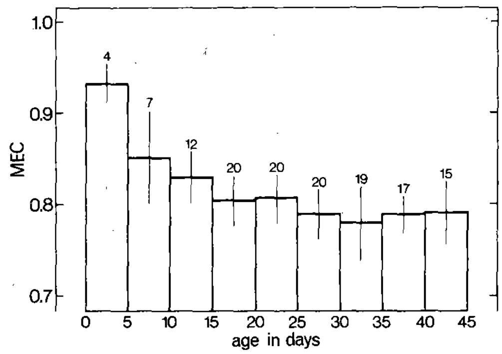


Fig. 56. Metabolizable Energy Coefficient (MEC) in relation to age (means ± 1 SD, sample sizes indicated) for a diet of laboratory mouse. The extremely high value in the first period is due partly to the fact that pellet production does not commence until after day 5.

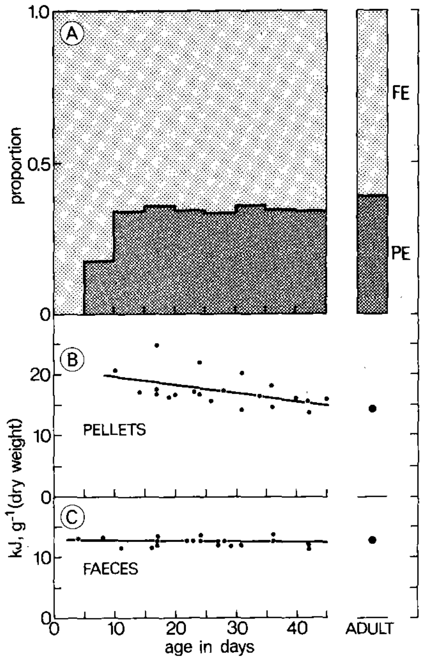


Fig. 57. Rejecta in the Long-eared Owl: (A) proportion of waste (in terms of energy) excreted in faeces (FE) and in the pellets (PE) and caloric content of pellets (B) and faeces (C) per g dry weight, in relation to age.

value that holds for adults at that period of the year (June—July). Pellet production sets in around day 8—9, and shortly after that time the proportion of the energy voided as pellets and as faeces stabilizes around values close to those of the adult (Fig. 57: 35% in pellets, the rest in the faeces, as compared to 40% in the pellets in adults).

Some interesting changes in the composition of the pellets occur with age (Fig. 57). Ash content (as % of the dry matter) increases significantly with age (which means that the caloric value declines). A hypothetical meal of 100 g dry weight (laboratory mouse) will contain 10.9 g ash. For adults this results in 30.7 g faeces (containing 3.2 g ash) and 17.2 g pellets (with 6.6 g ash) with a total ash output of 9.8 g. For a 20-day juvenile these values will be 26.1 g faeces (with 4.5 g ash) and 9.3 g pellets (with 2.7 g ash) for a total of only 7.2 g ash; the greater part has been retained. These figures probably reflect the higher intake of calcium, phosphate and other building materials necessary for the growing skeleton of the juveniles.

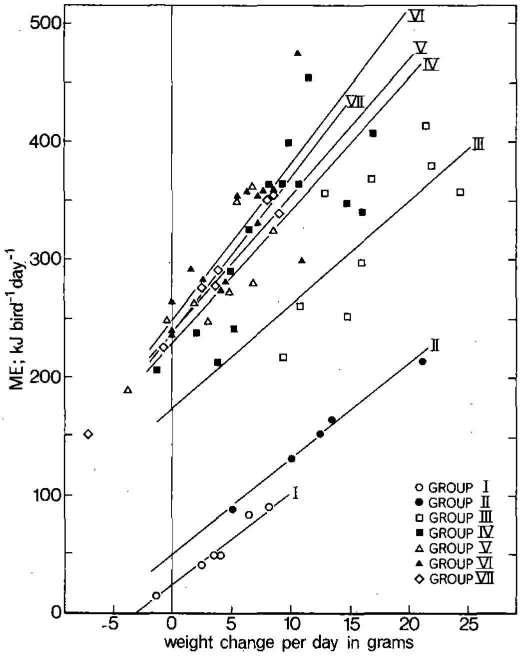


Fig. 58. Metabolized Energy (ME) in cage trials with growing Long-eared Owls (weight range and age of each group in Table 24) in relation to change in body weight. The lines of regression are shown and allow extrapolation to conditions of zero growth ("maintenance energy"). The slope gives the cost factor of weight change.

The data on metabolized energy are analyzed in Fig. 58, Table 24, showing ME per bird per day in relation to the weight change experienced. Linear extrapolation yields the energy requirement for maintenance without growth, which although an artificial concept in a growing bird allows comparison of the metabolic intensity with similar trials carried out on the adult birds (chapter 5). In fact, throughout nestling life the ME for zero growth ("existence metabolism" is the corresponding concept for adult ME) corresponds to a level of about twice BMR as measured at that age. More importantly, the slope of the linear regressions yields the cost factor, i.e. the energetic cost to produce weight gain. The slope increases with age, i.e. the cost of adding 1 g body weight increases from 7.9 kJ for owlets of about 30 g body weight to 13.1 kJ per g for juveniles of 280 g body weight. The latter value is close to the cost factor deduced from the ME trials with adults (13.5 kJ). As we have seen, the caloric content of one g body tissue is not constant, but increases with age, about doubling in the first five weeks of life hence this result is not unexpected. The data in Fig. 58 allow the reconstruction of the food requirement for owls at various ages to achieve

Table 24. Regression analysis of ME trials with nestlings

Groups	Mean body weight and age	Number of 1-day trials	ME$_0$ growth (kJ bird^{-1}day^{-1})	Cost of 1 g weight gain (kJ)	r
I	28 g (2 days)	n = 6	22.7	7.90	r = .99
II	81 g (8 days)	n = 5	49.4	8.15	r = .99
III	177 g (15 days)	n = 9	174.1	8.76	r = .74
IV	230 g (22 days)	n = 14	229.5	11.17	r = .80
V	254 g (30 days)	n = 9	239.4	11.48	r = .83
VI	279 g > 30	n = 15	248.0	13.13	r = .77
VII	301 g > 30	n = 8	241.2	12.91	r = .99

the growth rate typical for their age. Growth will be explained in the following section.

8.9. AN ENERGY BUDGET FOR GROWTH

It will be my aim here to integrate the growth data given in this chapter to obtain a general model of energy expenditure for the first 35 days of life. Data for BMR and for the ME at constant weight (ME extrapolated for zero growth) can be described by logistic equations fitted as was the equation for weight gain (Ricklefs 1967a):

$$\mathrm{BMR}\ (\mathrm{kJ\ bird^{-1}\ day^{-1}}) = \frac{132}{1 + e^{-0.291\,(t-10.8)}}$$

$$\mathrm{ME}_{\mathrm{O\ growth}}\ (\mathrm{kJ\ bird^{-1}\ day^{-1}}) = \frac{240}{1 + e^{-0.270\,(t-11.3)}}$$

In these equations t is age in days. Costs for growth were calculated by taking observed weight gain in the field data and multiplying this by the cost factor obtained from the ME trials with captive owls (given in Fig. 58). A slight additional cost of temperature regulation must be added. For the nestling period the data on parental absence (Fig. 47) when taken with the data on repercussions on the metabolic rate (Fig. 55) allow estimation of the additional cost of temperature regulation as a rising function starting at 1.5 kJ on day 10 to 7.7 kJ on day 20. After nest-leaving costs can be obtained from Fig. 55 directly, bearing in mind that the mean air temperature for June is 14.5 °C in my study area.

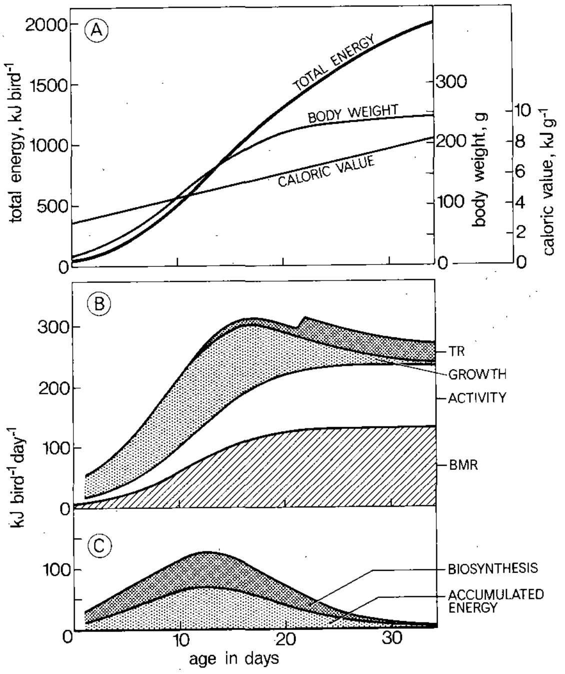


Fig. 59. Idealized energy budget for growth in the Long-eared Owl in relation to age (data in Appendix 3). Body weight and caloric content provide total energy incorporated during growth (A) while the components of energy expenditure are shown in (B) adding together to give the daily energy requirement to achieve normal growth; the growth component is replotted in (C) subdivided in the caloric increment ("accumulated energy") and the cost of biosynthesis.

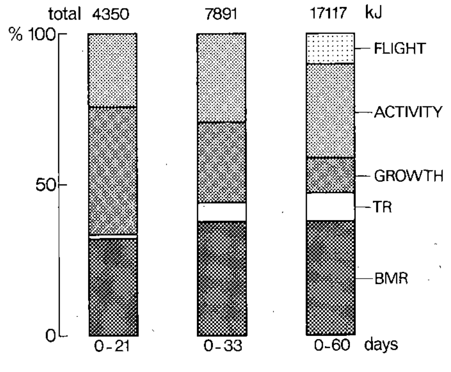


Fig. 60. Cumulative plots of energy expended on Basal Metabolic Rate (BMR), temperature regulation (TR), growth (including cost of biosynthesis), activity in the nest and flight, expressed on a percentage scale. Total energy per young given at top of bar. Day 0—21 is the period in the nest, day 0—33 is the period up to first flight and day 0—60 is the period up to independence.

We are now in a position to assemble the various costs. For each day of life, the cost of growth (increment × cost factor) is added to the ME for zero growth to obtain the "total ME" (see Appendix 3 where the values from the equations for growth and ME are entered for each day). To this must be added the "temperature regulation" cost to obtain total daily energy requirement. This total requirement can be subdivided into the inevitable BMR (by taking the smoothed values given by the logistic equation presented above, also entered in the Appendix) and the difference between BMR and ME for zero growth must represent the cost of activity. Fig. 59 presents the smoothed data, and Fig. 59B shows my estimate for the net energy requirement of the individual Long-eared Owl nestling up to day 35. It will be noted that the requirement increases steadily up until day 17 and remains at what may be termed a plateau value of some 300 kJ bird^{-1} day^{-1} thereafter. This ME figure can be translated into a food requirement with the aid of the conversion data given in Fig. 56. The cumulative energy allocation is clarified in Fig. 60 (for the period in the nest, for the period up to the first flight, and finally for the first 60 days of life respectively).

8.10 DISCUSSION

The calculations presented above for arriving at the cost of egg production conform to a method now widely employed, but nevertheless merit a word of caution. To begin with, the exact shape of the growth curve is not known and adoption of the asymmetrical pattern advocated by Ricklefs (1974) for example would increase cost by approximately 15%. On the other hand, Kendeigh *et al.* (1977) pointed out that at air temperatures below the lower critical temperature (LCT) a part of the energy calculated as cost of biosynthesis may contribute towards maintaining body temperature. Hence the cost of egg production according to the formula would be an overestimate. Despite these uncertainties in the exact cost of egg production (our computations gave 570 kJ for the entire clutch at a daily rate peaking at 73.3 kJ for a duration of four days, an increment equivalent to 61% BMR) there can be no doubt that this phase in reproduction is a major event in the energy budget of the female. According to the summary prepared by King (1973) the magnitude of the energy drain in the Long-eared Owl is comparable to that in gallinaceous birds which experience higher cost levels than passerines but do not reach the extremes posed by ducks and geese.

The figures presented for cost of incubation (following the formula devised by Kendeigh 1963) must also be regarded as tentative. Vleck (1981) recently compared the Kendeigh prediction with direct metabolic measurements of incubation cost (achieved by measuring oxygen consumption of incubating Zebra Finches, *Taeniopygia castanotis*). Vleck could confirm that incubation incurs an additional energetic demand as had previously been demonstrated by Biebach (1979) who presented empirical assessment of incubation cost in the Starling, *Sturnus vulgaris*. Although the mean levels as determined in Vleck's study were close to the Kendeigh prediction, the formula tended to overestimate incubation cost at moderate temperatures and underestimate cost at higher temperatures. Extending these findings to the Long-eared Owl, the Kendeigh prediction we have implemented may overestimate cost by as much as one-third (our estimate of an added cost equivalent to 26% BMR may thus require revision in the direction of 17%).

Turning now to the quantification of growth requirements for the growing brood, there are several ways in which our data can be compared to previous studies. Ricklefs (1968) showed that

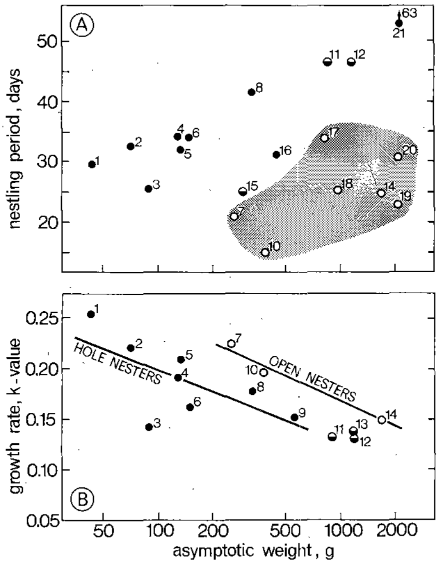


Fig. 61. Growth rate and nestling period in relation to asymptotic body weight in the *Strigiformes*: length of the nestling period (A) and growth rate K from the logistic curve fitted to field data (B). Species are identified and data sources given in Table 25. Open nesters (circles) have higher growth rates and leave the nest earlier than hole nesters (dots) at the same body weight.
Data for the duration of the nestling period (Glutz & Bauer, 1980) not mentioned in Table 25 are:

	Adult weight g	Nestling period days	Nest
Surnia ulula (15)	295	25	open/hole
Strix aluco (16)	450	31	hole
Strix uralensis (17)	810	34	open
Strix nebulosa (18)	990	25	open
Bubo bubo (19)	2050	23	ground
Bubo bubo (20)	2050	31	tree
Bubo bubo (21)	2050	63	cave

Table 25. Growth parameters for Strigiformes as derived from data of varions authors

Species	Adult weight (g)	A symptote (g)	K*	t_{10}-t_{90} (days)	Nestling period (days)	Nest**	Authority
1. *Micrathene whitneyi*	55	43	.252	17.5	29	H	Ligon 1968
2. *Glaucidium passerinum*	66	72	.221	19.9	32	H	Glutz & Bauer 1980
3. *Otus scops*	90	90	.141	31.2	25	H	Glutz & Bauer 1980
4. *Otus asio*	150	130	.190	23.2	34	H	Sumner in Ricklefs 1968
5. *Aegolius funereus*	120	135	.209	21.1	31	H	Klaus *et al.* 1975
6. *Athena noctua*	190	155	.160	27.5	34	H	Glutz & Bauer 1980
7. *Asio otus*	290	248	.225	19.5	22	O	this study
8. *Tyto alba*	314	330	.175	25.1	42	H	de Jong, pers. comm.
9. *Tyto alba*	408	570	.152	29.0	—	H	Sumner & Pickwell in Ricklefs 1968
10. *Asio flammeus*	347	380	.194	22.7	15	O	Hagen 1952, Daan pers. comm.
11. *Bubo virginianus* (male)	—	900	.133	33.1	47	O/H	Turner *et al.* 1981
12. *Bubo virginianus* (female)	—	1200	.131	33.6	47	O/H	Turner *et al.* 1981
13. *Bubo virginianus*	1175	1200	.138	32.9	—	O/H	Hoffmeister & Setzer in Ricklefs 1968
14. *Nyctea scandiaca*	1730 (♂) 2120 (♀)	1700	.149	30.7	25	O	Watson in Ricklefs 1968

*) K = growth constant calculated for the logistic equation
**) O = open nest, H = hole nest

the growth rate in altricial landbirds (data on 55 species including *Falconiformes* and *Strigiformes* were available for analysis at that time) could be closely predicted from the asymptotic weight achieved (larger birds growing more slowly). The value for the growth rate K derived from the logistic equation for my field data on the Long-eared Owl was 0.225, close to the predicted value of 0.239. Since the pioneering study of Ricklefs more data have become available for the Strigiformes, and I have plotted data for 14 species in Fig. 61 (the data sources are listed in Table 25). When open-nesting forms are treated separately from hole-nesters an interesting difference emerges. Open nesters achieve higher growth rates (and tend to leave the nest earlier, as shown in the upper panel of Fig. 61). Following Lack (1954) and Nice (1957) it can be argued that birds nesting in exposed locations tend to shorten the nestling period to minimize the risk of predation. The Long-eared Owl leaves the nest at 21 days, whereas the value expected on the basis of asymptotic body weight is approximately 33 days. Interestingly, this is the age at which first flight occurs in this species.

Summarizing, the Long-eared Owl is known to leave the nest prematurely, before the young owlets are capable of flight, and if we are to compare our data with other species the comparative analysis with hole-nesting owls indicates that a nestling period of 33 days would be the expected "fledging period". For this reason figures for both the first 21 days (the period actually spent in the nest) and the first 33 days (the period to first flight) are of particular interest.

In its simplest form the energy budget for growth entails the components of the total metabolized energy (ME) as follows:

$$ME = BMR + A + TR + G$$

where BMR = Basal Metabolic Range
A = Activity
TR = Cost of Temperature Regulation
G = Growth (both the caloric increment of growth and the cost of biosynthesis)

Unfortunately in most studies the cost of biosynthesis has not been assessed. To make my figures comparable I must therefore restrict myself to discussing the caloric increment of growth (the difference in caloric content with age).

Recently Dolnik & Yablonkevich (1982) have presented a growth budget for the Chaffinch, *Fringilla coelebs* derived from the same technique as in my study. When the two budgets are compared (Table 26) broad similarities are apparent. Perhaps the most unequivocal basis for

Table 26. Energy budget for a nestling Chaffinch (Dolnik & Yablonkevich (1982) and a Long-eared Owl

	Chaffinch (0—13 days)	Long-eared Owl (0—33 days)
Metabolized Energy	485 kJ	7891 kJ
Growth	80 kJ (16.6%)	1912 kJ (24.2%)
Activity	118 kJ (24.3%)	2482 kJ (31.5%)
Temperature Regulation	39 kJ (5.9%)	516 kJ (6.5%)
Basal Metabolic Rate	258 kJ (53.3%)	2981 kJ (37.8%)

Table 27. Allocation of energy to growth (caloric increment only) in nidicolous birds, expressed as percentage of total ME throughout the nestling period

Species	%	Authority
Phalacrocorax auritus	28	Dunn 1975a, 1975b
Mycteria americana	19	Kahl 1962
Larus canus	25	Kahru in press
Sterna hirundo	21	Ricklefs & White 1981
Sterna fuscata	24	Ricklefs & White 1981
Asio otus	24	this study (33 days)
Lanius collurio	29	Diehl & Myrcha 1973
Sturnus vulgaris	26	Westerterp 1973
Passer montanus	22	Myrcha *et al.* 1973
Passer domesticus	25	Myrcha *et al.* 1973
Passer domesticus	23	Blem 1975
Fringilla coelebs	17	Dolnik & Yablonkevich 1982

comparison entails the proportion of the nestling ME that is incorporated in the body (as proportion of ME). Table 27 provides an overview of this statistic in nidicolous birds (birds fed at the nest site by their parents). It will be noted that in most species approximately one quarter of the ME is incorporated in the tissues of the growing nestling, and our value for the Long-eared Owl conforms to this pattern.

This generalized statistic on energy allocation does not inform us on the efficiency of growth. My approach to this problem was to compute the slope of the ME trials in relation to weight change (Fig. 58). For the nestling period in the strict sense (21 days) enough trials are available to allow estimation of overall efficiency. According to my data the caloric increment of growth over the first 21 days is 1343 kJ (the difference between the caloric content of the hatchling and the nestling at 21 days) whereas the total cost of this growth according to the ME trials amounted to 1846 kJ (appendix 3). On this basis the overall efficiency of growth is 72.8%. This is a notoriously difficult parameter to estimate accurately, but in the literature the efficiency of protein synthesis is estimated to lie between 34 and 85% (Buttery & Boorman 1976, Kielanowski 1976) and for fat between 63 and 83% (Buttery & Boorman 1976). Our figure (for a mixture of fat and protein, see Fig. 52) is at least within this range. Ricklefs & White (1981) assume an overall figure of 67% in their calculations.

Dunn (1980) has recently provided an overview of energy allocation in nestling birds, based on conversion of the various studies in terms of BMR. There are some difficulties in this approach at very early ages, as BMR may not be well defined then (without a recognizable thermoneutral zone it is a moot point if BMR can be satisfactorily defined). My data when given in these terms (Fig. 62) must be interpreted against the background that BMR is not strictly measurable until approximately day 8 (Fig. 55). My tentative conclusion would be that ME is maximally approximately 4 BMR, and is thus comparable to peak values expressed as multiples of BMR in other species (Dunn 1980). Secondly in my data (from day 8 onwards) growth absorbs maximally 2½ BMR, again in line with maxima derived in other birds (Dunn 1980).

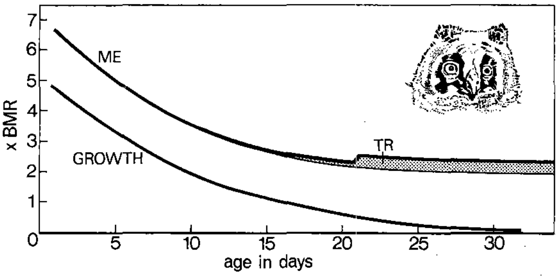


Fig. 62. Energy devoted to growth (estimated by mutiplying weight increments by cost factors, i.e. including cost of biosynthesis) and total Metabolized Energy (ME) and temperature regulation (TR) in relation to age, plotted as multiples of BMR as advocated by Dunn (1980).

9. PARENTAL ENERGETICS AND THE ANNUAL CYCLE OF BODY WEIGHT

9.1. INTRODUCTION

Now that food requirement of the growing nestlings has been quantified, the logical next step is to partition the incoming prey (the male is the sole hunter during the first 21 days of nestling life) among the nestlings and the female, and to explore the impact of the hunting activities on the energy requirement of the male. Before this computation can be done in the form of an energy budget we need to know the changes undergone in parental body weight during breeding, and it will be convenient to present all weight data at this point (9.2.). The next step is to explore what the energetic implications of these changes in body weight might be, by computing the expected cost of flight for the range of body weights actually found (9.3.). A partial integration with field data is then within reach, since we know the total food input to the nest on the basis of observation coupled with a weighing platform (9.4.) and can proceed to construct provisional energy budgets for the parents (9.5.).

9.2. ANNUAL CYCLE OF BODY WEIGHT

Data sources

Aside from parental weights obtained during the nestling period with the aid of the weighing platform (see p. 64) the field data comprise body weights (and wing lengths measurements) obtained when owls were captured (using mistnets and bal-chatris, p. 4). During my study we caught 196 individuals, and weights on an additional 117 Long-eared Owls were provided by S. Braaksma, J. Buker and F. Koning for other localities in the Netherlands and Dr. F. Goethe supplied weights for 59 migrants caught on passage on Helgoland (March—April) and October—November). The majority of the birds were caught during winter, generally around sunset (four individuals were trapped on the nest), and were weighed to the nearest 10 g using spring balances. In my data the sexes were distinguished on the basis of plumage characters. By examining traffic victims (in all of which sex was determined by dissection) I found that almost all individuals could be assigned to sex on the basis of the colour of the ventral feathers. In males the underside of the wing is sallow white whereas females have a much more ruddy colouring. In males the breast and legs are sallow brown, with brownish grey spots; whereas females have a more ruddy brown colouring on breast and legs, with highly contrast-

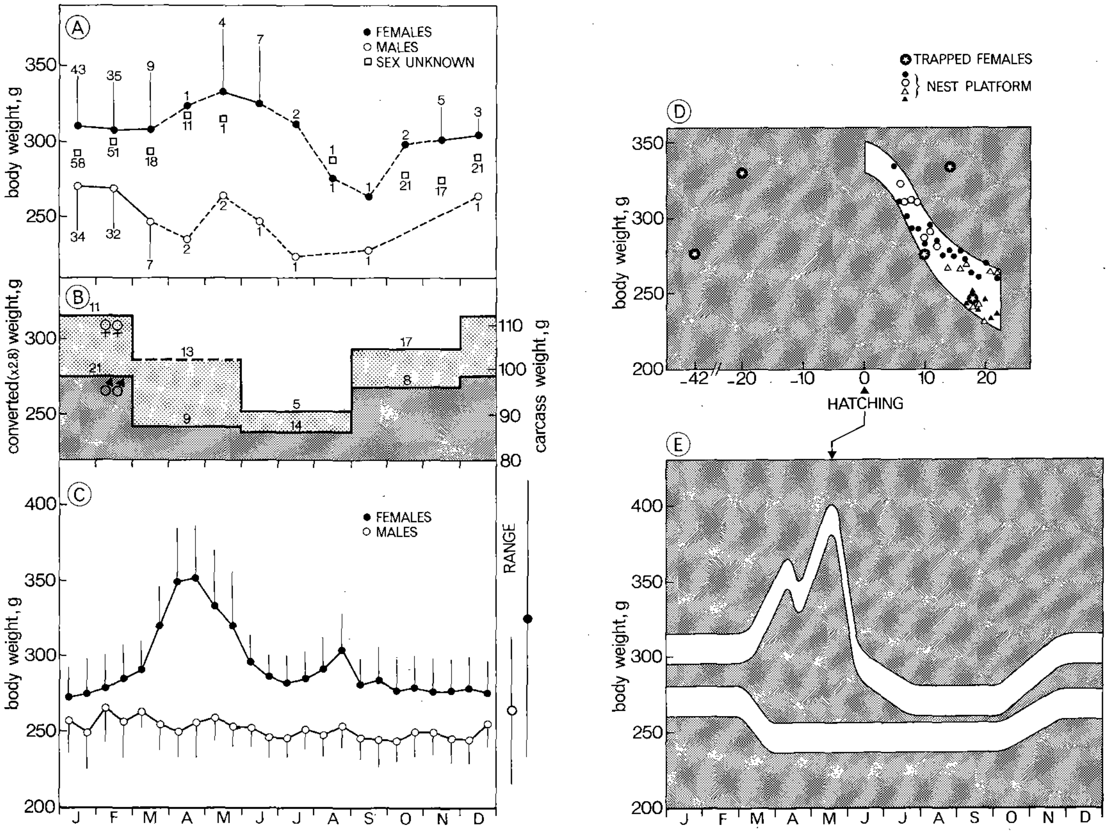


Fig. 63. Annual cycle of body weight in adult Long-eared Owls as determined from birds trapped in the field (A), carcass weights of birds killed by traffic (B), 14 captive owls held in outdoor aviaries (C), females trapped at the nest or weighed on the nest by means of the platform shown in Fig. 67 (D) and finally a generalized diagram showing probable annual cycle as distilled from these various sources (E). Means, sample sizes, and ± 1 SD are given where appropriate (given in only one direction for clarity).

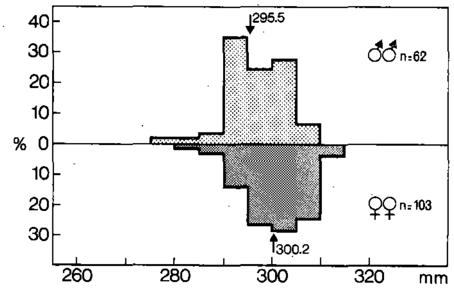


Fig. 64. Percentage distribution of wing lenth (flattened chord) for male (top) and female (bottom) Long-eared Owls in the study area. Means are indicated (for sexing technique see text).

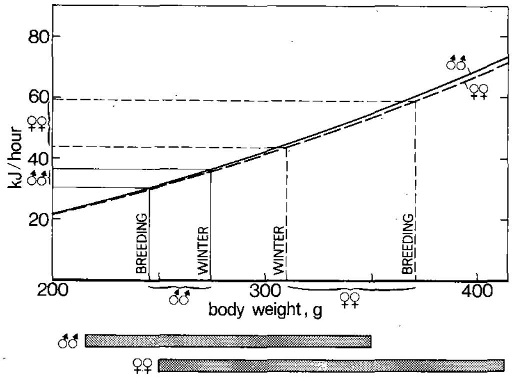
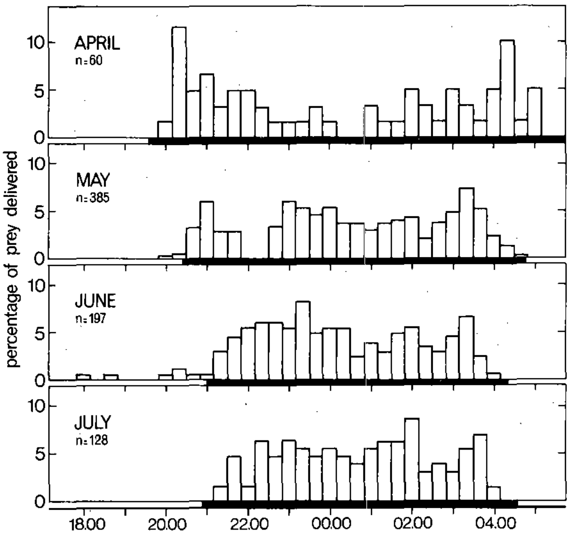


Fig. 65. Flight cost in Long-eared Owls as predicted by the Pennycuick formula in dependence on body weight (abscissa) and wingspan (note slight difference in cost line for the sexes). Expected values in winter and during breeding are indicated, derived from the mean weights found in Fig. 63 (measured range in body weight shown by blocs along bottom).

ing blackish brown spots. As a check on the reliability of this difference (which does not seem to have been described before, Glutz & Bauer 1980) 133 museum skins were examined and sexed on the basis of this plumage colour difference. Two observers (the author and J. Doevendans who regularly assisted in trapping) each sexed the skins, and each found (the same) 7 discrepancies between their classification and the information on the label. Thus in 95% of the cases the plumage characters were proven reliable, and it can be assumed that but few errors were made in the field.

Aside from these field data, the captive owls were weighed regularly throughout the year and the data have been analysed in forthnightly periods (here again sex was assigned according to plumage characters and in some cases confirmed by testosteron assay).

Finally a total of 97 carcasses were sexed and weighed, originating from taxidermists and hence without skin, head, of appendages. These data can be compared to intact owls by employing the conversion factor 2.8 (carcass weight × 2.8 = live weight intact owl). Most of these birds were killed in traffic, and for this reason females in breeding condition are lacking altogether.



Figs. 66. Distribution of prey deliveries at the nest in the course of the night per 20-minute interval based on 144 nights of observation. Sample size refers to number of prey delivered.

Results

Data from the various sources are collected in Fig. 63. The carcass data confirm that in the Long-eared Owl a reversed sex dimorphism in body size exists, the female being heavier (Earhart & Johnson 1970). For the carcass data, females average 14 g or 14.5% heavier (uncorrected data). This differential can also be estimated from the trapped birds for the period December—February (when body weight is relatively stable) and in these data the female is 14.1% (38 g) heavier (Fig. 63A). The female Long-eared Owl shows a spectacular cycle of change when the data are combined. The captive birds (Fig. 63C) provide an estimate of the magnitude of the weight change preparatory to breeding (about 60 g during March and April) confirmed for the field situation by the two females trapped 42 and 20 days before hatching (see Fig. 63D). Unfortunately there is a blank in the field data from that point until the young have hatched, but on the basis of my estimate of food input at this period I assume that a further 50 g or so are added to female body weight during incubation (the calculations will be presented below). From hatching on the females loses body weight rapidly as shown by the weighing platform data as well as the few indi-

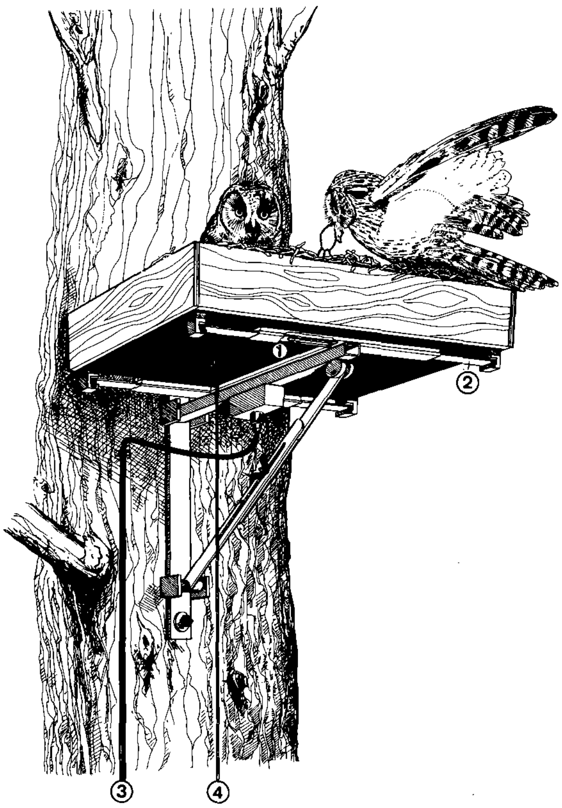


Fig. 67. Weighing platform used for obtaining prey weights and monitoring adult body weight at the nest of the Long-eared Owl (at which the male has just landed). 1 = tension strip, 2 = supporting bar, 3 = lead to meter output at observation post, 4 = attachment line for connecting brass weight for calibration of the platform.

viduals trapped (see Fig. 63D) and she experiences her lowest body weight of the annual cycle during the moult (Fig. 63A and B). These data have been combined in an idealized curve in Fig. 63E. For the male, change is less spectacular but there is evidence from the field (Fig. 63A and B) that during the nesting phase his body weight drops by about 30 g, and the idealized curve (Fig. 63E) has been drawn on that basis. In October both sexes return to their stable winter levels.

Wing length (flattened chord) measured outside the moult period is summarized in Fig. 64. Wing-length is slightly but significantly larger in the female (Student t-test, $p < .001$).

9.3. BODY WEIGHT AND FLIGHT COST: THEORY

It will be recalled that for the winter period applications of the most universal formula for predicting flight cost, that of Pennycuick (1972, 1975) resulted in a prediction which could be balanced against energy intake as deduced from the pellet method (p. 49). This model also provides a quantification of the repercussions of changes in body weight on the flight cost, and is given here in graphical form (Fig. 65) for the case of the Long-eared Owl (the prediction depends not only on body mass but also on wing shape). It will be appreciated that the drop in male body weight at the advent of the breeding season will reduce his hunting cost at a time when he is devoting more hours to flight than at any other time of the year. For the female, on the other hand, the weight cycle of reproduction, involving extensive deposition of fat, incurs a prohibitive rise in flight cost. At her peak weight (achieved about the time the young hatch) her flight costs are double those of the male.

9.4. DIRECT OBSERVATIONS OF FOOD CONSUMPTION IN THE REPRODUCTIVE PERIOD

Methods

During the incubation and the nestling period the female remains on or close to the nest. The male provides all prey eaten by the female and later by the owlets. Prey delivery by the male starts some time before incubation (Wendland 1957, pers. obs.) and gradually increases until by the start of incubation all food is delivered by the male. The female does not hunt until at least 20 days after hatching of the oldest young, after which her hunting activity gradually builds up again. In general the male announces his arrival (with a prey) by giving the male territorial call. The female answers with harsh barking at a high frequency. In most cases she receives her prey on the nest but sometimes she leaves the nest, and prey transfer occurs in a neighbouring tree. After a short period she comes back on the nest again.

Observations on the numbers of prey delivered per night were made during the incubation period (63 complete nights) and the nestling period (90 complete nights, including a few nights where the oldest young had already fledged). Distribution of the time of prey deliveries are given in Fig. 66.

Most nocturnal observations were carried out without the aid of a blind. The observer was sitting on the ground at a distance of 10—40 m from the nest. After a habituation period this observation method did not seem to influence the behaviour of the owls. Some observations, however, were made from a blind or a blind on a ladder. Mostly conventional binoculars were used, sometimes an infrared binocular was available. In two nest situations a 12 V electric light close to the nest that could be switched on from the observation post was used in order to facilitate observations. Due to difficulties in observation and because of the fact that the female sometimes receives her prey outside the nest, prey transfer was often not observed directly. However, the combination of vocalizations, with the appropriate behaviour of the male and the female made it possible to decide with a high degree of certainty whether a prey delivery had occurred or not. This decision based on behavioural criteria could be checked in the nestling situation where weight changes due to prey delivery were recorded with the weighing platform (see below). Nevertheless, data from a few observation nights is restricted to a maximum — minimum (difference never more than 2 prey) estimate of the total numbers of prey delivered by the male. In such cases the mean value was taken.

An attempt was made to stimulate Long-eared Owls to breed on the nest platforms on which were placed old Carrion Crow or Magpie nests. These platforms were erected on locations where in preceding years Long-eared Owls were found to breed, and the intention was to insert a weighing system under these platforms after the start of incubation. Unfortunately the owls did not lay on these platform-nests. For this reason it was necessary to erect the platform with the weighing system within a few meters of an occupied Long-eared Owl nest, and shift the nest afterwards (during the nestling period). With the aid of this system it was possible to collect data on female weight during the nestling period as well as the weights of the prey brought to the nest.

Fig. 67 shows the construction of this weighing system. The principle is based on a change in electrical resistance of the eight strain-gauges mounted on the two metal bars supporting the platform. This resistance change is measured with a bridge and an electronic amplifier, which is connected with the platform by a 50 m cable. The amplifier has a digital display. The system was regularly calibrated with a weight which could be operated at the observation post. The accuracy of the system depends on the environmental conditions (especially windspeed, shelter against wind and the stability of the tree) but was usually in the order of ± 2 grams.

In order to get information on the composition of the menu in the breeding period pellets of the adult owls and the young were collected whenever possible (see chapter 3). Additional information was available from uneaten prey remains found in the nest during inspection. All prey were weighed with a spring balance.

The total weight of the prey brought to the nest could be measured exactly in those situations where the weighing platform was used. In other situations the total weight was estimated using the observed prey delivery frequency and the average prey weight. Diet composition was based on the pellet analyses of that particular nest site during the period April—July. The average weight of the individual prey species was calculated from weight data on prey found in the nest, on weights obtained with the weighing platform and on weights of individuals trapped in the study area. In the few cases where nothing was known on the diet of the breeding owl pair the average prey of that breeding season was used (Appendix 1). For a few prey species literature data were used (especially for bird weights).

Results

Data on the numbers of prey delivered each night during the incubation, nestling and the start of the fledging period are given in Fig. 68.

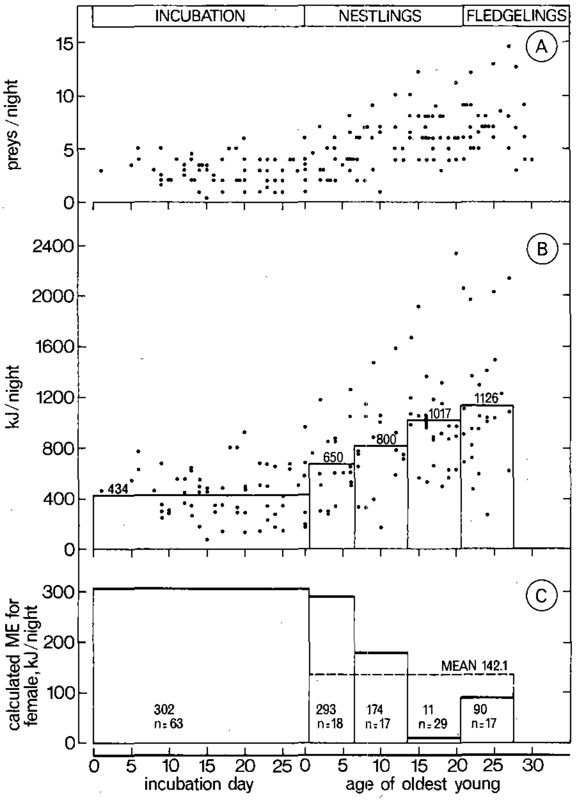


Fig. 68. Prey delivered at the nest in the course of the breeding period. A) Number of prey per night. B) Energetic equivalent of the prey; mean values are given for the incubation period and for each week after hatching. C) Calculated Metabolized Energy (ME) for the female in the same periods. A and B are based on all clutches, C only on 2, 3 and 4-egg clutches.

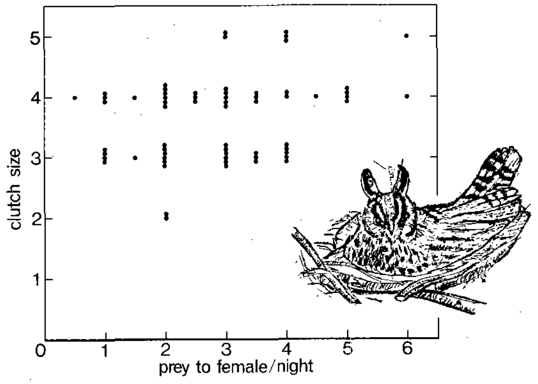


Fig. 69. Relationship between final clutch size and the rate of provisioning at the nest by the male. There is a significant positive relation between the two ($p < .05$).

There are 63 complete nights of observation during the incubation period. Prey delivery frequency varied during this period from 0 to 6 prey/night with a mean value of 2.83 (± 1.32) prey/night. During the 28 days of incubation there is no clear trend in prey delivery frequency. Hunting activity and/or success seems to be influenced by weather conditions. Numbers of prey brought to the nest during nights with rain are somewhat less than during rainless nights. The average value is 2.40 (n = 15) for rainy nights and 2.97 (n = 48) for rainless nights. This difference is however significant ($p < .01$ by Student's t-test). Fig. 69 shows the relationship between clutch size and the numbers of prey deliveries a night by the male. There is significant positive correlation ($r = 0.286$; $p < 0.05$), suggesting that females of successful hunters (males) lay large clutches.

After hatching the average number of prey brought to the nest shows a steady increase from 4.1 in the first week, 5.3 in the second week, 6.5 in the third week to 7.4 in the fourth week. In general the owlets leave the nest after 21—22 days, and although they stay for a few days in the nest tree observations become more difficult. Female hunting activity starts mostly in the fourth week after hatching. However, it is difficult to determine if food brought to the nest by the female is obtained by her own hunting activity or received from the male outside the nest area.

The caloric value for the main prey species, Common Vole, in spring was determined as 6.1 kJ/gram fresh weight (Fig. 29). The material was insufficient to analyze differences between years. Some additional determinations on caloric values of other prey species in spring did show some variation but, the number of determinations were insufficient to provide separate values for each. For this reason the *Microtus* value was employed for all prey.

Fig. 68 gives, in terms of kJ, the amount of food brought to the nest. During the incubation period the female receives on the average 435 kJ/night. Two weeks after hatching this value is more than doubled and the average prey delivery in the fourth week after hatching of the oldest young is 1126 kJ.

If we assume that all the food brought to the nest during the incubation period is wholy eaten by the female, it is possible to calculate her average ME during this period. The assumption that all prey is wholy eaten is of course a simplification. In some cases small fractions of the digestive tract might be rejected, but for prey smaller than 30—35 grams this will be negligible. For the largest prey, quite rare in the diet, an arbitrary weight value of 100 g (for rats, rabbits) is taken as the amount of food really eaten. Metabolized energy coefficient (MEC) for the female during the reproduction period was calculated as 0.70. This value is based on the average menu composition in the breeding seasons 1974—1978 (weight percentages! appendix 3), MEC for the different prey species and the seasonal trend (chapter 4.3.). Using this value of 0.70 the average ME of the female in the incubation period is 302 kJ (Fig. 68).

For the determination of the ME of the female during the nestling period we need information on how much energy the owlets take. The results of the energy metabolism measurements on five owlets raised in the laboratory, showing growth rates approaching field conditions closely, are given in chapter 8. These data, in combination with the average growth curves of nests with 2, 3 and 4 nestlings (extreme numbers of young are not considered here) give estimations of the ME for owlets with an average growth rate. Making use of the MEC values for young owls it is possible to calculate the GEI for the young. (In these calculations no correction is incorporated for brood size; it is assumed that the GEI per young is the same in broods of 2, 3 or 4 young).

Total amount of food brought to the nest (kJ) minus the GEI of the young and multiplied with 0.70 (MEC of the female) gives the ME of the female in the different periods after hatching.

Although the analysis of female energy consumption is somewhat indirect the overall trend is clear: after hatching the female receives less food than before and female food intake is minimal in the third week after hatching of the oldest young (± 11 kJ). In the fourth week the ME increases again. During the whole period up to four weeks after hatching the average female intake is about 142 kJ/night. This is less than half the ME during incubation.

9.5. BODY WEIGHT CHANGES DURING BREEDING AND PARENTAL ENERGY BUDGET

Table 28. Energy budget of the female Long-eared Owl during the nest phase (kJ bird^{-1}day^{-1})

	eggs	nestlings
BMR$_{day}$	72	79
BMR$_{night}$	47	40
TR$_{day}$	36	32
TR$_{night}$	32	24
Nonflight activity	20	20
Flight	10	9
Incubation/brooding	37	7
Total expenditure	254	211
Food intake (field)	302	142
Difference	48 (surplus)	69 (deficit)

A provisional energy budget for the female Long-eared Owl in the period when she is largely restricted to the nest is presented in Table 28. It will be noted that during the egg phase she enjoys a slight surplus of food intake over expenditure, and if we convert this energy surplus into a weight increase utilizing the cost factor derived from the ME trials (mean 13.5 kJ per g body weight change) then we find a daily increment of 3.6 g would result (48/13.5 = 3.6). For the entire incubation phase of 28 days this would allow a body weight increment of 100 g to be accumulated, but as I have pointed out I was unable to capture birds at the nest at the critical point to confirm the extent of the increment. During the nestling period the female suffers a daily deficit of approximately 69 kJ (Table 28) and this could theoretically be balanced by a weight loss of 5.1 g daily (assuming the same cost factor from the ME trials applies, namely 13.5 kJ per g weight change). Measured weight loss for the 16-day interval between nestling age 5 and 21 averaged 5 g in the weighing platform data (Fig. 63D) and is in accord with this estimation. After day 21 the female starts to hunt again, so it is probable that the magnitude of the body weight loss during the nestling phase is close to 100 g in all, and this is my strongest argument in favour of the deposition of a corresponding amount in the incubation phase. In any case the budget can be balanced with changes of body weight of this magnitude. Clearly the surplus body weight of the female serves as a buffer in the early nestling period, allowing the major share of the incoming food to be channeled into the growing nestlings; by accepting a surplus ration in the egg stage and undergoing a deficit during the nestling period the female reduces peak demand on the male's hunting ability.

In attempting to construct an energy budget for the male parent we are on much less firm ground. The period of peak performance is likely to be the nestling period, and it is in this period that our pellet method for estimating the daily ration breaks down. As was mentioned in chapter 4, it is not feasible to assign pellets found near or under the nest-tree to "male" or "female". The male shifts his daytime roost continually, and we were unable to assemble a sufficient sample of pellets for which we could be sure that they originate from the male. We must therefore have recourse to time-budget data in conjunction with ME$_{cage}$ values. On the basis of our observations at the nest, the maximum mean flight time for males hunting for the family was 5.5 hr per night (hunting by day is infrequent and can be ignored here). Our estimate is in substantial agreement with Wendland's (1957) observation of 6 hours each night. If we accept Pennycuick's prediction (Fig. 65) for flight cost, then the male requires 170.5 kJ per 24 hr for flight alone (5.5 × the hourly cost factor of 31 kJ). Assembling the budget as we did for winter birds (chapter 4), we assume that due to SDA and the spread of hunting throughout the night (heat is generated during flight) there will be no additional cost for thermoregulation during the nocturnal period. The ME$_{cage}$ value for May is 183.9 kJ per bird per day, and taking into account that 5.5 of the 24 hours are devoted to flight and already covered by the budget, we estimate that cost in the remaining 18.5 hr would be (18.5/24) × (183.9) = 141.8 kJ. This estimate includes temperature regulation costs of 13.7 kJ during the night, and if we subtract this value from the ME$_{cage}$ we are left with 128.1 kJ for all non-flight costs. The 24-hr total would then be 128.1 + 170.5 = 298.6 kJ, equivalent to 3.0 BMR (the BMR for males in May was determined at 98.4 kJ per bird per day). This crude estimate would mean that the male parent increases his level of expenditure by 30% compared to the non-breeding season (my original estimate of male parental working level at 4 BMR, reported in Drent & Daan 1980, was derived by assuming a flight cost factor of 12 BMR instead of the Pennycuick formula which predicts a cost factor of 7.6 BMR for flight in the breeding period). It is indeed unfortunate that the only nest where we were able to equip the male with a radio transmitter was disturbed by young naturalists during the weekend and failed to provide an independent attack on the energy budget of the male parent, which must be considered somewhat of an enigma until fresh data are forthcoming.

In the final chapter I will return to the problem of the division of labour between the sexes, and how this impinges on the degree of sex dimorphism observed in body weight.

10. MOULT

10.1. INTRODUCTION

Moult is one of the major events in the annual cycle of birds, and can potentially at least have a profound effect on the timing of the cycle. To begin with the production of new feathers will demand additional energy and/or specific nutrients. In the second place the loss of feathers in combination with the extension of the blood-vascular system in the pulp of the growing feathers will reduce the insulation and enhance the rate of energy loss of the bird during moult. Finally the loss of feathers may directly impinge on hunting success by reducing speed or manoevarability, and hence moult may be a time of reduced hunting ability.

Although most energetic studies indeed reveal an elevation of energy expenditure during the moult on the order of a 5—30% increment over the resting level, in some cases no overall increase has been detected (West 1968, Chilgren in: King 1980). This finding in itself does not mean that moult has no cost, because decreases in other energy demanding activities may mask the direct metabolic effects of moult (King 1980). The long duration of avian moult does mean that long-term trials are called for. In my study I followed the ME technique as well as short-term responses to ambient temperature of moulting birds as revealed by the monitoring of oxygen consumption in order to establish the energetic consequences of moult. Before entering on the cost of moult, a description and phenology will be given for the Long-eared Owl.

10.2. METHODS

Information on the plumage and the moult in the Long-eared Owl was obtained from different sources.

Plucking. Owls found dead were collected and stored in the freezer. For examination the bodies were defrosted and moult of the remiges and retrices noted. The length of all remiges and retrices was measured in a stretched condition, beginning at the point where they leave the skin. After taking these measurements all feathers were plucked, mostly a few at a time, by means of a tweezer. Counts were made separately for the different feather areas. Only one leg and wing was counted, so for total feather numbers these values were multiplied by two. Feathers were divided in flight feathers (primaries, secondaries and tail feathers) and body feathers (= all other feathers). This latter group was subdivided in three categories: *Contourfeathers*: feathers with a firm shaft and a vane (semiplumes, filoplumes and bristles were for practical reasons also classified in this category), *Down feathers*: soft feathers without or with short shaft and without a typical vane, *Growing feathers*: developing contour or down feathers with a feather sheath. After plucking of the flight feathers the length of the individual feather was measured again, now including the part which was normally buried in the skin. These feather measurements were used for the identification of moulted flight feathers found in the field. Primaries are numbered, following the usual convention, from the innermost outwards (P1—P10), the secondaries from the outermost inwards (S1—S13), the tail feathers from the central par outwards (T1—T6) as is clarified in Fig. 70. The fresh weight of the feathers of the different tracts and the weight of the individual flight feathers was determined just after plucking. Flight feathers and body feathers were then separately dried (± 24 hr 100 °C) and weighed again. The whole plucking procedure took about two days for one owl.

Inspection of museum skins. Long-eared Owl skins in the collection of the Zoologisch Museum, Amsterdam and the Rijksmuseum voor Natuurlijke Historie, Leiden were inspected for moult using the method described by Stresemann & Stresemann (1966). The date of collection and the sex (if known) was noted together with information on gaps in the flight feathers and the length of the growing flight feathers. Body feather moult was noted as present or absent from the original data collected when the skin was prepared. A total of 180 skins were examined of which only 13 were from the moult period.

Information on moulting captive owls. During 1974 and 1976 the moult pattern was observed in respectively 3 and 11 captive owls. Eight owls were kept in large outdoor flight cages, the others in individual small cages as was described in the ME trials. Two of them were kept outdoors, the others in temperature controlled cabinets at 15 °C with the same day-night regime as outdoors. All owls received laboratory mice ad lib. Although there was individual variation in the start and duration of the moult this seemed not to be related to different cage circumstances, and moult data for the different groups were pooled together. Each day cages were inspected for dropped flight feathers, and these were

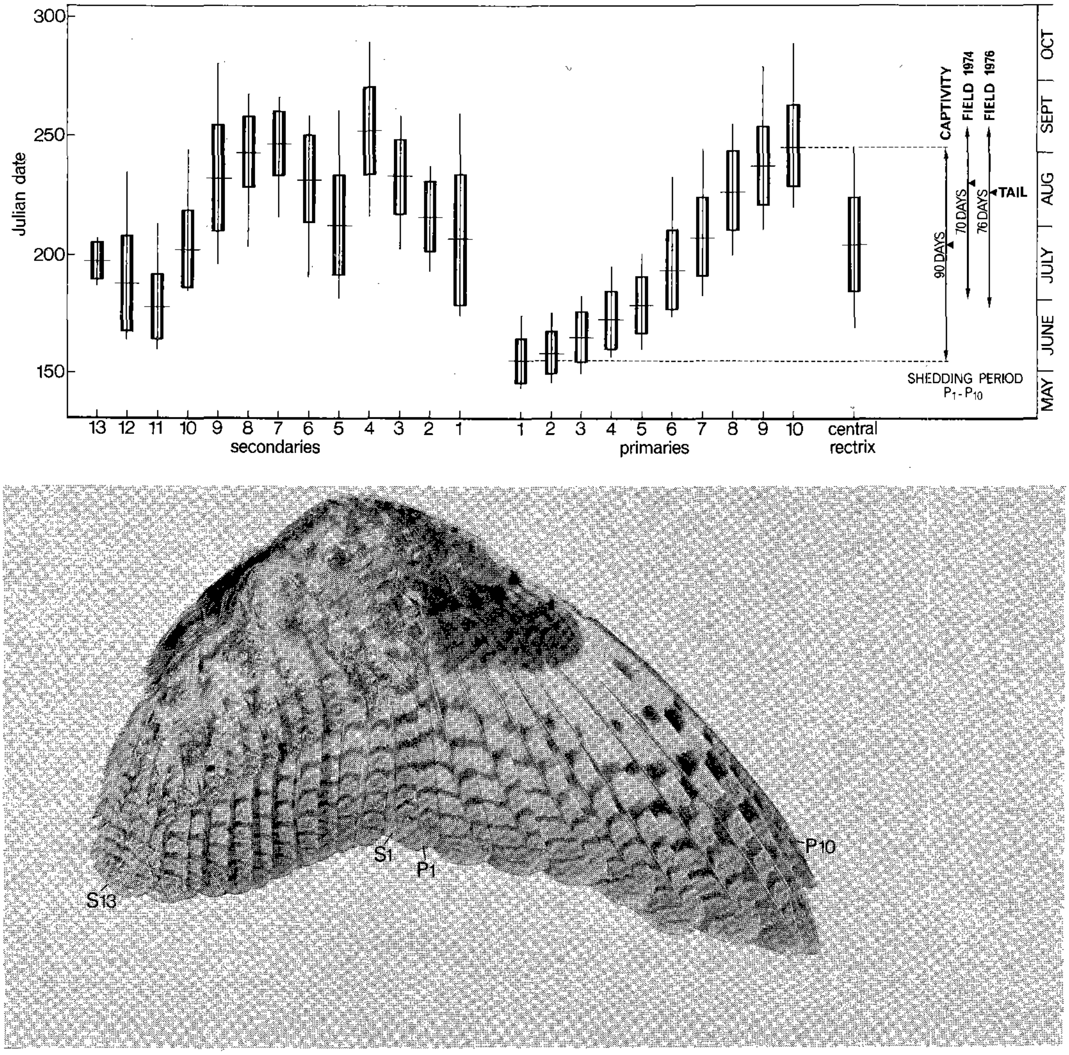


Fig. 70. Moulting phenology in the Long-eared Owl based on captive birds. Moult duration in captivity and in the field at right. Means, range and ± 1 SD are shown for shedding dates of secondaries, primaries and the central tail feather (the numbering of the flight feathers is shown in the photograph).

collected and measured. Sometimes flight feathers of communally housed owls were marked with waterproof dye to prevent misidentifications. Dropped body feathers were also collected, if possible daily, for the individually housed owls. Once a week these were collected (and if necessary cleaned) and weighed. All owls were weighed at least once a week and the length of the growing flight feathers and some wing coverts measured. In general feather growth in only one wing was measured as regular checks showed that the moult pattern in both wings remained in phase. For the tail only the central rectrix (T1) was measured as all rectrices were dropped within a few days and grew simultaneously.

Field data. During the moult period in 1974 and 1976 areas where owls were known to roost were regularly inspected for dropped flight feathers. The day between the preceding visit and date of collection was booked as the presumable dropping date. Primaries were identified by length. Rectrices, which could easily be recognized as they have a hooked shaft and vane equal in breadth on both sides of the shaft, could not be identified by number but as they are all dropped within a few days they give valuable information about the tail moult.

10.3. FEATHER NUMBER AND PLUMAGE WEIGHT

Total number of flight feathers (remiges and rectrices) is 58 subdivided in 10 primaries and 13 secondaries for each wing and 12 rectrices for the tail (see Glutz & Bauer 1980). Besides these feathers each wing has 4 alulae (Piechocki 1968). Total number of all feathers is high: a sample of nine birds throughout the year gives a mean value of 10.156 ± 837. Most numerous tracts are the capital tract (head), which accounts for about 36% of all feathers, the crural and femural tracts (both legs) with 17% and the wing coverts and humeral tract with 22%. Together with the tail coverts (1%) this will mean that the trunk has only 24% of the total number of feathers. About 10% of all feathers are down feathers (1042 ± 225).

The total number of feathers is about four times higher than predicted by the formula of Kendeigh (1970): $\log F_n = 2.97 + 0.178\ W$ (where F_n is feather number and W is body weight in grams). Substituting for a 280 g bird this gives an expected value of 2554 feathers for the Long-eared Owl. Even if we ignore the enormous number in the capital tract (including the facial disc) it is clear that this species has a incredibly high number of feathers, which might be an adaptation to a soundless flight.

Mean plumage weight, air dry and taken at various times of the year, is 31.6 ± 3.3 g ($n = 11$). This value can be subdivided in 9.3 g for the flight feathers and 22.2 g for all other feathers. Weight percentages (based on 22.2 g) for head, legs, wings and tail are 11.1%, 11.5%, 42.1% and 2.6% respectively, so the trunk has 32.7% of the weight of all feathers excluding the flight feathers.

One Long-eared Owl examined by Turček (1966) had a plumage weight of 10% of body weight. This value agrees with the mean value of 11.3% of body weight in this study (again 280 g was taken as a mean overall weight). Kendeigh's (1970) formula $\log F_w = -1.168 + 0.959 \log W$ (F_w is plumage weight) predicts a plumage weight of 15.1 g for a 280 g bird which is about half the actual value.

After feathers are replaced during moult they are subject to plumage wear till the next replacement (Newton 1967). An indication of this plumage wear, in terms of weight decrease, can be seen in Fig. 71 where total plumage weight (fresh weight) decreases from November (just after moult completion) to May (just before the onset of moult) according to $F_w = 35.1 - 0.960\ t$ ($n = 11$, $r = .61$, $p < 0.005$), where F_w is feather weight and t is the number of months after October. This means a weight decrease for total plumage weight of 19.1% till the next moult period. For Bullfinches Newton (1967) gives a weight change of 30% for total plumage weight.

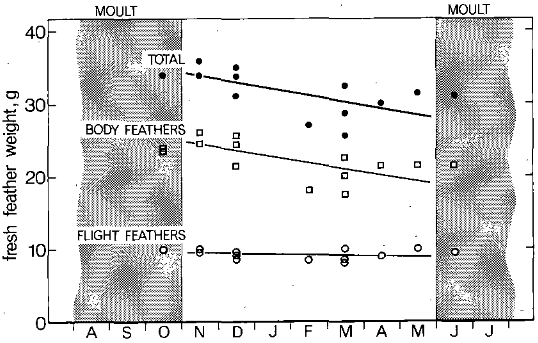


Fig. 71. Weight of the plumage of Long-eared Owls in the course of the year, the moult is shown as extending from June through October. Each symbol denotes an individual plucked owl.

Flight feathers show a small, non-significant, weight decrease: $F_w = 9.62 - 0.075\ x$ ($n = 11$, $r = .24$, $p > 0.05$). Because the number of contour feathers shows a decrease from 10.612 in November—December ($n = 4$) to 9750 in March—April ($n = 3$) it is likely that weight change also partly is due to actual feather loss during this period.

The water content of the plumage outside the moult period is about equal in November—December (11.7%, $n = 4$) and in February—April (10.8%, $n = 5$). One measurement of 21.4% water content during moult indicates a much higher water content of growing feathers as previously has been reported by Newton (1967), and others.

10.4. MOULT OF FLIGHT FEATHERS

A description of flight feather moult in the Long-eared Owl is given in Glutz & Bauer (1980) from observations by Piechocki and Sutter. Our own data confirm this description.

Flight feather moult starts with the shedding of P1. For all captive owls in both years the mean date of this event was 3 June (± 9.7 days, $n = 14$). For the captive owls the mean shedding dates of the other primaries, the secondaries and the rectrices are given in Fig. 70. Replacement of a new feather starts immediately after shedding the old one, so the figure gives also the mean start of feather replacement. All birds replaced their primaries in order from the innermost (P1) outwards to (P10) so in a strict descendent sequence.

Secondary moult is initiated with S11, which is shed soon after P4. Secondaries are renewed from three separate moult foci in each wing. One focus centres on S11 with a moult wave to S13 and S8. The second is S1 with a wave to S4 and the third is S5 with a wave to S8, as is presented in Fig. 70.

All 12 rectrices are lost within 1 to 9 days (mean: 5.1 ± 2.1 days, n = 13) shortly after P7 is dropped. The sequence of tail moult seems not to be very consistent although precise information is difficult to collect because the shedding period is very short. However, the outermost feathers (T6) are always lost after the innermost (T1) which suggest a centrifugal moult pattern as was supposed by Verheyen (1956). Primary wing coverts are shed a few days after the foregoing primary was shed. In general an intermediate wing covert is dropped halfway between the shedding dates of two successive primaries. On the contrary all secondary coverts are dropped at the same time, just after S12.

Three owls (out of the 14 observed) in captivity showed incomplete moult. In 1974 one owl (no 1) did not moult S2, 3, 4, 6, 7, 8. Primaries and tail did moult regularly. In 1976 owl no 7 did not moult S3, 4 and owl no 5 did not moult S13. Glutz & Bauer (1980) showed that incomplete secondary moult regularly took place. In those cases of incomplete secondary moult S3, 4, 6, 7, 8 were often not renewed, which is in agreement with our observations. The time between the shedding of primaries increases from an average of three days for P1—P2 to about 17 days for P6—7—8 but it decreases again for the distal end of the wing. This is shown in Fig. 72 where the corresponding data of Piechocki (1968) are also presented.

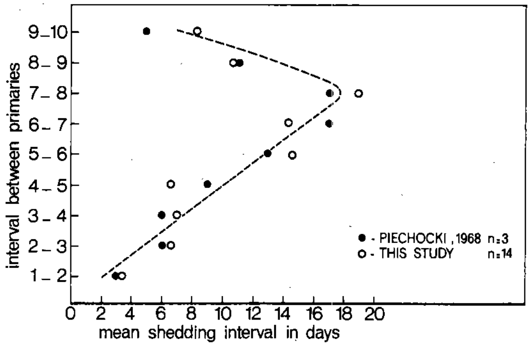


Fig. 72. Mean shedding interval between the primaries in captive Long-eared Owls.

A diagrammatic view of the gap in the outline of the wing in the course of the moult (Fig. 73) tends to support Gwinner's (1966) suggestion that the time interval in the shedding of adjacent primaries has evolved in relation to the growth rates of the regenerating feathers in order to minimize the period in which the wing-tip suffers loss of aerodynamic function. As in *Corvus corax* studied by Gwinner, maximal interprimary shedding intervals occur between primaries 7 and 8 which constitute the protruding wing-tip (Fig. 72). This idea deserves following up by subjecting wing mounts from various moult stages to analysis in wind tunnels.

A representative example of the growth of individual feathers for one bird (no 9) is given in Fig. 74. The mean period in which the feathers reach their final length varied from 27 days for S6 to 47 days for P8. Knowing the mean length

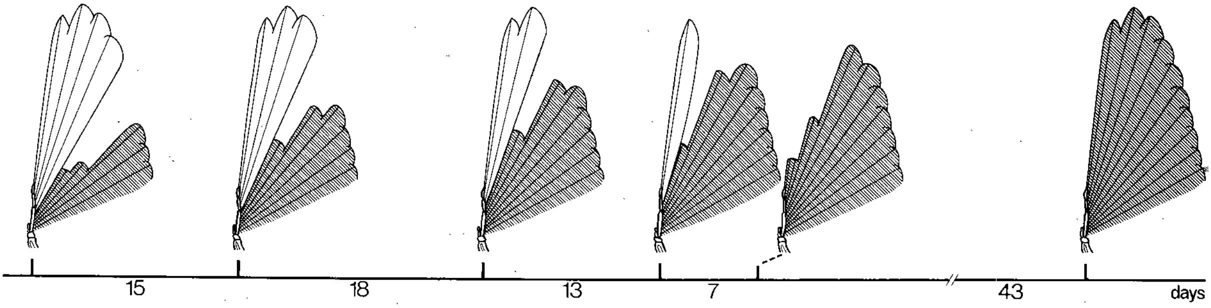


Fig. 73. Diagrammatic view of wing-tip during moult showing relatively rapid shedding of the last primaries, (scale in days, see also fig. 72 and text). New feathers are shown in grey, old ones in white.

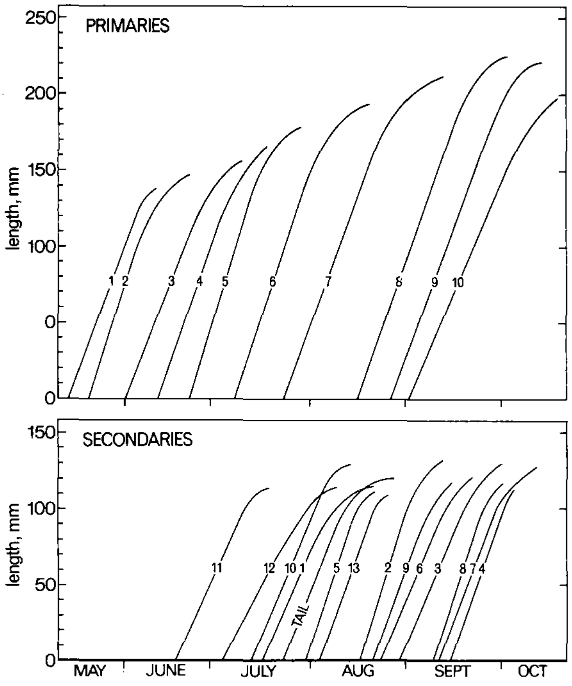


Fig. 74. Linear growth of individual feathers as measured in one captive owl (see text).

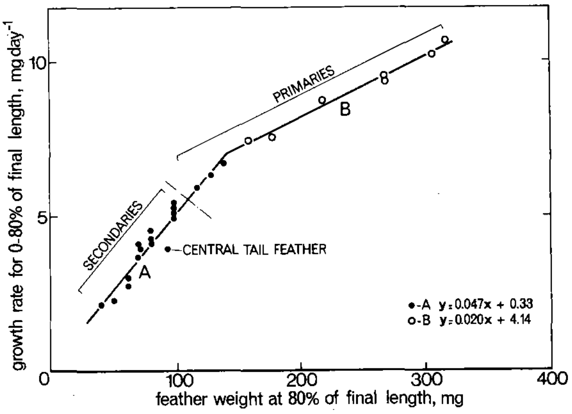


Fig. 75. Mean growth rates in the 10 primaries, 13 secondaries, and central tail feather for the linear period of growth (until 80 % of final weight is achieved) in relation to target weight (abscissa). The secondaries, tail, and primaries 1—3 appear to grow at a faster rate than primaries 4—10.

and weight of the different feathers calculation of the mean growth rate in mm day^{-1} and mg day^{-1} is possible. For growth rate expressed in weight the assumption was made that feather density was homogeneous. Because length increase slowed down as the final length was approached growth rate was calculated for the period during which feather growth is nearly linear, which was somewhat arbitrarily chosen as the period up until 80% of final length, has been reached. Length increase is highest in P4 (6.3 mm day^{-1}) and lowest in S12 (4.4 mm day^{-1}). Fig. 75 shows the growth data of the individual flight feathers. Although P8, 9, 10 have a somewhat lower growth rate (mm day^{-1}) compared to their length, weight increase is well correlated with feather weight. However, up to P4 this increase in growth rate is proportional to the increase in weight, but P4—P10 shows a less steeper slope.

Growth rate for juvenile flight feathers (measured were P1, 9, 19, S1 and T1; chapter 8) is about 10% slower compared to growth rate in moulting adults. However, in juveniles nearly all feathers grow at the same time, so the overall feather weight increase is much higher (see page ?).

Weekly growth of flight feathers (mg per week, fresh weight) was calculated for all individual owls using a simple formula

$$\Delta w = \frac{\Delta l \times W}{L}$$

where Δw = increase in weight for a growing feather
Δl = measured length increase
W = total weight of that particular feather
L = final length

Summing the weight increase of all growing feathers gives the total flight feather production in that week, which as a mean value for all owls, is given in Fig. 76. However, these values are based on weight data of dropped (old) flight feathers which were subject to feather wear. Actual data of feather production should then be corrected for this wear, which is about 9% of initial weight (calculated with the regression line for flight feathers for t = 11 months; Fig. 71). The total weight of flight feather production for captive owls is thus 9.00 g, a value which is close to 9.62 g of the October weight of flight feathers of plucked wild individuals. The difference is possibly due to heavier plumage wear in captivity compared to free-living individuals.

Flight feather moult could also be described by using a moult score. In general use is the

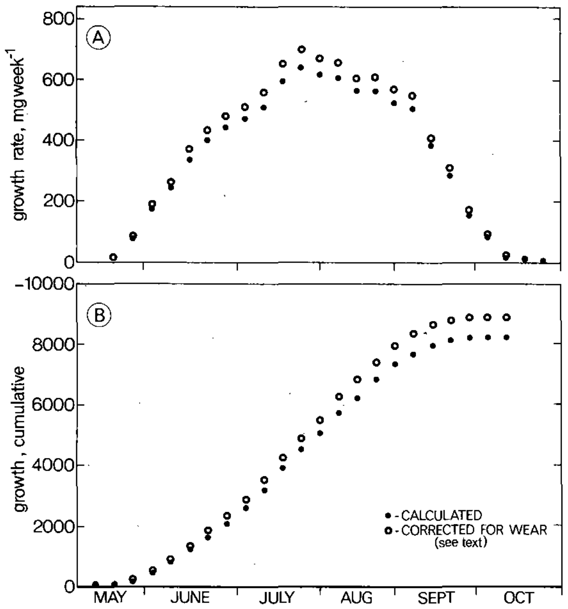


Fig. 76. Growth of flight feathers: (A) in mg new feather material per week, (B) idem cumulative. Data corrected for feather wear are shown by circles (see text).

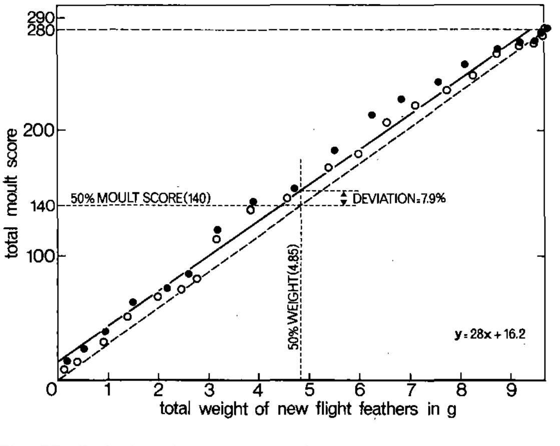


Fig. 77. Relation between moult score of the wing (see text) and total weight of new feathers added up to that point for two captive owls (indicated by dots and circles). The calibration curve (solid line) shows that moult score slightly anticipates progress of the moult as derived by weight increment (difference 7.9 % at the half-way mark). The total moult score, theoretically 290 (see text) is here equal to 280 because S13 was not included in the readings.

method described by Ashmole (1962) where each flight feather receives a score between 0—5 (0 = old feather, 5 = fully grown new feather). The maximum primary moult score is thus $(10 \times 5) \times 2 = 100$ points and maximal total moult score is $(29 \times 5) \times 2 = 290$ points. Fig. 77 shows the correlation between measured weight increase (not corrected for wear and calculated as described above) and total moult score for primaries, secondaries and rectrices for two captive owls. The correlation is highly significant ($r = .995$) but the elevation of the regression line is somewhat higher than the line which gives perfect one-to-one relationship.

The mean duration of flight feather moult (time of shedding P1 up to and including the time when all flight feathers are fully grown) measured in captivity is 134 ± 24.5 days. For comparing the moult duration and timing in captivity with free-living owls we can best take the period between shedding of P1 and P10 which covers roughly 70% of the total moult period. This period for 1974 and 1976 is given in Fig. 70. In both years moult seems to start later in the field than in captivity. This difference is

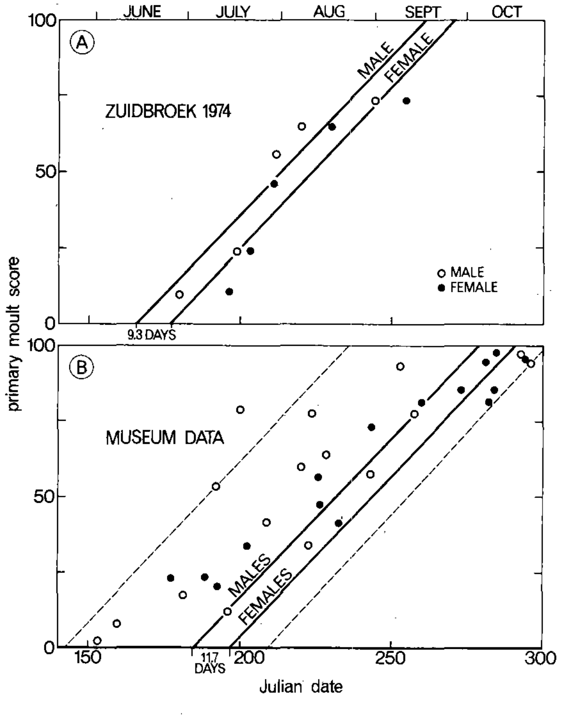


Fig. 78. Difference in moult phenology between the sexes as determined for two free living birds (A, solid lines are based on lineair regression) and based on museum collections (B, solid lines are the means of lines through every point, assuming a duration of primary moult score 0—100 from 93 days).

26 and 21 days respectively. The same time difference could be seen in the median shedding date of the tail feathers. However, primary moult seems to proceed faster in the field then in captivity because the mean shedding period was 73 days for the free-living owls and 90 days for the captive owls. The earlier start of captive owls might be due to the non-breeding status of these individuals as was earlier shown in finches (Newton 1966). However, caution is needed in interpreting these results because of different situations with respect to finding feathers. Recalculating Piechocki's data (1968) gives a mean duration of primary shedding period for one female Long-eared owl in captivity of 84 days in three successive observation years.

Stresemann & Stresemann (1966) and Piechocki (1968) suggested that males start earlier with moult then breeding females. Sufficient data were, however, lacking at that time. A combination of their data together with our museum data (Fig. 78) confirms a somewhat earlier start for males. Linear extrapolation for males and females gives a difference in starting date of about 12 days. Caution is needed in these data because they came from different localities and female status, breeding or non-breeding, is unknown. In 1974 the moult of one free-living pair could be followed to some extent by collecting dropped primaries. Primary moult score could be calculated and linear regression reveals a time difference of about 9 days between the male and female (Fig. 78).

In captivity, however, there is no difference between the sexes in the start of moult: mean commencement date for males is 3 June (± 12.5 days, n = 5) and for females also 3 June (± 8.5 days, n = 9). None of these individuals had achieved breeding condition however. Age of the owls seems to influence the duration of moult as can be seen in Fig. 79. Although there is a great scatter of points, 3 individual owls who were measured both in 1974 and 1976 show a decrease in moult duration. This was also found by Piechocki (1968) for one individual female who was measured in three successive years (Fig. 79).

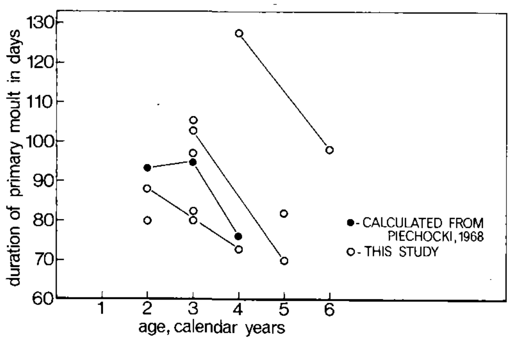


Fig. 79. Age effects in duration of primary moult in captive Long-eared Owls. Lines connect data of the same individual in consecutive years.

10.5. MOULT OF BODY FEATHERS

Weekly mean percentages of dropped body feathers for 9 owls are given in Fig. 80 for the period May through December. The mean total fresh weight of the collected body feathers during this period in both years is 16.6 g (n = 9). Fresh weight of body feathers just after moult is 23.3 g (page 70). From the linear regression in Fig. 71 it can be calculated that body feather weight decreases after November at about 3.5% per month. Weight decrease in this period will be due to feather loss and feather wear. The number of feathers lost is 1.6% each month after November, so feather wear will be about 3.5—1.6 = 1,9%. It then can be calculated that during the period May—November, if all body feathers were moulted, we should collect 17.8 g

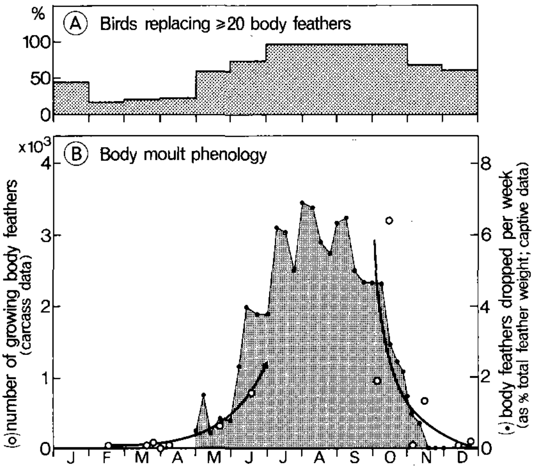


Fig. 80. Phenology of body moult: data from carcass analysis (A, n = 124) and carcass analysis and collection of shed feathers from captive birds (B, see key).

of body feathers for each owl. This is very close to the actual data of 16.6 g, so it may be concluded that the Long-eared Owl has a complete body moult each year. Outside the period of May—November, some owls show growing body feathers (Fig. 80). For February, March and April this is probably a "basal" level, necessary for (partial) replacement, but in December and January 50—60% of inspected skins show growth of downy feathers, which might be an adaptation to the winter period.

Some incidental measurements on wing covert feathers show a growth rate nearly identical to flight feathers (about 5 mm day^{-1}). This means that these feathers are fully grown about two-three weeks after they are dropped. If we assume that this is also valid for most of the other body feathers, we might calculate mean growth of all body feathers (mg week^{-1}) assuming a total feather weight of 25.5 g. Intensity of body feather growth and flight feather growth, both expressed in g week^{-1} are given in Fig. 81.

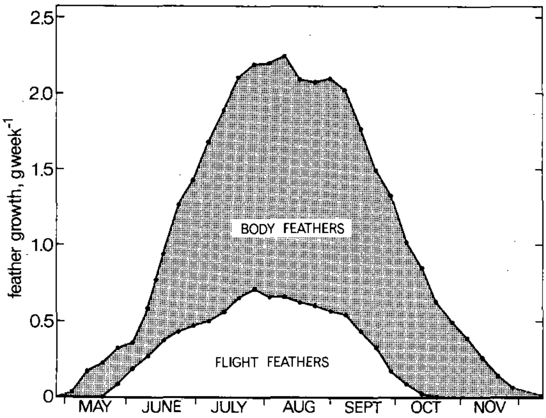


Fig. 81. Weekly increment in plumage weight throughout the moult (data from Fig. 76 and Fig. 80 combined).

During the moult peak in July, August and September about 2 g new feathers are built each week.

10.6. MOULT AND THE ENERGY BUDGET

As King (1980) has recently stressed in a thoughtful review, present whole-animal techniques do not allow an estimation of moult cost in itself, but rather the assessment of the energetic increment attributable to moult. This means that we are in a phase of empirical investigation, and cannot rely on theoretical predictions (based on efficiency of feather synthesis for example) to provide an answer meaningful in terms of the daily energy budget.

My approach to this problem has been to measure SMR (standard metabolic rate) in individual owls in the process of moult. These data allow reconstruction of the energy budget at rest (see discussion of the method in chapter 5). Levels of BMR related to the stage of moult (intensity of feather growth in weight) are given in Fig. 82 for six individual owls. With one exception (owl number 1) BMR is low in the premoult stage, increases as moult intensity goes up, and remains high as moult passes its peak. Combining these data (Fig. 83) analysis shows that in fact only the rise during the period of increasing moult intensity is significant. In effect, this means that in my data I can show that BMR is elevated as the Long-eared Owl enters the moult, but the return to normal levels after the moult has eluded measurement.

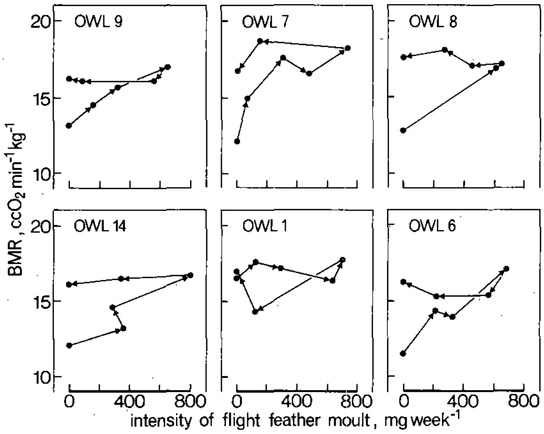


Fig. 82. Basal Metabolic Rate (BMR) in relation to intensity of moult. Arrows show time course of measurements for six captive owls.

A second source of data concern the ME$_{cage}$ trials. When the means for these trials (generally 5 days in duration it will be recalled) are plotted in relation to moult intensity we again obtain a significant rise as moult gathers momentum (Fig. 84, increase phase). As in the BMR data, the ME data from decreasing phase

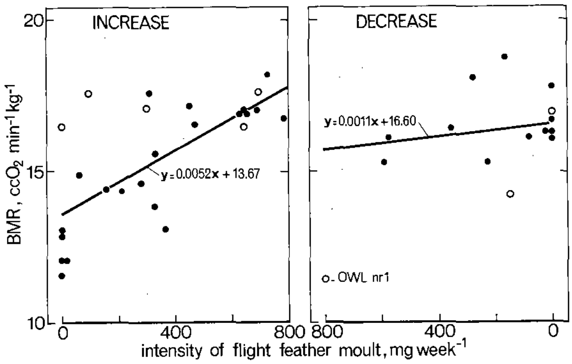


Fig. 83. BMR in relation to intensity of moult, summary of data in Fig. 82 with points separated for phase of increasing growth rate (left) and decreasing growth rate in the latter part of moult (right). The somewhat aberrant data of owl 1 are omitted from the calculation of lines of regression.

of moult fail to show a clear relation to moult stage.

Fortunately when the cost of maintaining a given gradient between body temperature and ambient air temperature is considered (the temperature coefficient, TC) the increasing and decreasing phases of moult intensity show agreement. As shown in Fig. 85 for the individual experimental subjects, and in Fig. 86 for the assembled data, both phases of the moult provide significant correlations. These data can be utilized to compute the energetic expenditure of an owl at rest at a given stage of the moult at the ambient temperature typical for that stage of the season (Table 29). According to these data, moult entails an increment in the daily energy budget of as much as 26 kJ per day (Septem-

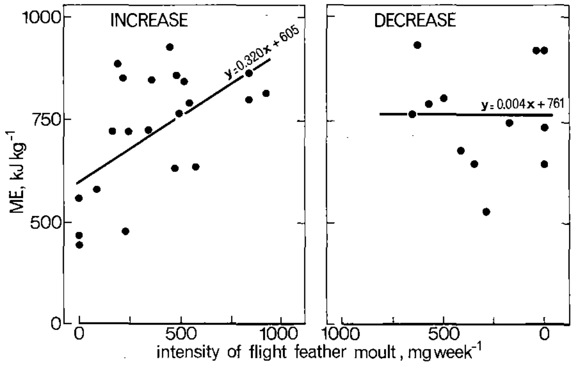


Fig. 84. Metabolized Energy (ME in kJ per kg per day) in the course of the moult (conventions for moult intensity as in Fig. 82) at 15 °C Lines of regression shown.

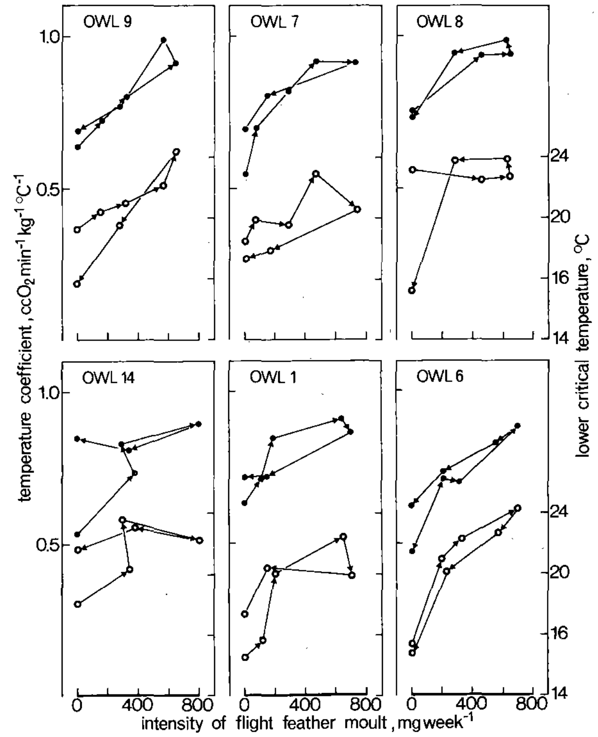


Fig. 85. Metabolic response to temperature during moult (temperature coefficient solid dots, scale at left, and lower critical temperature, circles and scale at right, both in relation to intensity of flight feather moult) for six captive owls.

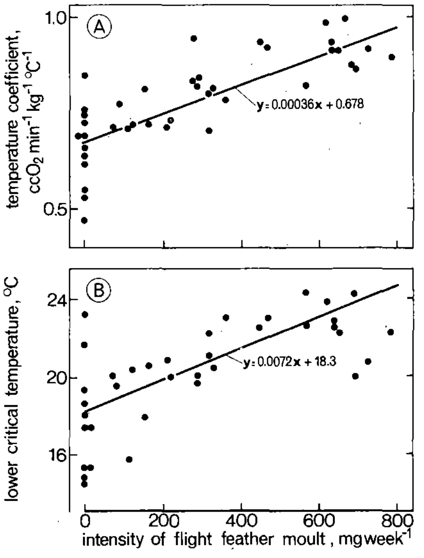


Fig. 86. Metabolic response to temperature during the moult, summary of data presented in Fig. 85 (temperature coefficient above, lower critical temperature below).

Table 29. Increase of Standard Metabolic Rate (△) as a consequence of moult

	Temperature coefficient* (ccO$_2$min^{-1}bird^{-1})	Mean ambient temperature (°C)	SMR measured (kJday^{-1}bird^{-1})	SMR "no-moult"** (kJday^{-1}bird^{-1})	△	% BMR
May (premoult)	.187	11.3	140	140	—	—
June (moult)	.187	14.4	124	117	7	6.5
July (moult)	.210	16.1	134	113	21	20.8
August (moult)	.210	15.9	135	114	21	20.8
September (moult)	.197	13.5	140	126	26	25.3
October (moult)	.197	9.8	159	143	16	15.6
November (postmoult)	.167	5.6	150	150	—	—
Mean					18.2	17.8

* see Table 16.

** assuming a temperature coefficient of .177 (= mean level of May and November).

ber). Over the entire moult period (June—October) the increment is equivalent to 0.18 BMR units. Expressed in another way, if we compute the (fictitious) budget of a non-moulting owl throughout this period, we find the daily SMR of the moulting bird is increased by 12½%. At the peak of the moult (September) the increment in daily energy expenditure (26 kJ) entails an increase of the daily ME on the order of 10%. These statistics do not mean that moult is potentially of no significance in influencing the timing of events in the annual cycle, but rather as we shall see when we compute repercussion of moult if timed differently, moult is so timed in the annual cycle that the cost increment is minimized (p. 79).

When the activity records of individual owls obtained by a radar system (p. 30) of monitoring movements in the ME cages were analysed, a compensatory effect became apparent. If we define the premoult level as 100%, the birds were found to reduce locomotory activity to 45%, at the peak of the moult (late August) and activity levels and had returned to 75% by October (final stage of moult). A similar depression of locomotion during moult has been reported for the Tawny Owl by Haarhaus (in Ceska 1980).

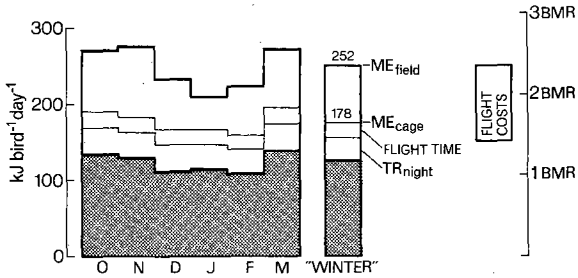


Fig. 87. Compatibility of field and laboratory estimates of energy expenditure during winter. Monthly means for ME$_{field}$ (Table 14) and ME$_{cage}$ (Appendix 4) are given. To obtain scope for flight cost, ME$_{cage}$ has also been computed for the non-flight hours only (= ME$_{cage}$-flight time correction). Cost of nocturnal temperature regulation is also shown (from chapter 5). Flight cost as derived from Pennycuick's formula is shown beside the winter mean (right).

11. FINAL DISCUSSION: THE ECONOMICAL HUNTER

What can we now say about the daily energy requirement for the free-living Long-eared Owl in the course of the year? For the period October through March, where we do not face the complication of intensive moult or breeding, Fig. 87 provides an overview of the energy available to the free-living owl (ME$_{field}$, as estimated by the pellet method, see Fig. 30) and the energy consumed by captive owls when maintained in small cages at the mean air temperature typical for the field (ME$_{cage}$, see chapter 6). As has been pointed out, these cage values basically represent expenditure of the perched quiescent owl. The two lines follow a similar course, and it has been argued (section 7.4.) that the difference represents the cost of flight incurred by the free-living owl. The difference between ME$_{field}$ and ME$_{cage}$ for the winter period as a whole, if we account for the time devoted to flight by accepting the telemetry estimate of 158 minutes per 24 hr and reduce the ME$_{cage}$ proportionally, amounts to 86 kJ per day. The cost of flight (for estimate by means of Pennycuick's formula see 7.4.) is approximately 104 kJ, so a slight discrepancy remains. This apparent energy deficit can be accounted for if it is assumed that the free-living owl minimizes the cost of temperature regulation during the night by profiting from the heat generated during flight and from the SDA of the meals taken then. In short, my conclusion is that the construction of an energy budget taking $\mathrm{ME}_{\mathrm{cage}}$ as the point of departure is a sound procedure in birds such as owls where cage locomotion does not provide a source of error. Koplin *et al.* (1980) have recently followed basically the same procedure in estimating daily energy expenditure for two raptors in winter, the American Kestrel, *Falco sparverius*, and the White-tailed Kite, *Elanus leucurus*. Their approach has been to estimate the $\mathrm{ME}_{\mathrm{cage}}$ (existence metabolism) and to add to this, as I have done, the cost of flight, to obtain the requirement of free-living individuals. For *Falco* an empirical measurement of flight cost was available, for *Elanus* this was estimated. When compared to direct field observations, the estimates for free-living were within 15% of the observed value for *Falco* (overestimated) and within 3% for *Elanus* (underestimated). These results are encouraging, and help justify extending the method to include breeding and moult. Before leaving the winter period, however, the question arises how the level of energy expenditure in the free-living Long-eared Owl compares to that in other birds at that time of year.

Outside the breeding period $\mathrm{ME}_{\mathrm{field}}$ in the Long-eared Owl varies from about 270 kJ/day in both fall and spring to a mid-winter low of only 211 kJ (Table 14) or in terms of the BMR as measured in this species from 2.7 to 1.9. The mean for the whole period (2.4 BMR; the median is 2.5 BMR) is reasonably close to the 2.6 BMR level suggested as typical for non-passerines outside the breeding period in a recent compilation (Drent *et al.*, 1978). In absolute terms, however, the value for the Long-eared Owl is lower than expected, for as we have seen, BMR is some 25% lower than predicted on the basis of body weight from the general equation for non-passerines (section 5.3.). The prediction of $\mathrm{ME}_{\mathrm{field}}$ for a 290 g non-passerine is 333 kJ/day according to the formula of Drent *et al.* (1978) and 363 kJ/day according to the compilation of Walsberg (1980) to mention only the most recent attempts at generalization. Walsberg's formula suffers the drawback that it is based on a very heterogeneous set of data including both passerine and non-passerine birds, and includes the three estimates for free-living owls provided by Graber (1962) which as we have seen are erroneous. Any regression of $\mathrm{ME}_{\mathrm{field}}$ on body weight is unlikely to provide more than a general indication of cost for a particular species, in view of the variation evident even in the limited sample of species so far. When $\mathrm{ME}_{\mathrm{field}}$ as determined by direct observation in birds of prey is considered in terms of BMR a spread of values for the winter period from 2.7 to 3.8 BMR emerges (Table 30) even when the data are restricted to recent studies based on extensive observations. Our conclusion must be that the Long-eared Owl operates at the lower end of the range delimited by field studies so far.

The question can be raised as to how we might explain the low energy requirements of the Long-eared Owl in relation to many other birds. As was demonstrated (section 5.3.) this species enjoys a far better insulation than would be expected of a bird that size, and indeed the plumage is remarkably dense and far heavier per unit surface than predicted on the basis of data from other species (section 10.3.). The impact that the reduced heat loss conferred by this

Table 30. Daily energy expenditure ($\mathrm{ME}_{\mathrm{field}}$) in free-living predatory birds outside the breeding season

Species	Body weight (g)	$\mathrm{ME}_{\mathrm{field}}$ (kJday^{-1})	BMR (kJday^{-1})	Ratio	Authority
Falco sparverius	119	180	67.3	2.67	Koplin *et al.*, 1980
Elanus caeruleus	243	417	110*	3.79	Tarboton, 1978
Elanus leucurus	331	474	135*	3.51	Koplin *et al.*, 1980
Asio otus	280	255	106	2.41	this study, August-March
Nyctea scandiaca	2086	1139	364	3.13	Gessaman, 1972

*) BMR estimated from a formula for Falconiformes provided by S. Daan.

improved insulation has on the energy budget of the free-living owl can be estimated with reference to the predictive relations recently derived for non-passerine birds in general by Gavrilov (1982). From Gavrilov's prediction the "standard non-passerine" at the body weight of the Long-eared Owl would require at least 67 kJ/day additional input to achieve balance during winter, i.e. an increase above the observed ME_{field} of some 30%. Put in another way, the superior insulation (low slope of the temperature coefficient) goes a long way towards explaining the discrepancy between the Long-eared Owl and other birds with regard to the level of energy expenditure.

As in many other bird species (Walsberg, 1980) it is not the period of winter cold but rather the breeding effort that entails the highest levels of daily energy expenditure (Table 30). In the Long-eared Owl we must consider the sexes separately, since there is a basic division of labour at this time. The female reaches her annual peak at the time of egg formation (daily requirement 302 kJ or 2.6 BMR) and the male has a rather protracted period of heavy demands. He takes the role of efficient hunter and provides not only for the female in the egg stage (when he operates at 2.7 BMR = 262 kJ/day^{-1}) but for the female and young in the nestling stage (when he reaches 3.0 BMR = 299 kJ/day^{-1}; for the male *Buteo regalis* provisioning the family Wakeley (1978) estimates the working level to reach 4.7 BMR). It has long been known that a similar division of labour occurs among many birds of prey (Tinbergen 1940), and is linked to a reversed sexual dimorphism in size (the females being larger than the males). Since the specialization of the smaller male as a hunter was first related to a minimization of flight cost by Mosher & Matray (1974) the "small but cheap male hypothesis" has gained support in subsequent analyses (Andersson & Norberg 1981, von Schantz & Nilsson 1981) and is an idea I favour too. The idea of the male slimming down in the breeding period to economize on hunting cost (Norberg 1981) whereas the female becomes restricted to the nest and lays down a fat depot that can serve as a buffer later on (section 9.5.) is thus a line of thought with an energetic background. To explain why the female is larger in the first place does not, in my opinion, necessarily follow from energetic considerations as presently understood, and an alternative argument (niche segregation) is often advanced (admirably summarized by Newton 1979). There is a pressing need for further work on the energetics of egg formation and fat deposition to help solve this enigma.

Turning now to ME_{field} at other times of the year, my study did not reveal an elevation in daily energy expenditure during the moult of more than about 10% (captive data, section 10.6.) and the field estimates (Table 14) are in accord. The extensive investigations of Dolnik and his colleagues on the Chaffinch (Dolnik & Gavrilov 1979, Dolnik 1982) suggest a similar moderate increment in that species during moult. It is a pity that I did not maintain captive owls at thermoneutrality throughout the moult in order to partition moult costs (into the components heat loss and biosynthesis) and I am unable to pursue the comparison in detail. My data do allow me, however, to predict the energy expenditure of moult as a function of air temperature, and hence to examine the repercussions of a shift in the timing of the moult. As was shown in Table 29, moult at the normal time involves an added daily cost of some 21 kJ in the peak months. If the entire moult process is shifted one month later, this daily cost factor is increased to 53 kJ/day, and a shift by two months incurs a daily cost factor of 75 kJ/day. In addition to this unfavourable cost aspect, a shift in moult in the Long-eared Owl would disturb its relation to the annual cycle of prey availability.

Ideally prey availability should be defined as prey captured per unit of investment by the predator (time and/or energy), but prey abundance can be taken as a first approximation. Computation from the extensive trapping statistics provided by Cavé (1968) yields a generalized pattern of the annual cycle of abundance of the Common Vole in the Netherlands, the primary prey of the Long-eared Owl (Fig. 88). It will be noted that moult occurs within the period of highest prey availability, and this can be no coincidence. Direct observation of raptors has demonstrated impaired hunting ability during the moult (*Falco tinnunculus*: Daan & Masman 1982; *Buteo buteo*: Sylvén 1982) of such magni-

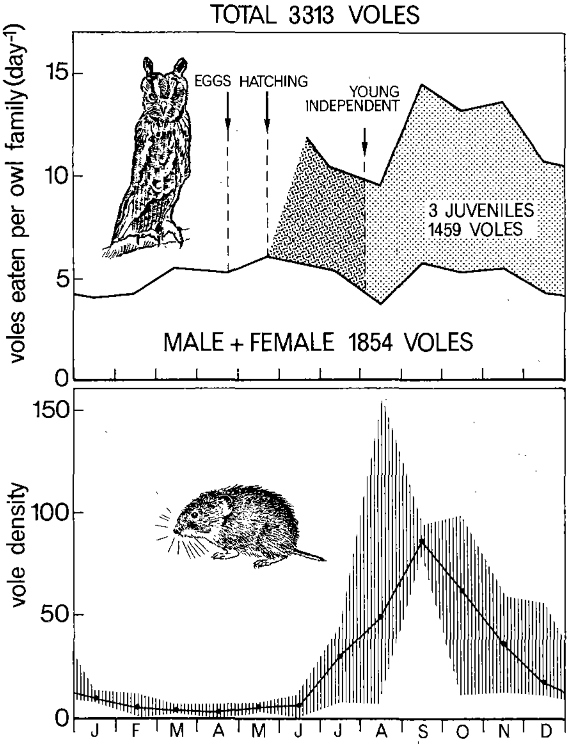


Fig. 88. Overview of the annual cycle in the Long-eared Owl expressed (at top) as number of voles eaten per day for a family unit (parents + 3 young). The GEI taken from Table 14 (adults), Fig. 60 (juveniles to 60 days) and data in section 9.5 (adults during breeding) has been converted to vole numbers taking account of the annual variation in body weight and caloric content (Fig. 29). Lower panel shows the annual cycle of abundance of *Microtus arvalis*, the predominant prey, as estimated by trapping data in the central Netherlands (assembled from Cavé, 1968, scale indicates voles per 1000 trap-nights).

tude that it is conceivable that this has been one of the factors shaping the timing of the moult in the course of evolution.

In order to synchronize moult and the period of maximum abundance of the major prey, the Long-eared Owl must breed relatively early, at a time when the annual increase in prey numbers has only just begun (the snap-trap data on which Fig. 88 is based probably underestimate the late spring surge in numbers, as natural foods are abundant at that time and the traps less effective than later on). An important result of this early start is that when parental feeding comes to an end and the young owlets must learn to feed for themselves, they too can profit from the annual food peak. The annual cycle in the Long-eared Owl is thus so timed that for each age category the period during which food acquisition is likely to be beset with difficulties (for the adults the moult, for the juveniles the first stages of independence) coincides with maximum food abundance. By way of illustrating how the Long-eared Owl exploits the abundance cycle of its major prey, I have entered the daily requirement (as measured in number of voles) in the top of the figure (Fig. 88). The suggestive mirror-effect led to the formulation of the adaptive advantage of the timing of events in the annual cycle. In theory at least the magnitude of the advantage conferred is open to investigation by following the fates of individuals whose timing in relation to the local food peak is known. Quantifying the penalty to the individual of a mismatch between the annual cycle and the food supply is liable to be a large undertaking and one I leave gladly to others.

12. ACKNOWLEDGEMENTS

I want to express my deep gratitude to Prof. Dr. R. H. Drent for giving me the opportunity to carry out this work and for his stimulating coaching during the progress of this study. I realize how much I am indebted to him especially for his investment during the preparation of the manuscript. In this context I should not forget to mention Mrs. N. Drent for her hospitality during the many evening sessions while we discussed the manuscript.

I want to thank my colleagues at the Zoological Laboratory for their valuable discussion on many parts of this study. Especially I want to mention Dr. S. Daan who showed a stimulating interest throughout this study and critically read the greatest part of the manuscript, Dr. K. Westerterp who introduced me to the technique of oxygen measurements, Dr. P. J. Drent who coached the pilot study at the "Vosbergen", Dr. J. B. Hulscher and Dr. J. Tinbergen. I also wish to thank Dr. J. Veen for his editorial assistance.

Nearly all members of the technical and administration staff of the Zoological Laboratory helped me in numerous ways. The late Mr. F. Bahlman, Mr. J. J. Holtman and coworkers gave the captive owls excellent care and Mr. A. de Haan provided the daily food for the owls by breeding laboratory mice. The late Mr. H. H. Molenberg, Mr. J. H. Nijboer, Mr. W. Kremer and his staff contributed to this study by making many ingenious instruments, while Mr. J. W. Koenes and his co-workers built the cages and other wooden elements. Mr. W. J. Beukema and his staff developed the electronical weighing machine among numerous other things. Mr. J. H. H. Suurd provided glasswork and chemicals while Mr. H. Eggen and Mr. H. Visscher were always running the administration in an optimal fashion.

Many many thanks go also to Mrs. H. Lochorn-Hulsebos for typing the manuscript and to Mr. D. Visser for preparing the excellent figures. I am grateful to Mr. E. Hazebroek for providing the owl vignets in Fig. 13.

Mr. T. Wierstra from the "Rekencentrum" of the University of Groningen kindly computed some of the metabolic data.

Mrs. P. Meyer-Boss assisted in many "daily routines" as part of her analytical schooling and during a major part of this study. Mr. J. Beukema assisted in the laboratory measurements. I am very grateful to them.

Mr. B. Nijhoff assisted in the fieldwork. His knowledge of the owls and the area was indispensable. Many thanks go to Mr. J. Doevedans en Mr. H. Esselink who cooperated in the trapping work, and to Mr. F. Koning, J. Buker, S. Braaksma and H. Sandée for allowing me to use their weight and other data.

Dr. F. Goethe, "Vogelwarte Helgoland", kindly provided me with weight data for Long-eared Owls and Mr. B. J. Speek and Mr. R. Wassenaar, "Vogeltrekstation Arnhem", allowed me to use their ringing data. The latter computed the ring recoveries from Long-eared Owls. Dr. J. Wattel, Zoölogisch Museum, University of Amsterdam, and Dr. G. F. Mees, Rijksmuseum van Natuurlijke Historie, Leiden, kindly allowed us to inspect their skin collections and I thank Drs. F. Fuchs for access to the carcass collection of the Rijksinstituut voor Natuurbeheer, Arnhem. Dr. J. Mertens, Instituut voor Oecologisch Onderzoek, Arnhem, kindly analyzed owl eggs, while Dr. I. N. Nilsson, University of Lund, Sweden, provided me with pellets from his area.

During the whole period when I was engaged in this study many students cooperated in parts of the work. Without their help such an extensive study would not have been possible. I'm very grateful to their devoted help and their permission to let me use their data. I want to mention here: D. de Groot, J. Haer, B. Hoentjen, W. Iedema, J. de Jong, W. Kuyer-Feitsma, W. Middelbeek, G. J. Punt, J. Vat, G. v. Veen, N. de Vries, J. Wanink and K. de Wit. In addition many 3rd year students helped during the yearly ecology course in the field or in laboratory.

Numbers of landowners, too numerous to mention, allowed me access to their property. I want to make an exception for "Natuurmonumenten" in particular for the Westerbroek study site and for the "Kraus-Groeneveld Stichting" for the Vosbergen estate. Mr. K. ter Veld kindly gave us permission to count owls at the roost located in his garden and to collect pellets there during several winters. Many naturalists gave me information on nest locations and on winterroosts. This valuable aid was very much appreciated.

Finally I want to express my gratitude to my wife Agnes, who apart from typing parts of the manuscript and doing many other odd jobs, facilitated me so much in doing this intensive work. Her stimulating force was vital in finishing this thesis.

13. SUMMARY

1. The period 1974—1979 was devoted to assembling an energy budget (see Fig. 1) for free-living Long-eared Owls in the northern Netherlands with a view towards identifying energetic bottlenecks of critical importance to the timing of the annual cycle in relation to seasonal variation in the abundance of the prey.
2. The diet of the Long-eared Owl was investigated by identifying prey remains in pellets and remains found at the nest (Table 6, Fig. 15). Small rodents predominated, with *Microtus arvalis* constituting 72% of all prey items (birds provided only 12.9% of prey biomass). Local variation was noted in the study area (Fig. 16) with a higher incidence of birds in the diet in built-up areas. The main dietary change associated with the vole cycle (Fig. 17) involves substitution of birds for voles as vole abundance declines. Compared to Nilsson's (1981) study in southern Sweden, the diet in my study area was more diverse and showed less seasonal variation (Fig. 18).
3. Food intake of free-living owls was derived from the pellets. First, pellet production was studied in captivity (for apparatus see Fig. 19) and it was found that pellets are cast not only during the daylight roosting period, but also during the night. There is a clear seasonal pattern in the incidence of night pellets (Fig. 20) related to the length of the dark period. Field experiments (where miniature radios were fed to free-living birds and subsequently recovered in the pellets) confirmed the production of night pellets, and intensive search yielded an adequate sample (Table 7). Integration of the laboratory trials and field data provided an estimate of the weight of the daily pellet output through the year for field conditions.
4. Feeding trials with captive owls provided information on the digestibility of the various prey species (expressed as the Metabolized Energy Coefficient, Fig. 27) and on the amount of dry matter reappearing in the pellets as residue (Fig. 27). Once species composition of the pellet is known, these data allow reconstruction of the food ingested (sample calculations in Table 14). This method provides a more reliable approach than counting prey remains in the pellets, on account of the loss of bony parts during digestion.
5. Combination of the information on the annual cycle of pellet production reconstructed for free-living birds, with an analysis of pellets from the field allow computation of daily pellet residue per prey type (Table 14) and hence of the daily gross food intake GEI (Fig. 30) throughout the period for which the pellets can be readily collected in the field (August through March).
6. Gross daily intake was corrected for the measured metabolizable energy coefficients (taking into account seasonal variation in digestibility, Fig. 28, and in caloric content of the prey, Fig. 29) to provide an estimate of net energy (metabolized energy) available for free-living owls outside of the breeding season (Fig. 30).
7. Indirect calorimetry (estimation of metabolism by measuring respiratory gas exchange) was employed to determine seasonal variation in Basal Metabolic Rate (BMR) and to quantify the cost of temperature regulation. BMR when expressed as energy expended per bird per day, the quantity we need for our energy budget, varies only slightly in the course of the year (Fig. 31).
8. Costs of temperature regulation show a strong seasonal variation under influence of the moult. In late summer, at the peak of the moult, the lower critical temperature reaches the highest value of the year (Fig. 33) and during a considerable part of the 24 hr the Long-eared Owl will have to metabolize in excess of BMR to maintain body temperature; the cost of maintaining a given gradient between body and ambient air is also maximal at that time of year (Fig. 35) on account of the reduced insulation value of the plumage.
9. The nocturnally active Long-eared Owl was found to show a reversed daily cycle in body temperature and metabolism, highest values being measured at night (Fig. 36, Fig. 37). Under conditions of prolonged fast-

ing the BMR gradually declines (Fig. 36) as has been deduced for other birds under starvation conditions.

10. A modified wind-tunnel and artificial sources of radiation were employed to simulate microclimate conditions in the day roost. Metabolic response (Fig. 38) showed that the effect of wind (increased heat loss) and of radiation (heat gain from the surroundings) are more or less in balance, and hence the results from metabolism chamber measurements can be applied to the field.
11. A literature compilation of BMR in *Strigiformes* shows the group to be relatively uniform in this respect, differences between species showing no simple correlations with distributional patterns. The overall level is lower than predicted by general compilations of BMR in non-passerine birds (Fig. 39).
12. Other components of energy expenditure were quantified by carrying out longterm balance trials with captive owls kept in small individual cages (where food intake, output of faeces and pellets, and body weight changes of the birds were monitored for periods of 5 days at a given temperature and light/dark regime). Analysis of these so-called ME trials (corrected for zero weight change) suggested that the heat increment of feeding (SDA) is not lost at temperatures below the thermoneutral zone, but can be completely utilized as a contribution towards the heat production required to maintain body temperature (Fig. 40). Moreover, comparison with the energy expenditure data of birds at rest in the respiration chamber indicated that cage locomotion incurred only a negligible increment in the budget of the caged birds. This means that, if due regard is paid to costs of temperature regulation and the compensatory effect of SDA, the ME trials provide a useful starting point for assembling the budget of energy expenditure for free-living birds.
13. Compilation of ME values for *Strigiformes* and *Falconiformes* confirms the weight exponent deduced by Kendeigh *et al.* (1977) for non-passerines in general, but the values lie at a lower intercept (as was the case in the BMR) Fig. 41.
14. The duration of flight activity was quantified with the aid of radio-telemetry whereby bearings on free-living owls could be obtained simultaneously from two vehicles equipped with directional antennas (methods see Fig. 42). Characteristics of the signal combined with information on displacement allowed flight to be distinguished in most cases from other activities such as preening. During hunting flight occurs in short bouts (Fig. 46A) and is strongly inhibited by rain and sleet (Fig. 44). During winter five Long-eared Owls were followed for prolonged periods, and flight time averaged 2.5 hours per 24 hr (Table 20).
15. Substituting Pennycuick's (1972, 1975) prediction for flight cost in the time-budget data for the Long-eared Owl in winter allows the budget to be balanced (Chapter 7: expenditure tallies with intake as derived from the pellet method) and therefore Pennycuick's model is applied for the rest of the year as well, as no independent estimate of cost of flight *per se* was undertaken.
16. Costs of gonadal growth, the production of eggs, incubation and brooding of the nestlings were estimated indirectly from current models provided by Kendeigh *et al.* 1977. The time-budget data for nest-care are given in Fig. 47.
17. Growth in the Long-eared Owl was studied by hand-rearing birds in captivity, and relating the laboratory measurements to the growth curve established for the field (Fig. 48 and Appendix 3). Linear growth (Fig. 49) and increase in weight (Fig. 50) were also measured for the plumage.
18. In the course of development the body composition changes (Fig. 52) and the caloric content per g fresh weight increases linearly (Fig. 51) allowing estimation of the caloric increments of growth.
19. There is an overshoot of BMR in the growing nestlings in comparison to the levels expected on the basis of the relation between BMR and body weight in adult *Strigiformes* (Fig. 53, 54) and temperature regulation becomes established only after the BMR has exceeded the level predicted for adults (Fig. 55).
20. Digestibility (Metabolizable Energy Coefficient) is high at first and declines gradually to adult levels (Fig. 56) accompanied by a progressive change in the caloric density of the pellets (Fig. 57). Balance data suggest that growing owlets extract more minerals from their food than adults do (requirement for bone development).
21. ME data when plotted in relation to change in body weight of the growing owlets allows estimation of the metabolic cost of adding increments to the body and permits extrapolation to zero growth (definition of maintenance energy, see Fig. 58 and Table 24).
22. Data from points 17 through 21 are integrated in an idealized energy budget for growth in the Long-eared Owl (Fig. 59 and Appendix 3) up until first flight and tentatively up to independence (Fig. 64). In the nestling period (first 21 days of life) the efficiency of biosynthesis of new tissue is estimated at 72.5%, and over the entire period until first flight (the first 33 days of life) growth (excluding cost of biosynthesis) accounts for 24% of all energy metabolized (a figure in close agreement with other studies in nidicolous birds, Table 27). According to this model temperature regulation is a minor cost until the owlets leave the nest, as the female parent is believed to maintain near-thermoneutral conditions. Activity is estimated to account for 31% of all energy metabolized up until first flight.
23. Analysis of growth rate in *Strigiformes* reveals that open-nesters such as the Long-eared Owl show accelerated growth rates and shorter nestling periods than hole-nesting owls of similar body weight (Fig. 61). The Long-eared Owl leaves the nest prematurely and achieves first flight at an age corresponding to nest departure in hole-nesting forms. For comparative purposes the growth model up to first flight (33 days) is most in line with other nidicolous birds.
24. The annual cycle of body weight in adult Long-eared Owls (Fig. 63) shows a marked differentiation between the sexes: body weight in the male is regulated at a lower level during breeding, when he alone provides food for the family. The female undergoes a long period of near-immobility at the nest, increasing sharply in weight due to fat deposition during the egg stage, and returning to normal levels during the nestling stage.
25. Data on food input to the nest (Fig. 68) obtained by means of a weighing platform (Fig. 67) are congruent with tentative energy budgets for the female (Table 28) and indicate a surplus during the egg stage sufficient to explain the weight increase in the nesting female. The

energy provided by drawing on this depot during the nestling stage allows the energy budget of the growing family to be met (growth requirement constructed from Fig. 59). The male doubles his flight expenditure during the breeding period (his flight time goes up to 5.5 hr per 24 hr).

26. Differences in flight activity between the sexes during breeding are seen as adaptations to reduce hunting costs; the buffer mechanism of fat deposition is energetically advantageous when linked with relative immobility (see predicted flight cost as a function of body weight, Fig. 65).
27. Phenology of the moult in the Long-eared Owl is described on the basis of field data and measurements on captive individuals (summarized in Fig. 70 and 80).
28. Metabolism measurements during moult (Fig. 85, Fig. 86) allow estimation of the elevation in energy expenditure associated with the moult (an increment of approximately 10% of the daily energy expenditure for free-living birds as compared to the subsequent period). Moult itself incurs a higher cost, but this is partly offset by a decline in locomotor activity at this time.
29. Energy expenditure for free-living Long-eared Owls in the course of the year is summarized in Fig. 87 and 88. Peak energetic demands (during breeding) fall relatively early in relation to the abundance of the main prey. It is argued that the timing of events in the annual cycle is related to hunting yield, and that the moult may be as critical a hinge-point as is reproduction.

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15. SAMENVATTING

Voor de veldornitholoog staat onderzoek naar de tijdsbesteding en de energiehuishouding van vrijlevende vogels centraal. Verwonderlijk is dit niet als we ons realiseren dat alle handelingen van een vogel gevolgen hebben voor de balans van energie-opname en -uitgave. Een evenwicht in deze balans en een goede verdeling van energiekostende processen door het jaar heen, in relatie tot het beschikbare voedsel zijn van belangrijke adaptieve waarde. Dit artikel beschrijft een onderzoek naar zo'n energiebudget bij de Ransuil. De centrale vragen in dit onderzoek waren: 1) hoe groot is de dagelijkse voedselopname (= energie-opname), 2) hoe kunnen we de energie-uitgaven onderverdelen en 3) hoe variëren deze uitgaven door het jaar heen. In dit verband willen we vooral ook de kosten van de twee belangrijke productieve processen (voortplanting en rui) bepalen, om de plaatsing in de jaarcyclus te leren begrijpen. Voor het beantwoorden van deze vragen was het noodzakelijk om naast veldonderzoek ook onderzoek in het laboratorium te doen met behulp van een aantal in gevangenschap gehouden uilen. De opbouw van zo'n energiebudget, tevens de indeling van het artikel, is samengevat in Fig. 1, waarbij links de methoden staan om te komen tot een schatting van de dagelijkse voedselopname en rechts de verschillende uitgaven.

Na een kort overzicht van de jaarcyclus van de Ransuil (Fig. 14) en het voorkomen in de provincie Groningen (Fig. 3) wordt de voedselsamenstelling besproken aan de hand van braakbalanalyses. Kleine zoogdieren domineren, waarbij de Veldmuis 72% van het prooitotaal uitmaakt (tabel 6, Fig. 15). De belangrijkste variatie in de prooisamenstelling toont verband met de veldmuizencyclus. In veldmuisdaljaren worden vooral vogels talrijker gegeten, hoewel ook in deze jaren de Veldmuis nog altijd meer dan 50% van de prooien uitmaakt. Lokale verschillen in de prooisamenstelling bestaan er vooral uit dat in het meer verstedelijkte gebied in en om de stad Groningen meer vogels worden geslagen.

Braakballen spelen ook een belangrijke rol in de schatting van de hoeveelheid opgenomen voedsel. Hiertoe was het eerst nodig om na te gaan hoeveel braakballen de Ransuil per etmaal produceert, aangezien hierover in de literatuur onduidelijkheid bestaat. Met behulp van een apparaat waarbij we de tijdstippen van de maaltijden en de tijdstippen waarop de braakballen werden geproduceerd konden registreren (Fig. 19) verkregen we hierin inzicht. Braakballen worden niet alleen overdag geproduceerd maar ook 's nachts, de actieve periode van de uil. Er bestaat een duidelijke seizoenstrend in de produktie van het aantal nachtbraakballen, verband houdend met de nachtlengte. Door middel van proeven in het veld ("witte muizen proef" en mini-radiozendertjes) kregen we een direct bewijs van de produktie van nachtbraakballen bij vrijlevende uilen. Door nu de laboratoriumgegevens te combineren met de veldgegevens was het mogelijk een schatting te maken van het totaal gewicht van de dagelijkse braakbalproduktie.

Bij in gevangenschap gehouden uilen hadden we ondertussen voor een aantal belangrijke prooisoorten vastgesteld hoeveel procent van het opgenomen voedsel als niet-verteerbaar materiaal in de braakballen terecht komt. Nu is het mogelijk om, uitgaande van de prooisamenstelling van de braakballen uit te rekenen wat één gram braakbal betekent in grammen opgenomen voedsel. De energie-inhoud van de prooisoorten werd bepaald met behulp van een bomcalorimeter. Dit wetende kunnen we nu de dagelijkse bruto energie-opname berekenen (GEI). Niet al het opgenomen voedsel is, zoals we gezien hebben, metaboliseerbaar voor de uil. Uit kooiexperimenten is gebleken dat, afhankelijk van de prooisoort en de tijd van het jaar deze metaboliseerbare fractie (MEC) varieert van 0.61 tot 0.79. Betrekken we deze gegevens nu in onze schatting van de dagelijkse voedselopname dan houden we de netto besteedbare hoeveelheid energie (ME) over. Voor de maanden augustus t/m november en voor maart is dit ongeveer 274 kJ per dag, terwijl in de maanden december t/m februari onze schatting wat lager uitkomen. In de eerstgenoemde periode betekent dit een bruto voedselopname van ± 52 g Veldmuis (ongeveer 3 muizen) per nacht. In de voortplantingsperiode is deze braakbal-methode niet goed bruikbaar, omdat de voedselopname van het wijfje een ander patroon vertoont en omdat braakballen van de jongen enigszins afwijken.

Aan de kant van de energie-uitgaven kunnen we in de eerste plaats de ruststofwisselings-component (basaalmetabolisme = BMR) en de kosten voor temperatuurregulatie (TR) onderscheiden. Deze werden bepaald m.b.v. indirecte calorimetrie (d.i. het meten van de zuurstofopname en de kooldioxydeproduktie). De BMR varieerde relatief weinig in de loop van het jaar, daarentegen vertoonden de kosten voor temperatuurregulatie wel een duidelijke seizoenstrend. In de late zomer, tijdens de piek van de rui, bereikte de laagste kritische temperatuur zijn hoogste waarde en was ook de helling van de temperatuurscoëfficient het steilst (Fig. 33). Dit wijst op een verminderde isolatie van het verenkleed. Uit een analyse van BMR gegevens voor verschillende uilensoorten blijkt deze groep overigens een lagere BMR te hebben dan voorspeld wordt door de algemene vergelijking voor niet-zangvogels (Fig. 39).

Andere componenten van de energie-uitgaven werden gekwantificeerd door 5-daagse balansmetingen, waarbij de uilen in kleine kooitjes werden gehouden en waarbij de voedselopname, de produktie aan braakballen en faeces tezamen met veranderingen van het lichaamsgewicht elke dag werden gemeten. Wanneer deze ME-metingen (gecorrigeerd voor constant gewicht) worden vergeleken met de zuurstofmetingen bij vastende uilen dan blijkt dat voor omgevingstemperaturen beneden de laagste kritische temperatuur een belangrijk deel van het zogenaamde warmteeffect dat bij de vertering van voedsel optreedt niet verloren gaat maar gebruikt kan worden voor de temperatuurregulatie. Opnieuw blijkt dat wanneer we de ME-metingen van uilen vergelijken met die van de niet-zangvogels van overeenkomstige gewichten de uilen minder energie verbruiken (Fig. 41).

Om te komen tot een energiebalans voor vrijlevende Ransuilen ontbreekt nu nog een belangrijke component, nl. de tijd en energie welke besteed wordt aan vliegen. De duur van de vliegactiviteit hebben we getracht te meten door een aantal uilen uit te rusten met een miniatuur radiozendertje. Deze uilen konden continue gevolgd worden met behulp van twee auto's uitgerust met draaibare peilantennes (Fig. 42). Veranderingen in het signaal tijdens het vliegen maakte het mogelijk om de vliegtijd per nacht te meten. In de winter bedraagt deze gemiddeld 2,5 uur, waarbij veel individuele variatie en variatie door weersomstandigheden mogelijk is (Tabel 20). De kosten van vliegen konden niet gemeten worden, maar substitutie van Pennycuicks (1972, 1975) voorspelling van vliegkosten, waarbij lichaamsgewicht en vleugellengte de belangrijkste parameters zijn, laten zien dat deze waarden de inkomsten-uitgavenbalans met elkaar in overeenstemming brengen.

In de voortplantingsperiode werden de kosten van de groei van de gonaden, de produktie van eieren en het bebroeden van de eieren en later van de jongen berekend met behulp van gangbare modellen zoals deze vooral door Kendeigh, Gavrilov en Dolnik (1977) zijn ontwikkeld. Daarnaast werd ook getracht een energiebudget van de opgroeiende jonge uilen op te stellen. De toename van het lichaamsgewicht en de lengte van de slagpennen werden in het veld gemeten. Van een aantal dode jonge uilen werd de lichaamssamenstelling geanalyseerd. In de loop van de ontwikkeling neemt de calorische waarde per gram vers gewicht lineair toe (Fig. 51), voornamelijk door een afname van het watergehalte.

Door jonge uilen met de hand op te fokken onder omstandigheden vergelijkbaar met de veldsituatie konden metingen worden verricht die anders niet of zeer moeilijk waren uit te voeren. Uit zuurstofmetingen bleek dat op lichaamsgewichtbasis de BMR van opgroeiende uilen hoger was dan die van adulte uilen en dat de temperatuursregulatie pas na 10—14 dagen grotendeels ontwikkeld was (Fig. 55). De MEC was in het begin hoog en nam geleidelijk af tot het niveau van de adulte uilen (Fig. 56). Voor de vorming van de botten haalden de jonge uilen meer mineralen uit hun voedsel dan adulte uilen.

Door nu de ME-metingen grafisch uit te zetten tegen de gelijktijdige metingen van de dagelijkse groei was het mogelijk door extrapolatie naar "nulgroei" de kosten te schatten van de lichaamsgroei (Fig. 58). Al deze gegevens uit gecombineerd veld- en laboratoriumonderzoek werden uiteindelijk geïntegreerd in een geïdealiseerd groei-energiebudget voor de periode tot 35 dagen na het uitkomen (Fig. 59, Appendix 3). In het veld verlaten de jonge Ransuilen na ongeveer 21 dagen het nest en vinden de eerste vliegpogingen na ongeveer 33 dagen plaats. Gedurende de eerste 21 dagen was de efficientie van de biosynthese voor de groei 72.5%. Over de gehele groeiperiode tot de eerste vlucht wordt ongeveer 24% van de totale ME in de groei geïnvesteerd, exclusief de kosten voor biosynthese. Deze getallen zijn in redelijke overeenstemming met gegevens van andere nestblijvende soorten. Wanneer we binnen de groep van de uilen de groeisnelheden vergelijken dan blijken de opennestbroeders als de Ransuil een hogere groeisnelheid en een kortere nestperiode te hebben dan in holen broedende uilen van gelijk lichaamsgewicht (Fig. 61).

Het energiebudget van de adulte Ransuilen in de broedperiode hangt nauw samen met de verschillen in taakverdeling tussen de beide sexen en de gewichtsveranderingen. In de winterperiode zijn de mannetjes gemiddeld 30 gram lichter dan de wijfjes (Fig. 63). In het voorjaar zorgt het mannetje voor de prooiaanvoer van het broedende vrouwtje en later ook voor de opgroeiende jongen. Het gewicht van het mannetje gaat in deze periode iets naar beneden, wat resulteert in lagere vliegkosten. Het vrouwtje ondergaat nu een lange periode van bijna immobiliteit. Tijdens de eifase gaat haar gewicht sterk omhoog door vetopslag. Daarna, in de nestjongfase gaat haar gewicht weer terug naar normale waarden, waarschijnlijk iets lager dan die in de winter. Door middel van continue observaties bij nesten, aangevuld met metingen m.b.v. een elektronisch weegplatform, konden we de totale voedselaanvoer bij het nest meten. Gedurende de eifase zien we dat er inderdaad een surplus aan voedsel wordt aangevoerd, voldoende om de gewichtstoename van het vrouwtje te verklaren. Na het uitkomen van de jongen neemt de prooiaanvoer van het mannetje verder toe doch het vrouwtje moet nu interen op haar eerder opgebouwde reserve. We zien de verschillen in vliegactiviteit tussen de sexen als een adaptatie om de gezamenlijke jaagkosten te reduceren. Het buffermechanisme van het vrouwtje is alleen dan energetisch voordelig als ze haar vliegtijd sterk weet te beperken (Fig. 65).

De phenologie van de rui van zowel vliegpennen als lichaamsveren werd vastgesteld aan de hand van veldgegevens en bij uilen in gevangenschap. In Fig. 70, 80 en 81 zijn de resultaten samengevat. Het totale verenkleed van de Ransuil is ongeveer 34 gram, aanzienlijk meer dan van andere vogels van gelijk lichaamsgewicht. Tijdens de piek van de rui wordt ongeveer 2,2 gram veren per week geproduceerd. Op grond van zuurstofmetingen schatten we de verhoging van de dagelijkse energie-uitgaven bij vrijlevende uilen tengevolge van de rui op ongeveer 10% in de periode van intensieve rui (juli t/m september).

In de slotdiscussie tonen we aan dat op grond van gegevens die beschikbaar zijn we de Ransuil in vergelijking met een aantal andere roofvogelsoorten moeten beschouwen als een buitengewoon economische jager. De energie-uitgaven buiten het broedseizoen zijn, uitgedrukt in BMR-eenheden duidelijk lager dan deze soorten, maar vergelijkbaar met een groot aantal andere niet-zangvogels. Aangezien echter BMR ook lager is vergeleken bij deze laatste groep is dus in absolute zin de Ransuil zeker "goedkoop" te noemen. De isolatie-waarde van zijn verenkleed kan deze lagere energie-uitgaven in belangrijke mate verklaren.

Tenslotte geeft Fig. 88 een berekening hoeveel voedsel (in termen van aantallen Veldmuizen) een Ransuil-familie op jaarbasis nodig heeft. Deze figuur laat tevens een jaarverloop van de Veldmuispopulatie zien, gebaseerd op gegevens van Cavé (1968). Rui vindt plaats in de periode van hoge dichtheden aan Veldmuizen. Omdat hun vliegvaardigheid door het ontbreken van een aantal veren waarschijnlijk achteruit gaat en het vliegen bovendien duurder wordt is dit extra belangrijk. (Lager jaagrendement is aangetoond bij de Torenvalk in deze periode, Daan & Masman, 1982). Verschuiving van de ruiperiode in de richting van de winter doet bovendien de kosten verder stijgen. Om het samenvallen van de voortplanting en de rui (cumulatie van kosten) te vermijden moet de voortplantingsperiode vrij vroeg in het jaar plaatsvinden. Bovendien kunnen nu en dat is zeker zo belangrijk de jongen op het moment dat ze zelfstandig worden profiteren van de veldmuizenpiek.

Appendix 1. Prey composition during the breeding season (April—June); percentages based on number

	1974	1975	1976	1977	1978	1974—1978
Microtus arvalis	76.3	63.7	59.9	78.8	55.1	66.8
Apodemus sylvaticus	10.8	5.5	20.3	11.4	24.8	14.6
Clethrionomys glareolus	0.2	—	1.6	0.4	—	0.4
Microtus agrestis	6.5	0.1	3.7	0.8	0.6	2.3
Micromys minutus	1.3	1.4	0.6	0.4	1.2	1.0
Sorex araneus	0.4	4.6	2.1	0.4	1.6	1.8
Mus musculus	—	0.2	—	—	0.8	0.2
Crocidura russula	1.2	3.1	—	3.1	0.7	1.6
Arvicola terrestris	0.1	—	—	—	1.6	0.3
Rattus norvegicus	0.1	—	—	—	0.7	0.2
Talpa europaea	—	—	0.1	—	0.5	0.1
Arvicola or *Rattus* (juv.)	0.3	—	0.5	0.4	—	0.2
Oryctolagus cuniculus/ *Lepus timidus* (juv.)	—	—	0.4	—	1.6	0.4
Sorex minutus	—	0.6	0.4	0.8	0.1	0.4
Neomys fodiens	—	0.2	—	—	—	0.0
Aves, body weight > 45 g	0.5	4.2	1.4	0.4	2.9	1.9
Aves, body weight 20—45 g	1.2	9.3	6.3	2.4	3.0	4.4
Aves, body weight < 20 g	1.3	6.7	2.2	0.8	5.3	3.3
Total number of prey	953	921	600	224	1054	3752

Appendix 2. Bird prey of the Long-eared Owl; results of pellet analysis and (a few) determined prey in nests. Combination of all data in the study area during the period 1969—1979

	Number	% of identified bird total (numbers)	Body weight (g)	% of identified bird total (weight)
Body weight larger than 45 g (mean 85 g)				
Turdus musicus	17		65	
Turdus viscivorus	1		100*	
Turdus pilaris	1		100	
Turdus merula	63		100	
Turdus philomelos	4		70	
Turdus sp., total	232	11.6	90	25.7
Sturnus vulgaris	211	10.6	80	20.7
Streptopelia turtur	1	0.0	100*	0.0
Vanellus vanellus	1	0.0	100*	0.0
Total identified	445			
Not identified**	298			
Total	743	22.7 (of all bird total)		53.5 (of all bird total)
Body weight between 20 and 45 g (mean 25 g)				
Fringilla coelebs/F. montifringilla	135	6.8	26	4.3
Pyrrhula phyrrhula	6	0.3	30	0.2
Passer domesticus/P. montana	640	32.1	28	22.0
Prunella modularis	14	0.7	23	0.4
Chloris chloris	3	0.15	28	0.1
Hippolais icterina	2	0.1	20	0.0
Erithacus rubecula	84	4.2	21	2.2
Total identified	884			
Not identified**	727			
Total	1611	49.2 (of all bird total)		34.1 (of all bird total)
Body weight smaller than 20 g (mean 15 g)				
Parus major	215	10.8	19	5.1
Parus caeruleus	103	5.2	12	1.5
Parus montana	3	0.2	10	0.0
Aegothalos caudatus	6	0.3	7	0.1
Parus ater	7	0.4	10	0.1
Parus sp., total	334	16.7	16	6.7
Carduelis carduelis	6	0.3	17	0.1
Carduelis spinus	238	11.9	13	4.1
Carduelis flavirostris	3	0.15	15	0.0
Carduelis cannabina	14	0.7	19	0.3
Troglodytes troglodytes	20	1.0	8	0.2
Regulus regulus	36	1.8	6	0.3
Regulus ignicapillus	1	0.0	6	0.0
Certhia brachydactyla	2	0.1	8	0.0
Phylloscopus sibilatrix	1	0.0	16	0.0
Anthus sp.	2	0.1	19	0.0
Hirundo sp.	1	0.0	19	0.0
Sylvia communis	1	0.0	10	0.0
Sylvia atricapilla	1	0.0	19	0.0
Sylvia borin	1	0.0	19	0.0
Sylvia sp.	5	0.25	10	0.0
Carduelis carduelis flammea	1	0.0	14	0.0
Total identified	667			
Not identified**	256			
Total	923	28.1 (of all bird total)		11.7 (of all bird total)
Birds total identified	1996			
Birds total not identified	1281			
Birds total	3211		36	

*) 100 g was arbitrary chosen as upper limit of prey weight eaten.

**) A number of prey were only classified according to the three classes of body weight.

Appendix 3. Parameters of the growth budget of the Long-eared Owl

Age (days)	Mean body weight (g) and sample size	Smoothed body weight (g)	Daily increment (g) × cost factor (kJ) = growth (kJ)	$ME_{0\,\mathrm{growth}}$ (kJ bird^{-1})	TR (kJ bird^{-1})	ME_{total} (kJ bird^{-1})	BMR (kJ bird^{-1})
0	17.4 (14)	19.3		10.8			5.5
1	18.8 (10)	23.6	4.3 × 7.9 = 34.0	14.0	—	48.0	7.2
2	24.1 (22)	28.9	5.3 × 7.9 = 41.9	18.0	—	59.9	9.5
3	33.5 (18)	35.2	6.3 × 7.9 = 49.8	23.1	—	72.9	12.4
4	45.8 (17)	42.5	7.3 × 8.0 = 58.4	29.3	—	87.7	16.0
5	54.0 (16)	51.1	8.6 × 8.0 = 68.8	37.0	—	105.8	20.6
6	63.7 (18)	60.8	9.7 × 8.1 = 78.6	46.3	—	124.9	26.2
7	70.8 (19)	71.7	10.9 × 8.1 = 88.3	57.2	—	145.3	32.8
8	91.4 (17)	83.7	12.0 × 8.2 = 98.4	69.8	—	168.2	40.5
9	104.3 (24)	96.6	12.9 × 8.3 = 107.1	83.9	—	191.0	49.1
10	118.3 (19)	110.1	13.5 × 8.4 = 113.4	99.2	—	212.6	58.4
11	129.3 (21)	124.0	13.9 × 8.6 = 119.5	115.1	1.5	236.1	67.9
12	132.9 (18)	137.5	13.9 × 8.8 = 122.3	131.3	2.4	256.0	77.4
13	155.2 (27)	151.4	13.5 × 9.0 = 121.5	147.1	3.3	271.9	86.4
14	167.2 (28)	164.3	12.9 × 9.3 = 120.0	161.9	3.5	285.4	94.7
15	180.1 (29)	176.3	12.0 × 9.7 = 116.4	175.4	3.6	295.4	102.0
16	194.4 (27)	187.2	10.9 × 10.1 = 110.1	187.3	3.8	301.2	108.2
17	200.1 (28)	196.6	9.7 × 10.4 = 100.9	197.6	4.0	302.5	113.3
18	212.9 (29)	205.5	8.6 × 10.6 = 91.2	206.2	5.0	302.4	117.5
19	208.9 (21)	212.8	7.3 × 10.8 = 78.8	213.3	6.0	298.1	120.9
20	214.9 (29)	219.1	6.3 × 10.9 = 68.7	219.1	7.0	294.8	123.5
21	223.8 (28)	224.4	5.3 × 11.0 = 58.3	223.7	7.7	289.7	125.5
22	225.6 (21)	228.7	4.3 × 11.1 = 47.7	227.4	37.7	312.8	127.1
23	228.4 (24)	232.4	3.7 × 11.2 = 41.4	230.2	38.1	309.7	128.3
24	233.3 (12)	235.4	3.0 × 11.2 = 33.6	232.5	38.5	304.6	129.2
25	246.2 (12)	237.8	2.4 × 11.3 = 27.1	234.2	38.9	300.2	129.9
26	239.2 (9)	239.8	2.0 × 11.3 = 22.6	235.5	39.0	297.1	130.4
27	224.5 (9)	241.4	1.6 × 11.4 = 18.2	236.6	39.1	293.9	130.8
28	228.6 (9)	242.7	1.3 × 11.4 = 14.8	237.4	39.2	291.4	131.1
29	235.4 (9)	243.8	1.1 × 11.4 = 12.5	238.0	39.3	289.8	131.3
30	230.5 (8)	244.6	0.8 × 11.4 = 9.1	238.5	39.4	287.0	131.5
31	248.7 (4)	245.3	0.7 × 11.4 = 8.0	238.8	39.5	286.3	131.6
32	232.5 (2)	245.8	0.5 × 11.4 = 5.7	239.1	39.5	284.3	131.7
33	269.5 (2)	246.3	0.5 × 11.4 = 5.7	239.3	39.5	284.5	131.8
34	244.0 (2)	246.6	0.3 × 11.5 = 3.5	239.5	39.5	282.5	131.8
35		246.9	0.3 × 11.5 = 3.5	239.6	39.5	282.6	131.9

For derivation see text. The column "smoothed body weight" refers to the daily values predicted from the logistic growth equation fitted to the field data. It will be noted that growth as here given includes the cost of biosynthesis. The column $ME_{0\,\mathrm{growth}}$ provides the metabolic cost at zero growth derived from the balance trials. ME_{total} = Growth + $ME_{0\,\mathrm{growth}}$ + TR.

Appendix 4. Monthly variation in Metabolized Energy measured in small cages (ME_{cage}) at temperatures close to the mean month temperature

	ME_{cage} (kJ bird^{-1}day^{-1})	Number of 5 day trails	95% confidence interval	Mean body weight (g)
January	168.0	3	150.5—185.5	290.3
February	160.4	3	111.7—209.1	290.2
March/April	197.0	7	166.0—228.0	350.9
May	183.9	10	157.2—210.6	287.1
June	186.3	5	142.6—230.0	261.8
July	229.6	5	191.5—267.7	266.2
August	266.0	5	232.5—300.5	266.0
September	215.3	5	196.3—234.3	268.6
October	191.5	8	172.4—210.6	285.5
November	184.8	5	131.1—238.5	262.8
December	168.0	1	—	286.0