Ecological energetics of the long-eared owl (Asio otus)

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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

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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.

14. REFERENCES

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