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## The annual cycle of the kestrel *Falco tinnunculus*

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## Chapter 7

### Epilogue

The kestrel research project of the Department of Zoology (University of Groningen) aims to evaluate the evolutionary benefits endowed on individuals by the temporal order in their behaviour. In the tradition of the Animal Ecology Section of the department, founded by the late Prof. Dr. L. Tinbergen, the project has taken an empiry - rather than theory-based approach to the problem of temporal organization. With the maturation of behavioural ecology as a branch of science the skeleton of theory often tends to outgrow the flesh of empirical data. Frequently the question 'how should an individual behave?' is answered and the answer then compared with reality. Our approach has been to quantitatively describe the real situation first and then ask what the consequences of alternative strategies would be.

Such consequences should eventually be measured in the currency of reproductive fitness. The relationship between behaviour and fitness is rarely immediate. The present thesis therefore investigates the daily balance of energy intake and expenditure as an intermediate link. This choice is based on the consideration that daily energy balance on the one hand reflects short-term results of behavioural decisions, on the other hand affects survival and hence reproductive prospects. The project extends the earlier research of Wijnandts (1984) on the nocturnal Long-eared owl to its diurnal counterpart as a vole hunter, the European Kestrel. This intermediate sized bird combines visibility with an overseable home range of about 400 ha. A broad background of knowledge on reproduction and population biology was assembled by Cavé (1968). In the earlier stages of the project the daily organization of hunting and feeding were analyzed (Rijnsdorp et al. 1981) and its consequences for energy expenditure and reproductive perspective estimated (Daan & Aschoff 1982).

The present thesis is the result of a joint enterprise, supported in particular by the participation of many students, to firmly establish the daily energy budget of the freeliving bird throughout its annual cycle as well as of major factors in the environment and the animals

behavioural and physiological repertoire which affect the energy budget. The primary conclusions drawn from this work can be summarized as follows:

We started by addressing the question of constraints on the time spent foraging per day (chapter 2). The use of time of freeliving kestrels was analysed on the basis of 417 dawn-to-dusk observations of focal birds, including 18 in which male parents were put under increased demand from their brood by removing prey brought to the nest. Kestrels obtained their prey (92% common voles, Microtus arvalis) primarily by flight-hunting. On average no more than 3.6 hours per day was spent in flight-hunt, by males provisioning their broods in summer. Neither in winter, when food is hard to come by and hunting yields are low (2.2 small mammals per hour flight-hunt), nor in summer (average yield 4.7), with high food demands from the nest, was hunting time constrained by daylength. Analysis of foraging modes showed a predominance of the low cost-low yield technique of perch-hunting in winter. This is incompatible with Schoener's (1971) classic principles of time minimization and energy maximization which both would predict flight-hunting to be the preferred mode. It rather suggests that non-breeding kestrels minimize daily energy expenditure, as demonstrated earlier for non-breeding sunbirds (Pyke 1979). The breeding situation is characterized by sexual task differentiation: females refrain from foraging, males hunt virtually only from windhovering flight, the increased yield of which renders additional perch-hunting futile.

Male parents restricted total flight to 4.6 hours per average day. Since experimental fasting of the brood induced them to expand their efforts for several days, we argue that it is not energy expenditure itself which constrained parental effort. With flight hours increasing beyond 4.6 per day, energy intake levels off at  $430 \text{ kJ.day}^{-1}$  (chapter 2) suggesting that energy intake limits the number of flight hours sustained without loss of condition. Male parental foraging strategy is thus compatible with energy maximizing within digestive constraints.

The time budget analysis in chapter 2 provided the basis for the energy budget developed in chapter 6. Several major factors in the balance of energy intake cannot be accurately inferred from available data on other species. We therefore devoted separate chapters to the

measurement of natural energy intake (chapter 3), energy expenditure in flight (chapter 4), the costs of moult and digestion in excess of basal metabolic rate and thermogenesis (chapter 5).

Assessment of metabolizable energy intake (chapter 3) was based on meal frequency and size estimation (primarily from handling times calibrated against mass of cached prey items) in association with assimilation quotients established in laboratory trials. Size selection of voles caught, transferred to dependents, cached and eaten was taken into account. Female energy intake peaked during egg-laying, while males gorged especially during parental care. Winter intake rates were reduced in both sexes, in concordance with the winter energy minimization strategy. To meet seasonal peak energy demands the kestrel appears to use various options: increased daily energy intake, accumulation and mobilization of body reserves, and changes in energy allocation to thermogenesis and activity.

Energy expenditure during flight (chapter 4) was assessed independently by two techniques. Trained kestrels were flown indoors once per day over a distance of 125 m and their flight time, energy intake and oxygen consumption during the non-flight portion of each 24 hours recorded. By inference energy expenditure during directional flight was found to be 13.8 Watt. Doubly labeled water turnover measurements on birds in the field gave a value of 14.6 Watt for directional + wind-hovering flight. The close resemblance of both values led to the conclusion that one cost factor can be applied to all non-soaring flight of birds in the field. This factor is close to a value (15.1 Watt) derived from a new allometric equation developed for avian flight costs based on measurements of energy expenditure, body mass, wing span and wing area.

For the analysis of moult costs (chapter 5) we established energy intake, mass change,  $O_2$ -consumption in daytime and at night in year-round trials of fasting and fed tethered kestrels in the laboratory, and compared the results with moult intensity. Relating thermoneutral oxygen consumption and metabolizable energy intake with moult intensity yielded cost factors for feather synthesis of 109 and 125  $\text{kJ.g}^{-1}$  dry plumage respectively, much lower than the figures of 391 and 372  $\text{kJ.g}^{-1}$  previously available from three species of songbirds. Increased plumage

synthesis efficiency may be due either to the protein diet of kestrels or to their larger size and reduced basal metabolism.

In the process of establishing moult costs we obtained the cost factors for basal metabolism, thermoregulation and heat increment of feeding. Basal metabolic rate is 12% higher in males than in females of the same body mass and is proportional to body mass ( $W^{1.0}$ ) within individuals, in contrast to the wellknown interspecific proportionality to  $W^{0.73}$  and interindividual proportionality to  $W^{0.67}$ . Thermoregulatory costs at subthermoneutral temperatures increased by 58% during moult. The heat increment of feeding, assayed by comparison of metabolic rates following a meal and during fasting, declined linearly over 20 hours after the meal, and accumulated to 16.6% of the metabolizable energy content of the meal. At low temperatures the heat increment of feeding only partially substituted energetic costs of thermogenesis.

In chapter 6 we reconstructed the daily energy budget of the species by three independent methods: (1; TEB) from the time budgets in chapter 2, making use of energy cost functions derived in chapter 4 and 5, with corrections for thermogenesis based on the power drawn by heated taxidermic kestrel mount to wind, radiation and temperature; (2; DME) from metabolizable energy intake (chapter 3), corrected for energy retained in body mass change; (3; DLW) from doubly labeled water turnover in 28 freeliving birds. DLW and TEB methods were significantly correlated ( $r = 0.832$ ), although TEB values on average overestimated DLW by 7%. In average DEE per month and per sex, TEB values were 12% above the corresponding estimates from food intake. We argue that occasionally meals not observed cause underestimation of DEE by the food intake method, while unknown energy saving mechanisms adopted by birds in the field cause a slight overestimation of DEE by the TEB method.

After making global corrections for these small discrepancies, we analysed by computer simulation the energetic consequences of (1) the timing of mmoult with respect to the reproductive cycle and (2) the phase relationship of the reproduction-moult-overwintering cycle to the annual environmental cycle. We concluded that moult just after reproduction reduces the annual energy turnover in the kestrel to a minimal amount, and that for minimization of energy turnover a 2-month window of phase relationships is available, with egg laying starting in

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late April to late June. The concentration of egg laying in late April suggests other than energetic benefits for the parents, but is compatible with a general strategy of energy minimization. We shall later analyse the fitness benefits accrued to the nestlings from early breeding. The present analysis of energy expenditure strategies further opens new perspectives for evaluating the consequences of inter- and intra-individual variations in timing of the annual cycle.