

ENERGY EXPENDITURE DURING FREE FLIGHT IN TRAINED AND FREE-LIVING EURASIAN KESTRELS (*FALCO TINNUNCULUS*)

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ABSTRACT.—During directional flight trained Eurasian Kestrels (*Falco tinnunculus*) in the laboratory expended 13.8 W. Free-living birds expended 14.6 W during nonsoaring flight that included both directional flight and wind hovering. The former value was obtained by combining food balance and indirect calorimetry techniques, the latter by doubly labeled water ($D_2^{18}O$). Because the energy-expenditure rates are so similar for directional flight alone and for wind hovering and directional flight combined, we argue that the value for either mode of kestrel flight may be used to analyze time-energy budgets.

We predicted avian flight costs (e_f) from an equation based on published data on flight costs in 14 species (body mass 3.8–1,000 g):

$$e_f = 17.360M^{1.013}b_w^{-4.236}s_w^{1.926} \text{ W,}$$

where M is body mass (g), b_w is wing span (cm), and s_w is wing area (cm²). Inclusion of the morphological data with body mass significantly improved the prediction of flight cost [$r^2 = 0.84$ vs. $r^2 = 0.75$ without b_w and s_w , $F_c(2,18) = 5.34$, $P < 0.05$]. Received 8 May 1986, accepted 29 November 1986.

QUANTIFICATION of the components of daily energy expenditure will improve the understanding of the behavior of free-living birds. This can be achieved by combining time-activity budgets with estimates of the various cost factors (e.g. basal metabolism, thermoregulation, flight; Koplín et al. 1980, Mugaas and King 1981). Energy expenditure during flight is increased greatly relative to during other behaviors (e.g. Berger and Hart 1974). Therefore, even though little time may be devoted to flight, an error in the estimate of the flight cost will produce a considerable error in the total daily energy expenditure estimated from time-activity models.

Available allometric equations that predict flight cost in birds are based solely on body mass (e.g. Berger and Hart 1974, Kendeigh et al. 1977, Butler 1980) and provide only a rough estimate of power consumption. Energy expenditure during flight varies among birds of the same mass, according to flight pattern and the aerodynamic and behavioral properties of the species (Nisbet 1967, Utter and LeFebvre 1970, Hails 1979, Dolnik 1982, Flint and Nagy 1984).

The Eurasian Kestrel (*Falco tinnunculus*) has two distinct modes of powered flight: (1) directional flapping flight and (2) wind hovering, which is flapping flight against the wind with

zero ground speed (Videler et al. 1983). We determined energy expenditure in kestrels during powered flight. We used this information to quantify total daily energy expenditure of the Eurasian Kestrel throughout its annual cycle (Masman 1986).

We used two techniques to determine flight cost. The energy budgets of trained, free-flying kestrels in the laboratory were reconstructed by monitoring daily metabolizable energy intake, oxygen consumption during rest, and time spent flying per day, from which the energy expenditure during directional flight was estimated. In the field we measured daily energy expenditure of free-living kestrels by a doubly labeled water ($D_2^{18}O$) technique (Lifson et al. 1955). Time spent flying was recorded simultaneously. Energy expenditure during combined directional flight and wind hovering was estimated from the correlation between daily CO_2 production and time spent in flight.

METHODS

Food balance and indirect calorimetry.—Three adult wild Eurasian Kestrels (1 male, 2 females) were caught by bal-chatri (Cavé 1968) and trained by falconry methods (Glasier 1978) to fly along an indoor hallway (135 × 3.0 × 2.5 m) back and forth between two falconers. Within 3 weeks the kestrels flew up to 20

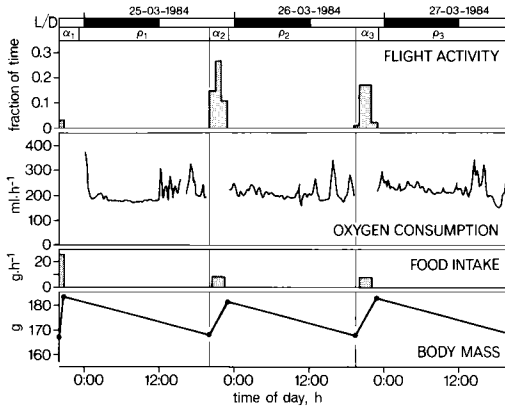


Fig. 1. Experimental design of food-balance trials combined with indirect calorimetry. Example of 3 consecutive experimental days for male J, 24–27 March 1984. Indicated are L:D cycle, active phase (α) during which the bird was fed and flown, resting phase (ρ) during which oxygen consumption was monitored, and body mass as determined at the beginning and end of the active phase.

km/day. During this period body mass decreased and stabilized.

The daily energy budget was recorded by monitoring daily gross energy intake (I , kJ/day), total energy content of feces and pellets excreted per day (L , kJ/day), fluctuations in body mass (ΔM , g/day), energy expenditure during rest (e_p , kJ/h), duration of rest (ρ , h/day), and duration of the flight session in the hallway (α , h/day). The daily ($\alpha + \rho = \text{ca. } 24$ h) energy budget was described by the equation:

$$I = L + \Delta M\epsilon + \rho e_p + \alpha e_a \text{ kJ/day}, \quad (1)$$

where ϵ is the energetic equivalent of body mass change (kJ/g) and e_a is the metabolic rate (kJ/h) during the flight experiment.

Daily gross energy intake (I) was determined by weighing the food provided during the flight sessions (Fig. 1). The food consisted of small cut-up pieces of laboratory mice offered after each transit flight in the hallway. Food intake was corrected for water loss due to evaporation. The food was dried to determine water content ($\bar{x} = 0.64$, SD = 0.01, $n = 10$) at 75°C and combusted in a Gallenkamp Adiabatic Autobomb calorimeter. Mean wet-mass energy content was 9.23 kJ/g (SD = 0.70, $n = 10$). Fat content was determined by extraction with petroleum ether, and protein content was estimated by ashing the fat-free residue, assuming a negligible carbohydrate content (Kendeigh et al. 1977). The fat fraction of ash-free dry mass was 0.29 (SD = 0.47, $n = 10$), and therefore the protein fraction of ash-free dry mass was 0.71 (SD = 0.47, $n = 10$).

To determine the total energy lost (L) all ejecta were collected during flight sessions and the resting period. Feces and pellets were separated and dried at 70°C to constant mass. Energy contents of feces and pellets were determined as described for the mouse carcasses.

Fluctuations in body mass (ΔM) were recorded by weighing the kestrels to the nearest 0.1 g at the beginning and end of each experimental session (Fig. 1). We kept body mass as constant as possible by adjusting the daily ration.

Energy expenditure (e_p) over the resting period (ρ) was measured as oxygen consumption in an open-flow system using an Applied Electrochemistry S3A oxygen analyzer. On 15 of the experimental days the carbon dioxide concentration was measured simultaneously with a Binos infrared gas analyzer (Masman 1986). The ratio of oxygen consumption and CO₂ production (RQ), both calculated following Hill (1972), varied from 0.80 to 0.84, indicating the consumption of carbohydrates in addition to fat and protein.

We calculated the mass ratio of lipids, proteins, and carbohydrates combusted to assign an energy equivalent to the volume of oxygen consumed to correspond to the RQ measured. The diet did not supply carbohydrates; thus, gluconeogenesis (Lardy 1966) must have taken place, as demonstrated in Black Vultures (*Coragyps atratus*; Migliorini et al. 1973). We assumed protein to be the substrate for gluconeogenesis (Stryer 1981) and estimated the amount of protein converted into carbohydrate. We assumed the ratio of protein and fat catabolized in total to equal that in the mouse diet (0.71:0.29) because the body mass of the kestrels remained constant. We used this diet composition and the measured RQ to calculate the energy equivalent (see Appendix). We found energy equivalents for oxygen consumption of 19.8–20.2 kJ/l for RQ values of 0.80–0.84.

Energy expenditure during the flight sessions (e_a) was estimated from Eq. 1. The kestrels flew for only part of the time (t_f , h/day) during the flight sessions, however. After each flight of 125 m, which took an average 14.5 s, the birds took an average of 31.8 s to feed. Thus, the overall energy expenditure during the flight session was:

$$\alpha e_a = t_f e_f + (\alpha - t_f) e_{nf} \text{ kJ/day}, \quad (2)$$

where e_f represents the energy expenditure during flight (kJ/h) and e_{nf} represents the energy expenditure during sitting between the transit flights (kJ/h). Combining Eqs. 1 and 2 gives:

$$I - L - \rho e_p - (\alpha - t_f) e_{nf} = e_f t_f + \Delta M\epsilon \text{ kJ/day}, \quad (3)$$

where all variables were measured except flight cost (e_f), the costs of sitting during the flight session (e_{nf}), and the energetic equivalent for body mass change (ϵ). We calculated the best-fit value for these three variables from the 49 equations from each experi-

mental day (Eq. 3) by multiple linear regression analysis through the origin, where the left-hand side of Eq. 3 was the dependent variable. However, the correlation between the time spent flying (t_f) and the time spent sitting ($\alpha - t_f$) during each experiment was too strong to determine a definite value for the three variables. We reduced the number of unknown variables by assuming the metabolic rate during sitting between the transit flights was equal to the metabolic rate directly after the flight session and before the lights were turned off.

Doubly labeled water method.— $D_2^{18}O$ was used to measure CO_2 production (see Lifson and McClintock 1966, Nagy 1980) in free-living Eurasian Kestrels. Birds were captured either at a nest box, by net, or elsewhere by baited spring nets, Verbal leg-hold traps (Steward et al. 1945), or bal-chatri (Cavé 1968), and weighed to the nearest gram. An initial 25- μ l blood sample was obtained from the posterior tibial vein and flame-sealed. Birds were injected subcutaneously in the abdomen with $H_2^{18}O$ (95.3 atom %) and D_2O (99.8 atom %) mixed in a ratio of 2:1. We injected $[0.45 \times 2^{n-1}]$ ml mixture/kg, where n is the number of half-life times of ^{18}O ($T_{1/2}$, days) the experiment was planned to last. We calculated $T_{1/2}$ on the basis of body mass (M , g) as $T_{1/2} = 0.152M^{0.37}$ (K. A. Nagy pers. comm.). After injection the bird was held in a dark box for 3 h to allow complete equilibration of the isotopes in the body water. Body mass was determined again, an initial sample of isotopically enriched blood was taken, and the bird was released. Birds were recaptured 22–74 h after release. Body mass was determined and a final blood sample was taken (Fig. 2).

We used 10 doubly labeled water (DLW) experiments of reproductive kestrels that include continuous time-budget observations (Masman 1986). We studied 2 females just before egg laying (April–May) and 4 males and 3 females (one individual twice) during the nestling phase (June–July). Behavior was recorded on average for 90.4% (range: 75–100%) of all daylight hours during the experiments. Total flight time was estimated by correcting the observed time to that projected for the whole daylight period (Masman 1986).

Blood samples were stored at 5°C and analyzed at the Laboratory for Isotope Physics in Groningen. Water was extracted by vacuum distillation, and the same sample was analyzed for both isotopes by isotope-ratio mass-spectrometry. The 2H and ^{18}O enrichment of the water was calculated, taking fractionation effects during the analyses into account (W. G. Mook pers. comm.).

The CO_2 production of the birds was calculated using Eq. 35 of Lifson and McClintock (1966). Body-water volumes were determined by calculating the dilution space for the injected ^{18}O molecules, from the enrichment of the first sample after injection (Schoeller et al. 1980). In all our DLW experiments

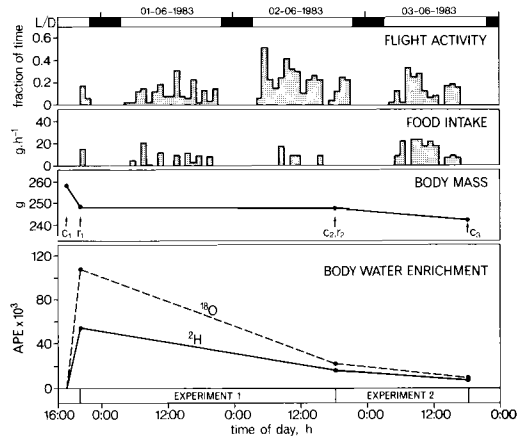


Fig. 2. Experimental design of DLW method as applied in the field. Example of 2 consecutive experiments on female 345 during the nestling phase, 31 May–3 June 1983. Indicated are L:D cycle, fraction of time spent in flight and food intake as derived from continuous activity protocol between release (r) and capture (c), body mass, and body-water enrichments for ^{18}O and 2H as determined from the blood samples.

body-water content averaged 65.9% (SD = 5.9, $n = 13$) in males and 67.7% (SD = 5.1, $n = 18$) in females (Masman 1986). These mean values were used when the amount of isotopes injected was not known accurately.

From the diet of kestrels in the study area we deduced the two extreme energy equivalents for CO_2 possible and converted carbon dioxide production to energy expenditure. The diet consisted almost entirely of common voles (*Microtus arvalis*), which as dry mass contain mainly protein (76.2%, SD = 3.2, $n = 15$) and fat (10.2%, SD = 3.9, $n = 20$) (Masman et al. 1986). The RQ during rest, when no conversion from protein into carbohydrates occurs, was calculated as 0.74, assuming that fat and protein are oxidized in a ratio identical to that in the diet. During exercise, notably flight, gluconeogenesis occurs, and glycogen will be used as fuel in the muscles (Parker and George 1975, Butler et al. 1977). When all protein available in the diet was converted to carbohydrates, the calculated RQ was 0.92. The corresponding energy equivalents for these extremes are 0.566 and 0.502 kJ/mMol CO_2 , or, for the intermediate RQ of 0.83, 0.528 kJ/mMol CO_2 produced. These values were derived using the same principle as for the indoors experiment (see Appendix).

Average daily metabolic rate was calculated as total CO_2 production (mMol/g) divided by experiment duration (days). Experiment duration was always close to whole multiples of 24 h (ranges of duration: 0.83–1.15, 1.92–2.33, and 3.09 days), so we refrained from adjustments for circadian phase. Time spent in flight

TABLE 1. Estimated ($\bar{x} \pm SD$) energy expenditure during flight (e_f) in trained birds and the energetic equivalent of body mass change (ϵ). Values were derived by multiple regression on energy-budget data from 49 food-balance trials in combination with indirect calorimetry. Estimates based on days during which body mass increased and days during which it decreased are statistically indistinguishable. For correlation coefficients (r), $P < 0.01$ in all cases.

Experiment	e_f	ϵ	n	r
Body mass increased over 24 h	13.1 \pm 5.8 W	9.91 \pm 2.45 kJ/g	27	0.763
Body mass decreased over 24 h	13.9 \pm 4.4 W	9.42 \pm 2.09 kJ/g	22	0.715
All	13.8 \pm 3.1 W	9.56 \pm 1.39 kJ/g	49	0.746
All	0.078 \pm 0.017 W/g	9.63 \pm 1.40 kJ/g	49	0.745

(t_f , h/day) was calculated as total flight (hours of directional flight plus flight hunting) during the experiment, divided by experiment duration (days).

Validations of the DLW technique by concurrent measurement of CO₂ production were made previously in 8 bird species ranging in body mass from 14 to 384 g (LeFebvre 1964, Hails and Bryant 1979, Weathers et al. 1984, Westerterp and Bryant 1984, Williams and Nagy 1984, Williams 1985). These measurements had an average error of +0.4%, but the errors range from -7.1 to +8.0%.

To check our procedures we used the DLW technique simultaneously with two other methods, for two trials each: a gravimetric method (absorption of CO₂ by Ascarite; Haldane 1892) in 2 resting birds and infrared CO₂ analysis (Masman 1986) in 3 birds. The mean discrepancy between the DLW method and the alternative methods (AM), calculated as 100(DLW - AM)/AM, was +2.2% (SD = 5.0, $n = 8$). We conclude that our measurements were as accurate as reported for other bird species and can be used to estimate daily energy expenditure in free-living Eurasian Kestrels.

RESULTS

Energy expenditure during flight in trained birds.—

During 49 experimental days the time spent flying (t_f) ranged from 6 to 2,397 s/day, with corresponding flight distances of 0.014 and 20.12 km/day. Daily gross energy intake (I) ranged from 19.19 to 224.67 kJ/day. The metabolized fraction of the energy in the food, $Q = (I - L)/I$, was 0.81 (SD = 0.04, $n = 49$), which is similar to the values measured by Kirkwood (1981, 0.79) and Masman (1986, 0.78). Daily changes in body mass (ΔM) were small ($\bar{x} = +1.9$ g/day, range: -5.8 to +5.1) relative to body mass. Resting metabolic rate (e_r) averaged 1.34 W (SD = 0.25, $n = 49$).

The best-fitting values for energy expenditure during flight (e_f) and the energy equivalent of body mass change (ϵ) in Eq. 3 were calculated by multiple regression (Table 1). The calculated

e_f and ϵ estimates for days with a body mass increase and for days with a body mass decrease were indistinguishable statistically ($t_{45} = 0.11$ for e_f , $t_{45} = 0.15$ for ϵ , $P < 0.05$). We therefore combined data to estimate e_f and ϵ . Energy expenditure during flight was estimated as 49.7 kJ/h (13.8 W, SD = 3.1, $n = 49$), and we found no relation between body mass and e_f , probably because of the small range of body mass.

The second unknown variable in Eq. 3 was the energetic equivalent of body mass change (ϵ). The value of 9.6 kJ/g in trained kestrels (\bar{x} mass = 180.2 g, SD = 14.0, $n = 3$) was low relative to values found in other experiments with the Eurasian Kestrel. For kestrels fed *ad libitum*, an equivalent of 19.2 kJ/g (SD = 6.5, $n = 18$) was reported earlier (Masman 1986). Kirkwood (1981) found an energetic equivalent of 12.1 kJ/g catabolized for a kestrel with a decreasing body mass. The observed energy equivalent of body mass change depends on the composition of the mass lost. Catabolism of body fat yields 37.9 kJ/g, while that of muscle yields 20.5 kJ/g dry tissue (Ricklefs 1974). During catabolism of protein, however, a more or less fixed fraction of the mass lost is water (Sheng and Huggins 1979). Total body water as a percentage of the lean feather-free mass in kestrels was 71.0% (SD = 3.1, $n = 9$) in 3 individuals from Kirkwood (1981) combined with 6 individuals analyzed in our laboratory. We estimated an energy equivalent of 5.9 kJ/g mass change during protein catabolism, assuming that during mass loss, because of decreased lean body tissue, the ratio of protein to water was 0.29:0.71. Using the equivalences of 37.9 kJ/g for catabolism of fat and 5.9 kJ/g for protein, we calculated from the energetic equivalent actually observed (9.6 kJ/g) that the trained birds we studied used body fat and body protein in a ratio of 1:4 during mass decreases.

Energy expenditure during flight in the field.—

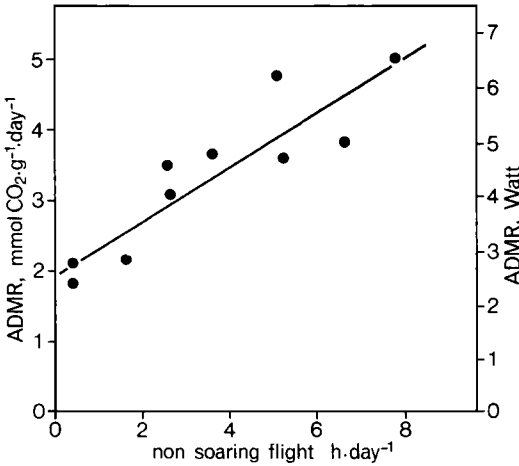


Fig. 3. Average daily metabolic rate (ADMR) as a function of daily time spent in nonsoaring flight. ADMR expressed in mass-specific CO₂ production as measured by DLW and as energy expenditure per bird (mean body mass = 213 g) using an energy equivalent of 0.528 kJ/mMol CO₂. Each dot represents one experiment lasting at least 22 h. The equation for the regression is $ADMR = 1.97 + 0.385t_i$ mMol CO₂ · g⁻¹ · day⁻¹.

Average daily metabolic rate (ADMR) of free-living kestrels, measured by D₂¹⁸O as CO₂ production, increased with time spent in nonsoaring flight (*t_i*, Fig. 3), as described by the equation:

$$ADMR = 1.97 + 0.385t_i \text{ mMol CO}_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1} \quad (4)$$

(*r* = 0.897, *n* = 10, *P* < 0.001, intercept: SD = 0.29, slope: SD = 0.067). Assuming that energy expenditure during nonflight activity did not vary systematically with flight time, the slope of the regression estimates the difference between flight and nonflight energy expenditure and the intercept estimates nonflight energy expenditure. Hence, *e_i* can be estimated as $1.97 / 24 + 0.385 = 0.467$ mMol CO₂ · g⁻¹ · h⁻¹ (SD = 0.068). For a kestrel of 213 g (mean mass of all experimental birds) energy expenditure during flight was estimated as 13.7 and 15.5 W for RQ values of 0.92 and 0.74, respectively. An intermediate RQ of 0.83 yielded an estimate of 14.6 W (SD = 2.1). The intercept of the regression implied an energy expenditure during nonflight activities of 1.97 mMol CO₂ · g⁻¹ · day⁻¹ (SD = 0.29), which is equivalent to 2.6 W (RQ = 0.83) for a kestrel of average mass. Daily energy

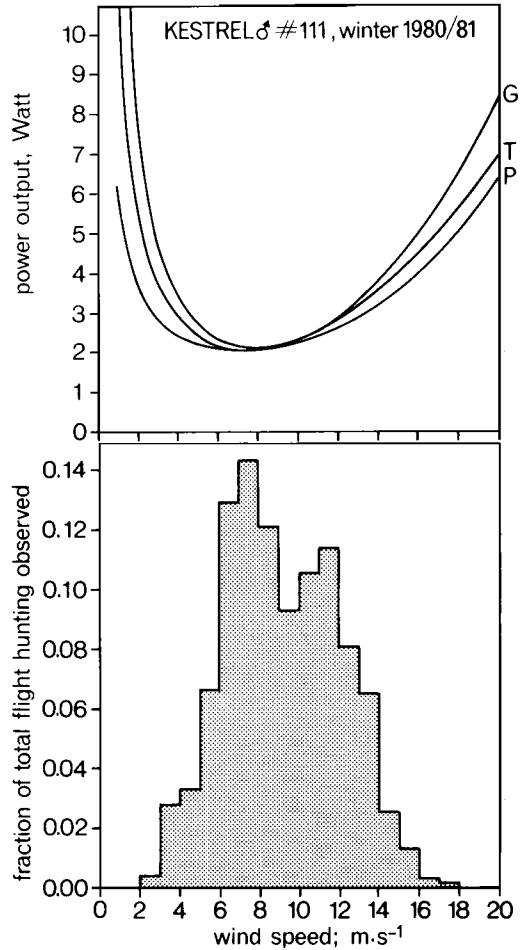


Fig. 4. Comparison of flight costs, as predicted by aerodynamic theories, and time allocated to wind hovering by a wintering free-living male under different prevailing wind speeds. Top: Power output during flight as a function of flight speed as predicted by equations of Pennycuik (P), Tucker (T), and Greenewalt (G) for a male kestrel (body mass = 213 g, wing span = 73.8 cm, wing area = 708 cm²). Bottom: Fraction of total time allocated to wind hovering (32.1 h) at different wind speeds in one free-living male kestrel (#111) during winter (data collected by H. v. d. Leest and H. Waterbolk).

expenditure for nonflight activities was calculated from time-budget and laboratory data on basal metabolic rate, thermoregulatory costs, and the heat increment of feeding (Masman 1986) as 2.1 W (SD = 0.4, *n* = 63) for males during reproduction (\bar{x} mass = 191 g, SD = 11, *n* = 63), which is close to the nonflight cost estimated by these DLW measurements.

TABLE 2. Estimated energy expenditure during flight in 58 bird species. The categories of method used are: wind-tunnel studies (W), mass change over long flights (M), and doubly labeled water technique (D). Where available, wing span and wing area are indicated. Species numbers refer to Fig. 5.

Species	Body mass (g)	Flight cost (W)	Method	Wing span (cm)	Wing area (cm ²)	Source
1. <i>Ocreatus u. underwoodii</i>	2.7	0.53	W	—	—	Schuchmann 1979b
2. <i>Calypte costae</i>	3.0	0.70	W	—	—	Lasiewski 1963
3. <i>Selasphorus sasin</i>	3.36	0.96	W	—	—	Epting 1980
4. <i>Selasphorus sasin</i>	3.5	1.4	W	—	—	Pearson 1950
5. <i>Regulus regulus</i>	3.8	0.29	M	14.3	32.2	Nisbet 1963
6. <i>Archilochus alexandri</i>	3.96	1.18	W	—	—	Epting 1980
7. <i>Calypte anna</i>	4.1	2.0	W	—	—	Pearson 1950
8. <i>Amazilia tzacatl</i>	4.4	0.52	W	—	—	Schuchmann 1979a
9. <i>Calypte anna</i>	4.71	1.32	W	—	—	Epting 1980
10. <i>Amazilia cyanifrons</i>	4.8	0.65	W	—	—	Schuchmann 1979a
11. <i>Amazilia fimbriata</i>	5.7	1.43	W	—	—	Berger and Hart 1972
12. <i>Eulampis jugularis</i>	8.3	2.1	W	—	—	Hainsworth and Wolf 1969
13. <i>Vermivora peregrina</i>	10.9	2.21	M	—	—	Raveling and LeFebvre 1967
14. <i>Spinus spinus</i>	12.46	2.93	M	21.4	68.0	Dolnik and Blyumenthal 1967
15. <i>Spinus spinus</i>	12.5	2.98	M	21.4	68.0	Dolnik and Gavrillov 1973
16. <i>Riparia riparia</i>	12.7	1.60	D	—	—	Westerterp and Bryant 1984
17. <i>Riparia riparia</i>	13.7	2.05	D	—	—	Turner 1982a, b
18. <i>Nectarinia kilimensis</i>	14.7	4.09	W	—	—	Wolf et al. 1975
19. <i>Erithacus rubecula</i>	16.3	1.57	M	22.7	88.0	Nisbet 1963
20. <i>Hirundo rustica</i>	17.7	1.34	M	33.0	135.0	Lyuleeva 1970
21. <i>Delichon urbica</i>	17.81	1.01	D	29.2	92.0	Hails 1979
22. <i>Delichon urbica</i>	18.1	1.26	D	29.2	92.0	Westerterp and Bryant 1984
23. <i>Hirundo rustica</i>	18.99	1.30	D	33.0	135.0	Hails 1979
24. <i>Delichon urbica</i>	19.0	0.95	M	29.2	92.0	Kespaik 1968
25. <i>Dendroica striata</i>	19	1.18	M	22.7	75.0	Nisbet et al. 1963
26. <i>Erithacus rubecula</i>	19	6.5	D	22.7	88.0	Tatner and Bryant 1986
27. <i>Hirundo rustica</i>	19	1.62	D	33.0	135.0	Turner 1982a, b
28. <i>Euplectes franciscanus</i>	19.3	7.3	W	—	—	Teal 1969
29. <i>Catharus fuscescens</i> / <i>Seiurus aurocapillus</i>	19.6	2.21	M	—	—	Hussell 1969
30. <i>Delichon urbica</i>	20.2	1.08	M	29.2	92.0	Lyuleeva 1970
31. <i>Spizella pusilla</i>	21.0	7.7	W	—	—	Teal 1969
32. <i>Guiraca caerulea</i>	21.6	8.1	W	—	—	Teal 1969
33. <i>Melospiza melodia</i>	21.9	1.55	M	—	—	Nisbet 1963
34. <i>Fringilla coelebs</i>	22.0	5.33	M	28.5	102	Dolnik and Blyumenthal 1967
35. <i>Fringilla coelebs</i>	22.3	4.25	M	28.5	102	Dolnik and Gavrillov 1973
36. <i>Fringilla montifringilla</i>	23.25	5.06	M	28.1	123	Dolnik and Blyumenthal 1967
37. <i>Fringilla montifringilla</i>	23.3	4.61	M	28.1	123	Dolnik and Gavrillov 1973
38. <i>Zonotrichia albicollis</i>	24.0	9.0	W	—	—	Teal 1969
39. <i>Meliphaga virescens</i>	24.3	2.46	W	—	—	Collins and Morellini 1979
40. <i>Passer domesticus</i>	29.3	10.9	W	—	—	Teal 1969
41. <i>Pyrrhula pyrrhula</i>	29.5	5.61	M	—	—	Dolnik and Gavrillov 1973
42. <i>Oenanthe oenanthe</i>	31	4.5	M	—	—	Nisbet 1963
43. <i>Hyllocichla fuscescens</i>	31.5	4.53	M	—	—	Hussell 1969
44. <i>Melospittacus undulatus</i>	37	40.8	W	—	—	Tucker 1966
45. <i>Icterus galbula</i>	38.0	17.5	W	—	—	Teal 1969
46. <i>Heterophasia capistrata</i>	38.1	12.5	W	—	—	Teal 1969
47. <i>Apus apus</i>	40.4	1.84	M	42.0	165	Lyuleeva 1970
48. <i>Ramphocelus flammigerus</i>	44.6	23.2	W	—	—	Teal 1969
49. <i>Progne subis</i>	50.5	3.88	D	—	—	Utter and LeFebvre 1970
50. <i>Scardafella squammata</i> <i>ridgwayi</i>	50.9	23.5	W	—	—	Teal 1969
51. <i>Lamprospere superbus</i>	54.4	15.9	W	—	—	Teal 1969
52. <i>Hesperiphona vespertina</i>	59.3	11.09	W	—	—	Berger et al. 1970
53. <i>Turdus iliacus</i>	69.3	28.4	W	—	—	Teal 1969
54. <i>Sturnus vulgaris</i>	72.8	9.15	W	—	—	Torre-Bueno and LaRochelle 1978
55. <i>Sturnus vulgaris</i>	75	9.0	D	39.5	192.0	Westerterp and Drent 1985

TABLE 2. Continued.

Species	Body mass (g)	Flight cost (W)	Meth-od	Wing span (cm)	Wing area (cm ²)	Source
56. <i>Cyanocitta cristata</i>	94.2	28.9	W	—	—	Teal 1969
57. <i>Falco sparverius</i>	120	13.8	W	—	—	Gessaman 1980
58. <i>Pluvialis dominica</i>	140	8.96	M	—	—	Johnston and McFarlane 1967
59. <i>Colaptes auratus</i>	146.5	43.9	W	—	—	Teal 1969
60. <i>Sterna fuscata</i>	188	4.7	D	84.0	625.5	Flint and Nagy 1984
61. <i>Falco tinnunculus</i>	213	14.6	D	73.8	708	This study
62. <i>Columba</i> sp.	254	33.1	M	—	—	Pearson 1964
63. <i>Corvus ossifragus</i>	275	22.5	W	—	—	Bernstein et al. 1973
64. <i>Larus atricilla</i>	340	25.66	W	—	—	Tucker 1972
65. <i>Columba livia</i>	384	25.9	D	66.0	630	LeFebvre 1964
66. <i>Larus delawarensis</i>	427	21.6	W	—	—	Berger et al. 1970
67. <i>Columba livia</i>	442	30.5	W	—	—	Butler et al. 1977
68. <i>Corvus cryptoleucus</i>	480	30.40	W	—	—	Hudson and Bernstein 1983
69. <i>Larus marinus</i>	800	36.29	M	—	—	Dolnik and Gavrilov 1973
70. <i>Anas platyrhynchos</i>	1,000	44.2	M	90	928	Dolnik and Gavrilov 1973
71. <i>Anas rubripes</i>	1,026	78.0	W	—	—	Berger et al. 1970

DISCUSSION

Energy expenditure during flight.—An airborne kestrel may engage in soaring (no wing movements), directional flight (flapping flight and soaring combined), or wind hovering (flapping flight and soaring combined, with zero ground speed; see Videler et al. 1983). Energy expenditure during soaring has been measured only in Herring Gulls (*Larus argentatus*), and was 1.5–2.4 times the resting metabolic rate (Baudinette and Schmidt-Nielsen 1974, Kanwisher et al. 1978). Such low energy expenditure during soaring relative to flapping flight is assumed to be a general phenomenon (Pennycuick 1972).

During directional flight and wind hovering energy expenditure is higher than for other activities. Because the time spent wind hovering and flying were correlated strongly in free-living kestrels ($r = 0.802$, $n = 10$, $P < 0.01$), it was not possible to distinguish those two variables in the analyses of the relation between energy expenditure (determined by DLW) and time allocation. However, energy expenditure during directional flight in trained birds (13.8 W, SD = 3.1) was not distinguishable from that during combined directional flight and wind hovering in the field (14.6 W, SD = 2.1). We therefore assumed the cost of directional flight was identical to that of wind hovering in kestrels.

There are further arguments for the hypothesis that the costs of directional flight and wind hovering are similar in kestrels. During wind

hovering, flight speed depends on the prevailing wind velocity because the kestrel has to fly against the wind to remain stationary. Aerodynamic theories (Tucker 1974, Greenewalt 1975, Pennycuick 1975, Rayner 1979) predict energy expenditure during flight to be dependent on flight speed, especially at high and low wind speeds (Fig. 4). Most wind hovering by kestrels occurred when wind speeds were 6–12 m/s, the range where flight costs are predicted to be minimal and relatively constant (Fig. 4). This range also encompasses average flight speeds recorded during directional flight in the field (8.3 m/s; Videler et al. 1983) and in the laboratory [8.6 m/s, average over 24 values from long-distance (>80 m) sessions, SD = 0.4]. Therefore, most wind hovering and directional flight probably occurs at about the same air-speed.

Predictions of flight costs.—Aerodynamic theory (Tucker 1974, Greenewalt 1975, Pennycuick 1975) provides estimates for mechanical power output during flight. To predict energy expenditure for a bird during flight (e_i), a muscular-efficiency factor (power output: power consumed) is necessary. This efficiency has not been determined precisely for any avian species. The muscular efficiency of quadrupedal locomotion ranges from 70% in large animals to 7% in small animals (Heglund and Cavagna 1985), which contrasts with the classic assumption of peak efficiencies of 20–25% for all muscular work (e.g. Tucker 1974). Instead of deriving a prediction

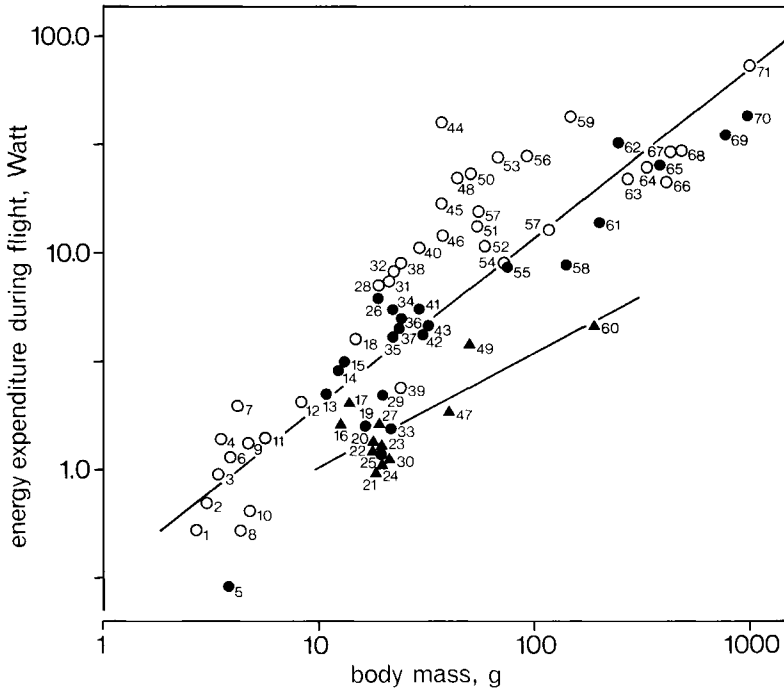


Fig. 5. Energy expenditure during flight in 57 bird species as a function of body mass. Numbers refer to species listed in Table 2. Open symbols = wind-tunnel studies, closed symbols = non-wind-tunnel studies, triangles = extremely aerial species (EAS; see text). Upper line = linear regression on all data points; lower line = linear regression on EAS (see text).

of power consumption during flight (e_f) from theory, we used aerodynamic theory to estimate muscular efficiency during flight once we had measured flight cost. Power output during flapping flight at a speed of 8.5 m/s for a 0.215-kg kestrel, with a wing span of 0.73 m and wing area of 708 cm², was predicted as 2.17 W (Tucker 1974), 2.10 W (Pennycuik 1975), or 2.09 W (Greenewalt 1975). We found an energy consumption of 14.6 W, or a muscular efficiency of about 15%. We combined flapping and gliding flight, however, and this efficiency may be over-estimated.

Empirical predictions for flight cost may be derived from allometric analysis (Berger and Hart 1974, Kendeigh et al. 1977, Butler 1980). Because the variation in measured avian flight costs at any given body mass is great, the regressions cannot provide a precise prediction for a single species. Aerodynamic theory implicitly suggests that such empirical predictions should be improved considerably by including morphological characters in addition to body mass. We compiled available data on flight energy

expenditure for 57 bird species (Table 2, Fig. 5) and categorized the data on the basis of the methods used and the aerodynamic properties of the species concerned.

There was considerable discrepancy between results from wind-tunnel studies and those from studies that used methods applied to unrestrained birds (Fig. 5). This effect was analyzed by comparing wind-tunnel and non-wind-tunnel studies. We restricted this comparison to birds that do not habitually forage on the wing during large parts of the day, thus excluding the "aerial feeders" (Hails 1979) and the "extremely aerial species" (Flint and Nagy 1984). The data were reduced to 36 wind-tunnel studies and 23 studies on free flight. Both subsets had a statistically significant relation between body mass (M) and flight cost (e_f). In the wind-tunnel studies $e_f = 0.471M^{0.786}$ W ($n = 36$, $r = 0.903$, $P < 0.0001$, $M = 2.7-1,026$ g); for non-wind-tunnel studies $e_f = 0.305M^{0.756}$ W ($n = 23$, $r = 0.917$, $P < 0.0001$, $M = 3.8-1,000$ g). These allometric relations had similar exponents ($t_{55} = -0.285$, not significant) but different intercepts

TABLE 3. Relation of time allocation (flight, h/day), flight cost (multiples of BMR), wing loading (g/cm^2), and aspect ratio ($\text{span}^2/\text{area}$). Flight costs were predicted using the equation of Dolnik (1982): $e_t = 2.5(1 - \ln t_t/24) \times \text{BMR}$, where t_t is time spent in flight (h/day). Species numbers refer to Fig. 6.

Species	Body mass (g)	BMR (W)	Flight (h/day)	Wing loading (g/cm^2)	Aspect ratio	Flight cost			Source
						Measured	Predicted	Percentage difference	
1. <i>Erithacus rubecula</i>	19.0	0.313 ^a	0.5	0.263	5.86	22.6	12.2	-85.2	Tatner and Bryant 1986
2. <i>Sturnus vulgaris</i>	75.0	0.915	2.5	0.414	8.126	9.8	8.1	-21.0	Tinbergen 1981, Westerterp and Drent 1985
3. <i>Merops viridis</i>	33.8	0.297	2.6	—	—	13.3	8.0	-66.3	Bryant et al. 1984
4. <i>Hirundo tahitica</i>	14.1	0.177	3.3-8.3 ^b	—	—	10.0	7.5-5.2	-57.5	Hails 1984, Westerterp and Bryant 1984
5. <i>Hirundo rustica</i>	19.1	0.325	9.1	0.133	8.067	4.8	4.9	+2.0	Westerterp and Bryant 1984
6. <i>Progne subis</i>	47.7	0.693	7.1-9.9 ^c	—	—	5.9	5.5-4.7	-15.7	Utter and LeFebvre 1970, 1973
7. <i>Delichon urbica</i>	18.1	0.307	12.5	0.207	9.268	3.4-4.8	4.1	0.0	Westerterp and Bryant 1984
8. <i>Riparia riparia</i>	12.9	0.245	12.7	—	—	6.5	4.1	-58.5	Westerterp and Bryant 1984
9. <i>Apus apus</i>	40.4	0.541 ^a	16.6	0.219	10.691	3.4	3.4	0.0	Lyuleeva 1970, Dolnik 1982
10. <i>Sterna fuscata</i>	187.0	0.986	18.1	0.299	11.281	4.8	3.2	-50.0	Flint and Nagy 1984
11. <i>Falco tinnunculus</i>	213.0	0.903	1.7-4.6 ^d	0.346	7.691	16.2	9.1-6.6	-106.4	This study

^a BMR estimated by allometric equation of Aschoff and Pohl (1970) or as measured by authors.

^b Time allocation during nonbreeding season and nestling phase.

^c Time allocation for males and females.

^d Time allocation during winter and males in nestling phase.

($t_{56} = -3.48, P < 0.001$). Flight costs predicted from wind-tunnel studies were therefore approximately 50% greater than those from non-wind-tunnel studies. This difference was due both to differences in flight performance caused by forcing birds to fly in a wind tunnel (Greenewalt 1975) and to the extra costs caused by the equipment attached to the bird (Tucker 1974). We conclude that the most realistic predictions of flight costs are obtained by excluding wind-tunnel studies. Thus, all further analyses were restricted to non-wind-tunnel studies.

Hails (1979) and Dolnik (1982) drew attention to the fact that species that spend most of the day in the air tend to have lower flight costs (per hour) than species that fly sporadically during the day. Dolnik analyzed the normalized flight-cost factors (multiples of BMR) against average flight time per day. He suggested that a smooth curve adequately described the avail-

able data and provided the most reliable flight-cost factors for converting time-budget data into energy units. We reproduce Dolnik's predictive relationship in Fig. 6 (top) and have inserted data from 11 other studies where flight costs (non-wind-tunnel studies) and time-budget data are well established (Table 3). Although the trend of Dolnik's estimator is confirmed, several recent findings, unavailable to Dolnik, deviate from expectation (Table 3). The kestrel data showed an energy expenditure during flight that is at least 78% above the value predicted by Dolnik. This prediction was dependent on the time allocated to flight per day, a parameter that varies with season and sex (Table 3). This makes application of Dolnik's estimator imprecise. However, his analysis stressed again that "extremely aerial species" may be adapted for predominantly aerial behavior during the day. These adaptations may be behavioral (Withers

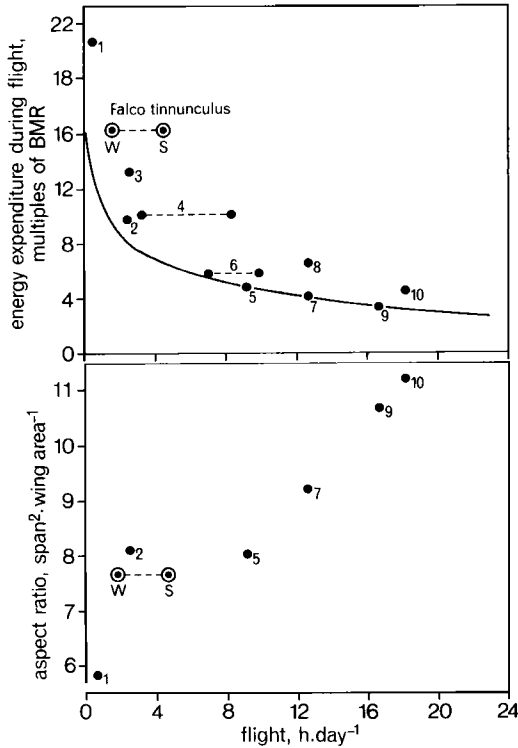


Fig. 6. Time allocated to flight in relation to estimated flight costs (top) and in relation to aspect ratio (bottom) for 10 species where flight costs and time-budget data were available. Solid line = Dolnik's (1982) prediction for the energy expenditure during flight (e_f , in multiples of BMR) estimated from time spent in flight (t_f , h/day): $e_f = 2.5(1 - \ln t_f/24) \times \text{BMR}$. Numbers refer to species listed in Table 3. Each dot represents e_f and BMR as reported by the authors, or BMR as predicted by Aschoff and Pohl (1970) when no measurements were available. For the kestrel two data points are included: W = winter (average for males and females), S = summer (average for males during the nestling phase).

and Timko 1977, Pennycuick 1983, Wiens 1985), physiological (Viscor et al. 1985), or morphological. Hails (1979) identified the morphological adaptations of extremely aerial species as relatively long wings and a low wing loading, to generate lift and favor gliding (Pennycuick 1972). This decreases the overall power required for flight. The aspect ratio (AR = wing span²/wing area) of a bird indicates such adaptations. We plotted the aspect ratio of 7 species vs. time spent in flight (Fig. 6, bottom) and found a consistent trend of more time in flight associated with a higher aspect ratio and lower flight

cost, although this feature is largely brought about by the preponderance of extremely aerial species.

To incorporate morphological data, in addition to body mass, in an equation that predicts flight costs, we used the equations of Greenewalt (1975) for the relationship of minimum power output (PO_{mp}) and power output for minimum cost of transport (PO_{mr}). These equations include the variables mass (M , g), wing span (b_w , cm), and wing area (s_w , cm²):

$$PO = KM^{1.394}b_w^{-1.378}s_w^{0.189} W, \quad (5)$$

where K ($W \cdot g^{-1} \cdot \text{cm}^{-3}$) is a constant that depends on the option chosen by the bird, PO_{mp} or PO_{mr}. We found morphological data for 23 non-wind-tunnel studies, either in the original publications or in Greenewalt's (1962, 1975). The data, excluding one aviary study of *Erethacus rubecula*, on foraging birds flying at extremely low velocities (Tatner and Bryant 1986), were analyzed by multiple regression. We used Greenewalt's (1975) equation for power output (PO) as a template and yielded the following equation:

$$e_f = 17.360M^{1.031}b_w^{-4.236}s_w^{1.926} W. \quad (6)$$

Inclusion of the morphological data improved the correlation coefficient significantly [$r(e_f, M) = 0.866$, $r(e_f, M + b_w + s_w) = 0.918$, $F_c(2,18) = 5.342$, $P < 0.05$] and increased the total explained variation in the flight cost from 75% to 84%.

Because $b_w^{-4.236} \times s_w^{1.926}$ in Eq. 6 approximates the inverse of the square root of the aspect ratio [$(b_w^2/s_w)^{-2}$], the aspect ratio largely explains the variation accounted for by b_w and s_w separately. The exponents in Eq. 6 differ markedly from theoretical values (Greenewalt 1975). Greenewalt's equations predict power output during flapping flight, however, while ours includes cost estimates for birds flying naturally, combining gliding and flapping flight.

Our analysis still leaves 16% of the variation in flight cost unexplained. This may be due to variation in the data that was not taken into account, such as actual flight speed, behavior while aloft, and the methods used in the different studies. Another source of variation may be the use of morphological data from populations different from those in which the energy expenditure during flight was measured. Future developments of aerodynamic theory and broadening of the empirical basis may improve

the predictive value of allometric equations. To convert time-budget data into energy units without undertaking independent studies of flight costs, we believe allometric equations must include morphological data in addition to body mass.

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APPENDIX. Calculation of the energy equivalent of oxygen consumed using diet composition and respiratory quotient.

The energy equivalent of oxygen consumed (EE) depends on the ratio of carbohydrates, lipids, and proteins catabolized. We derived this ratio from the mass ratio in the diet and the respiratory quotient (RQ) as follows:

$$EE = EE_c P_c + EE_l P_l + EE_p P_p \quad \text{kJ/l O}_2 \quad (1)$$

where EE_c, EE_l, and EE_p are the energy equivalents (kJ/l O₂) for catabolism of pure carbohydrates, lipids, and proteins, respectively (Table A1); and P_c, P_l, and P_p are the fractions of total O₂ consumed in the oxidation of carbohydrates, lipids, and proteins. For the P-values the following relationships hold:

$$\begin{aligned} P_c &= C_c / (RQ_c X), \\ P_l &= C_l / (RQ_l X), \text{ and} \\ P_p &= C_p / (RQ_p X), \end{aligned} \quad (2)$$

where C_c, C_l, and C_p are the CO₂ (Mol) produced in carbohydrate, lipid, and protein catabolism; RQ_c, RQ_l, and RQ_p are the RQ-values (Mol CO₂/Mol O₂) known for the oxidation of these substrates (Table A1); and the total O₂ consumption (X) is:

$$X = (C_c / RQ_c) + (C_l / RQ_l) + (C_p / RQ_p) \quad \text{Mol O}_2 \quad (3)$$

The total CO₂ produced is:

$$RQX = C_c + C_l + C_p \quad \text{Mol CO}_2 \quad (4)$$

TABLE A1. (From Schmidt-Nielsen 1979.)

Fuel	Energy equivalent (kJ/l O ₂)	Respiratory quotient
Carbohydrates	EE _c = 20.9	RQ _c = 1.00
Lipids	EE _l = 19.7	RQ _l = 0.71
Protein	EE _p = 18.4	RQ _p = 0.74

We further know for lipids that:

$$C_l = (0.76/12)L \quad \text{Mol CO}_2, \quad (5)$$

where 0.76 = g carbon/g lipid (Kleiber 1961) and L is the mass fraction of lipids in substrate oxidized. For protein catabolism the situation is more complicated. Protein is not catabolized completely but with an efficiency of q . The diet of the kestrels contains virtually no carbohydrates, and all carbohydrates oxidized are first formed in gluconeogenesis (Lardy 1966) from protein (Stryer 1981). We assume that both protein catabolism and gluconeogenesis have the same efficiency because both follow the urea cycle pathway (Scrutton and Utter 1968).

Therefore,

$$C_p + C_c = (0.44/12)Pq \quad \text{Mol CO}_2, \quad (6)$$

where 0.44 = g carbon/g protein (Kleiber 1961), P is the fraction of protein in substrate oxidized, and q is the efficiency of protein metabolized. For q we assumed a value of 0.9 (Kirkwood 1981). We further assumed that the ratio between protein and lipid metabolized was equal to the ratio in the diet (P:L).

If P, L, and RQ are known, C_e , C_p , C_l , and X can be solved from Eqs. 3-6, and used to solve Eqs. 2 and 1.
