direction, and average flight speed of different species at varying wind speeds and varying wind directions relative to that of the bird.

The methods we have suggested cannot be applied to birds that are attracted to a ship. Estimating absolute densities of these birds poses a problem that remains unresolved, primarily because little is known about the distance from which a given species of bird will respond to a ship. Progress along these lines has been made by Haney et al. (in press), who estimated response distances of some species of seabirds being attracted to ephemeral food sources. More studies of this sort are needed.

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Cost of Short Flights in the Willow Tit Measured with Doubly-labeled Water

ALLAN CARLSON AND JUAN MORENO[1]
Department of Wildlife Ecology, Swedish Agricultural University,
P.O. Box 7002, S-75007 Uppsala, Sweden; and
Department of Zoology, Uppsala University, P.O. Box 561, S-75122 Uppsala, Sweden

Accurate measurement of the daily energy expenditures (DEE) of free-living birds depends on the use of realistic values for energy expended in high-cost activities like flight (Mugaas and King 1981, Weathers et al. 1984). Aerodynamic theory (Pennycuick 1968, 1975, Tucker 1970, Greenewalt 1975, Rayner 1979),

[1] Present address: Museo Nacional de Ciencias Naturales–C.S.I.C., J. Gutierrez Abascal 2, 28006 Madrid, Spain.

material balance (Kespaik 1968 as cited in Hails 1979), and wind-tunnel studies (Teal 1969, Torre-Bueno and LaRochelle 1978) have been employed for determining avian flight costs. Allometric equations based solely on body mass (Berger and Hart 1974, Kendeigh et al. 1977, Hails 1979) and standard multiples of basal metabolism (King 1974) are routinely used to estimate flight costs in studies of energy budgets (Goldstein 1988). The validity of aerodynamic models and wind-tunnel studies for predicting the energetic costs of free flight has been questioned on the basis of studies

TABLE 1. Individual activity and energy budgets for six Willow Tits.

Bird	Body mass (g)	Temp (°C)		Percent of aviary time record-ed	Hours in		Han-dling (h)	Night rest (h)	Aviary time budget[a]			DEE (kJ/day)
		Day	Night		Aviary	Cage			Perching	Foraging	Flying	
A	10.7	18.1	12.0	93.7	3.0	3.9	0.05	17.1	2.59 (86)	0.36 (12)	0.05 (2)	33.05
B	11.8	18.4	12.0	68.2	4.0	2.9	0.05	17.1	3.43 (86)	0.44 (11)	0.14 (4)	38.90
C	12.7	19.7	13.0	42.1	5.0	1.9	0.05	17.1	3.85 (77)	0.45 (9)	0.70 (14)	43.42
D	11.5	18.2	11.0	93.5	6.0	0.9	0.05	17.1	5.33 (88)	0.47 (8)	0.19 (3)	32.89
E	11.6	18.2	12.0	72.0	6.9	0.0	0.05	17.1	5.43 (79)	0.44 (6)	1.05 (15)	43.20
F	10.5	19.6	12.0	99.3	6.9	0.0	0.05	17.1	5.90 (86)	0.77 (11)	0.26 (4)	37.10

[a] In hours, with percent in parentheses.

using doubly-labeled water (Flint and Nagy 1984, Masman and Klaassen 1987). Standard multiples of basal metabolic rate (BMR) have been shown in dou-bly-labeled-water studies to grossly underestimate flight costs in some species (Tatner and Bryant 1986), while they overestimate costs for other species (Flint and Nagy 1984). Recently, the inclusion of aerody-namic properties of the species concerned have led to improvements in the predictive value of allometric models (Masman and Klaassen 1987).

Differences in flight costs are associated with dif-ferent foraging models. Aerial feeders that habitually forage on the wing during large parts of the day employ low-cost flight at metabolic rates ranging from 2.9 to 5.7 BMR (Hails 1979, Flint and Nagy 1984), whereas the short flights employed by some nonaerial foragers can cost as much as 23 BMR (Tatner and Bryant 1986). We determined the impact of time spent in flight on daily energy expenditure measured with doubly-labeled water in the Willow Tit (*Parus mon-tanus*). We used a large aviary, an approach only fea-sible for measuring the cost of short flights (Tatner and Bryant 1986). The foraging mode of Willow Tits is characterized by frequent flights of short duration (Moreno et al. 1988). This pattern makes very high costs of short flights improbable in the face of rela-tively low metabolic rates in the field (Moreno et al. 1988). By studying a nonaerial forager that flies fre-quently, we aimed to broaden the empirical basis for broad generalizations about the implications of for-aging mode and general ecology for avian flight costs.

We captured six Willow Tits in Lunsen forest near Uppsala (59°50′N, 17°40′E), central Sweden during the autumn of 1986. Birds were housed individually in 0.6 × 0.4 × 0.3 m cages, kept on an outdoors diurnal cycle, and fed on a diet of sunflower seeds and meal-worms. They were conditioned to the laboratory for two weeks before the DEE measurements.

Measurements of DEE were performed on birds flying in a large aviary (12 × 6 × 4 m) furnished with hanging pine branches and feeders at both ends. All individuals were accustomed to the aviary during four days before the DEE measurements. On the day of

measurement, each bird was weighed, loaded with 0.05 ml $D_2{}^{18}O$ (from a mixture containing 5 g of 51.6 atom % $H_2{}^{18}O$ and 1.29 g of 99.95 atom % D_2O. An RQ of 0.80 has been used for converting from milliliters of CO_2 to kilojoules) and kept in a dark box for 1 h to allow equilibration of labeled water in the body water pool. Half times ($T\frac{1}{2}$ days) of ^{18}O was calculated on the basis of body mass (M) in grams as

$$T\tfrac{1}{2} = 0.152M^{0.37} \qquad (1)$$

(K. A. Nagy pers. comm.; Masman and Klaassen 1987). This yields for an 11.5-g Willow Tit a half time for ^{18}O of 0.37 days.

Blood was sampled from a brachial vein and stored in flame-sealed microhematocrit tubes for later anal-ysis at the Centre for Isotope Research of the Uni-versity of Groningen, Netherlands. The labeled bird was then released in the aviary. This occurred in all cases at 0900. At 1600, the bird was recaptured, trans-ferred to its housing cage, and kept in darkness until 0900 the next morning, when we weighed the bird and took the second blood sample. A 7-h day (0900–1600) is representative for the natural day length dur-ing midwinter in Uppsala.

To manipulate flight time, the aviary session was interrupted by a variable period spent in the housing cage. Five of the six birds were randomly assigned to one of five treatments: 3, 4, 5, 6, or 6.9 h in the aviary, with a replicate of 6.9 h. Those birds with less than 6.9 h in the aviary had the day divided at midday, when they were captured and held in the housing cage with access to food and water for 1 to 4 h. The two individuals that spent 6.9 h in the aviary were subjected to the same capture procedure as the rest, but were released back into the aviary. The distur-bance caused by capture in the aviary represented about 5 min per day.

The 24-h day of the measured birds can be divided into: (a) the light period, when they were either mov-ing freely in the aviary or kept in the small housing cage; (b) the night rest period, which was the same for all individuals; and (c) the time needed to capture and handle the birds in the aviary and before second
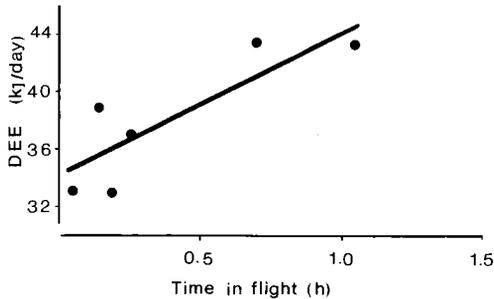
Fig. 1.   Energy expenditure by Willow Tits in relation to time spent in flight. Regression slope of 10.05 (SE = 3.19, t = 3.16, P < 0.05) and intercept of 34.09 (SE = 1.71, t = 19.99, P < 0.001).

samples were taken (which also was constant). The activity of the birds while in the aviary was continuously recorded on a datalogger. We noted three behavioral categories—perching, flying and foraging. Foraging includes hopping on branches, feeding at feeders, and handling food.

Time budgets of the labeled birds expressed in behavioral categories are shown in Table 1. The proportion of time in the aviary covered by time budgets differed because of technical details, but are assumed to be representative. On average, Willow Tits perched during 83.7% of aviary time, foraged for 9.6% of the time, and flew for 6.8% of the time in the aviary. The coefficients of variation for the average percentage of aviary time were 5.6, 23.6, and 87.2, respectively. The large coefficient of variation for flight indicates large individual differences in the tendency to fly in the aviary. For birds A and D, we recorded their flight speed in moving between branches 9.6 m apart. On average, these flights took 2.0 ± SE of 0.4 s (n = 35), which gives a flight speed of 4.7 m/s.

Willow Tits forage by continuously moving between trees, and hopping and flying inside trees (Alatalo and Moreno 1987, Moreno et al. 1988). In a field study, Willow Tits spent on average 2 s flying between trees close together and 45 s in every tree, of which 1 s was spent flying between branches (Moreno et al. 1988). Thus, 6.4% of the time was spent in flight, which is very close to what we observed in the aviary. The short 2-s flights in the aviary also are similar to the frequent flights employed while the birds moved between close trees. If we assume that Willow Tits forage continuously during the 7-h day in winter, they would make more than 500 such intertree flights daily. The durations of Willow Tit flights observed in the aviary and in the field are more than double those measured in European Robins (*Erithacus rubecula*) in an aviary (0.78 s; Tatner and Bryant 1986). The average flight speed of Willow Tits is 22% higher than in the European Robin, but 11% less than the minimum power speed (V_{mp} = 5.3 m/s) predicted by Pennycuick (1990).

TABLE 2.   Wing characteristics of Willow Tits and European Robins.

	Body mass (g)	Wing area (cm²)	Wing loading (g/cm²)	Aspect ratio[a]
Willow Tit	11.5 ± 0.8	64.1 ± 2.5	0.179	5.47
European Robin[b]	18.6	70.8	0.263	7.33

[a] (Wing span)²/wing area.
[b] Tatner and Bryant (1986).

The average DEE measured with doubly-labeled water is 38.09 ± 4.66 kJ/day for a 11.5-g Willow Tit, which represents a metabolic intensity of 2.03 BMR using the allometric prediction for the rest phase of Aschoff and Pohl (1970; 18.76 kJ/day). However, if we use the nighttime BMR measured by Reinertsen and Haftorn (1986; 23.51 kJ/day), we obtain the low value of 1.62 BMR. The average DEE we measured in captive conditions is 7.6% lower that the measured under field conditions in the same area (Moreno et al. 1988).

Daily energy expenditure was positively correlated with time spent in flight (Fig. 1). From the linear regression equation

$$\text{DEE (kJ/day)} = 34.09 + 10.05T_f, \qquad (2)$$

where T_f is hours in flight (P < 0.05, r^2 = 0.71), we deduce that for every hour a Willow Tit spends in flight, there is an increment in DEE of 10.05 kJ/day. Following the arguments put forward in Flint and Nagy (1984), maintenance metabolism should be added to the incremental cost of flight to give the total cost of flight. In the case of the Willow Tit, adding a maintenance cost of 34.09 kJ g^{-1} day^{-1} (the intercept of the regression line) yields an estimate of the total cost of short flights in Willow Tits to 11.47 kJ/h. This is equivalent to a metabolic intensity of 11.7 BMRnight or 9.1 BMRday (Reinertsen and Haftorn 1986). These figures are slightly lower than the usual multiple of 12 BMR used to estimate flight costs in studies of energy budgets (King 1974, Goldstein 1988).

Flight costs of Willow Tits predicted from the allometric equation of Hails (1979), which includes only body mass, are 24.3% lower (8.56 kJ/h) than our value. Incorporating wing morphology of Willow Tits (Table 2) in the allometric equation of Masman and Klaassen (1987) leads only to a minor improvement (8.94 kJ/h or 21.0% lower). The short flights of Willow Tits, thus, are relatively costly compared with predictions derived from studies of sustained flight. On the other hand, the flight expenditure of another non-aerial forager, the European Robin, has been estimated to be 23 BMRnight (Tatner and Bryant 1986). The flights of European Robins apparently are two times as costly as those of Willow Tits. This difference could be accounted for partly by the fact that Euro-

pean Robins used in the experiment performed very short flights, which involve mainly accelerating and deaccelerating, two energetically costly exercises (Norberg 1989).

European Robins have relatively high wing loading and a high aspect ratio (Table 2). The high aspect ratio indicates relatively long wings, which may be an adaptation to the migratory habits of this species. Willow Tits' short wings with a low aspect ratio (Table 2) enable them to engage in rather slow maneuverable flight, which is advantageous when foraging in trees (Norberg 1989). Furthermore, Willow Tits are sedentary (Ekman 1979) and, thus, seldom undertake long flights. The two species differ also in foraging mode. European Robins spend only small proportions of their time in flight (East 1982), and their foraging mode involves mostly hopping with infrequent sallies from perch to ground (East 1980). Willow Tits engage in short flights and move continuously between trees and between branches in search of food (Moreno et al. 1988).

Avian flight costs depend on body mass and aerodynamic properties, and how these relate to foraging mode and flight gait. This interaction is illustrated in our data for the Willow Tit, where morphological adaptations serve to reduce the energy cost of frequent short flights, which represent the major mode of locomotion used by this species. Selection probably favored the development of these characteristics, since they would lower DEE by reducing the cost of flight and by increasing foraging efficiency. The same adaptations may have evolved in other resident forest species.

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Daily Energy and Expenditure by Black-capped Chickadees (*Parus atricapillus*) in Winter

WILLIAM H. KARASOV, MARGARET C. BRITTINGHAM,[1] AND STANLEY A. TEMPLE
Department of Wildlife Ecology, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA

Daily energy expenditure (DEE), or field metabolic rate (FMR), has been determined in more than 25 species of birds (Nagy 1987, Weathers and Sullivan 1989). Based on these measurements, some authors have suggested that sustained metabolic rates (sensu Peterson et al. 1990) of wild birds may be constrained to three to five times standard (or basal) metabolic rate (SMR; e.g. Drent and Daan 1980, Peterson et al. 1990). Furthermore, it has been proposed that the limits constituted by the sustained metabolic rate may limit clutch size (Drent and Daan 1980) and latitudinal range boundaries (Root 1988, Peterson et al. 1990).

The available measures of DEE in passerines are greatly biased towards measures made during the reproductive season. Only Moreno et al. (1988) reported DEE of free-living passerines during winter in cold temperate habitats. We report on DEE of free-living Black-capped Chickadees (*Parus atricapillus*) during winter in Wisconsin, measured with doubly-labeled water (DLW).

Our measurements complement a study on the impact of wintertime supplemental feeding on the ecology of wild birds (Brittingham and Temple 1988, 1991). Though the current study was based on a small number of birds ($n = 5$ on two days) visiting a feeder, the data greatly extend our knowledge about the magnitude of energy expenditure during a time of year when expenditure is thought to be high and energy availability is thought to be limiting (Lack 1954, 1966, Fretwell 1972).

The study site was in a rural area of Dane County, Wisconsin, composed primarily of deciduous woods with intermittent openings. Chickadees are year-

around residents, and adults remain in the same area throughout winter; in the spring, they breed near their winter home range (M. C. Brittingham, pers. observ). We used mist nets to capture chickadees on the morning of 14 December 1985, when they visited a feeder.

We used a Hamilton glass syringe to inject birds intramuscularly with 45 µL water containing tritium (0.33 mCurie/mL; ICN) and oxygen-18 (95%). Birds were put into small paper sacks for 1 h. Previously, we concluded that this was sufficient time for complete equilibration, because dual sampling in the same species showed that tritium activity was, relative to 60 min: 1.01 ± 0.01 (ratio, $n = 2$) at 30 min; and 0.98 ± 0.02 ($n = 3$) at 90 min. We collected 70 to 100 µL of blood from a clipped claw or from the jugular vein. Birds were released at the feeder following weighing (± 0.01 g). Birds were caught with mist nets, weighed, and blood-sampled again either 24 h later (1 bird), or 48 h ($\pm$SE of 0.7) later ($n = 4$ birds). It is important that birds were weighed on the day of recapture at a time of day within 1.5 h of the time of day they were weighed on the initial day, because body mass cycles with time of day in winter (M. C. Brittingham, pers. observ.). Blood samples were stored in flame-sealed heparinized capillary tubes at 4°C pending analysis.

Blood was microdistilled to obtain pure water (Wood et al. 1975), and 2- or 5-µL samples were assayed in replicate for tritium by liquid scintillation. Three 7-µL samples were assayed for oxygen-18 content by proton activation (Wood et al. 1975). We used Nagy's (1980:eq. 2) equation to calculate CO_2 production, and Nagy and Costa's (1980:eq. 6) equation to calculate water influx. We calculated initial total body water by dilution of oxygen-18, and final total body water was taken as the product of the measured mean initial fractional water content (0.675 ± 0.012, $n = 5$) and final body mass. We converted the volume of CO_2 expired to kilojoules energy metabolized by assuming

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[1] Present address: School of Forest Resources, The Pennsylvania State University, University Park, Pennsylvania 16802, USA.