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

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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 (±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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an RQ of 0.85 and, hence, a ratio of 24.0 J/mL CO_2 (Schmidt-Nielson 1975).

Hourly air temperature (T_a) was measured with a thermocouple at 1 m above the ground in the shade. During the 48-h period of the study, the minimum T_a was $-14.6°C$, the maximum approximately 4.5°C, and the average $-10.1 \pm 0.4°C$. Initial body mass was 11.63 ± 0.35 g ($n = 5$). Recapture mass of the bird caught after one day was the same as the release mass, but all four birds caught after two days lost mass ($-3.2 \pm 1.1\%$; paired t-test, $t = 2.87$, $P = 0.07$). The bird caught after one day had the highest calculated CO_2-production rate, but among the five birds the coefficient of variation was remarkably low (6.5%). The CO_2 production averaged 238 ± 7 mL g^{-1} day^{-1} (range 215–258), corresponding to a daily energy expenditure of 65.5 kJ bird^{-1} day^{-1}. Water influx was 5.1 ± 0.2 mL/day, of which 1.7 mL/day was due to metabolic-water production (assuming 0.026 mL H_2O/kJ metabolized; Schmidt-Nielson 1975) and 3.4 mL/d was preformed water (in food, or from drinking or eating snow).

Root's (1988) analysis of winter-range boundaries and avian energetics implied that bird species are limited to wintering in areas where they do not have to raise their FMR much beyond 2.5 times the basal level (Peterson et al. 1990). The FMR of chickadees in our study (238 J g^{-1} h^{-1}) was 2.95 times Chaplin's (1976) measurement of chickadee basal metabolism during the resting phase (80.6 J g^{-1} h^{-1}). This agrees closely with FMR of 2.2 to 2.9 SMR measured in three species of *Parus* in central Sweden in winter (average $T_a = -6°C$; Moreno et al. 1989). The winter metabolic rates of parids studied so far are no higher than those observed in passerines feeding nestlings (3.38 ± 0.35 SMR, $n = 9$ species; Weathers and Sullivan 1989).

The energy expenditure of free-living chickadees was 26% below that measured in chickadees housed in outdoor aviaries at similar winter temperatures (Howitz 1981). Because the technical accuracy of the labeled-water method is about $\pm 10\%$ (Nagy 1987), this difference underscores Nagy's (1987) point that free-living animals experience physical conditions and exhibit behaviors that can result in differences in energy expenditure of $\pm 50\%$ between the captive and free-living situations.

Tits in the genus *Parus* probably reduce winter expenditure through selection of roosting microhabitats and nighttime hypothermia (Moreno et al. 1988). Chaplin (1976) measured resting metabolism of hypothermic chickadees as a function of temperature. Based on those measurements and average temperatures during the two nights of our study (-8.8 and $-11.9°C$), we estimate that no more than 29.7 kJ/day was expended during 14 h of nighttime roosting, or 45% of total FMR. The actual value is lower, because chickadee roosting cavities offer insulation and reduce net radiative heat loss. Partitioning daytime expenditure into costs associated with thermoregulation and activity is difficult due to uncertainty about

the bird's conductance and whether heat generated during activity substitutes for thermoregulation.

Brittingham and Temple (1991) estimated that chickadees obtained at least 21% of their daily energy needs at feeders in winter. Based on the more accurate results from our study, the value appears slightly higher—about 29% of daily needs.

In summary, the energy expenditure of free-living chickadees in winter was about three times their basal rate of expenditure. This is not notably different from rates of expenditure of other passerines feeding nestlings at other times of the year. Because our winter study was based on only five individuals, more research on winter energy expenditure of free-living birds is warranted.

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Exotic Birds: A Growing Problem with No Easy Solution

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In the Western Hemisphere, it began at least 1,400 years ago in Polynesia and has continued at an ever-accelerating rate since then; it has resulted in the extinction of indigenous species and the disruption of natural communities; it has caused untold economic losses and other hardships for some human beings while bringing joy, recreation and profit to others; it has been both promoted and condemned by governments and by common citizens; and, finally, it has generated enough controversy to warrant the attention of the AOU Conservation Committee, which is preparing a detailed report. *It* is the establishment of free-living populations of bird species outside their natural ranges as a result of human activities. Many of these exotic birds, now established components of the American avifauna, have been imported from distant zoogeographical realms, but others have been translocated within the Nearctic region. In all cases, these alien birds have had help—sometimes substantial—from human beings and would not have immigrated or dispersed naturally.

The first exotic bird in what is now the United States almost certainly was the Red Junglefowl (*Gallus gallus*) imported by Polynesians from southeastern Asia to the Hawaiian Islands and to other islands throughout the Pacific. Since then, the number of free-living exotic birds in the United States and its territories has grown by an estimated 75 species imported from other countries and 22 species translocated within U.S. territory (S. A. Temple and D. M. Carroll, unpubl. manuscript). Many additional species have been imported or translocated, but they failed to become established as self-sustaining wild populations.

Figure 1 traces the historical accumulation of nonnative bird species in the United States. The rate of importation of exotics remained low until the mid-

1800s, when streamships and then airplanes provided ways to rapidly transport birds to the United States from distant places. Many of these imported species successfully established wild populations. The acceleration in the rate of importation and establishment of new species shows no signs of slowing; the apparent leveling of the rate during the last decade reflects only my uncertainty about which exotic species first detected in the wild during the 1980s have actually become established as self-sustaining populations.

The origins of imported exotics that are now established in the United States are diverse with 26% from the Neotropics, 47% from Eurasia, 22% from Africa, and 4% from other regions. Imported and translocated exotics have not become established uniformly throughout the United States. Hawaii and Florida have the highest proportions of their breeding avifaunas composed of exotics (18% and 9%, respectively). In most states, exotic birds account for less than 5% of the breeding avifauna.

How did the 97 exotic birds become established in regions outside their natural geographic range? Some exotic species have been able to expand their ranges into new areas because human activities inadvertently removed previous range limitations or barriers to dispersal. Many were intentionally imported or translocated in accordance with existing laws, while others were introduced intentionally but illegally. In many cases, establishment in the wild was accidental, involving escapes from captivity.

Birds that have expanded their geographic ranges in response to human-caused changes in the environment are examples of natural dispersal made possible by unnatural events. In the United States, northward range expansions in response to new sources of winter food, such as bird feeders, and eastward dis-