Winter and Breeding-season Energetics of Nonmigratory White-crowned Sparrows

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The lives of most temperate-latitude birds are organized on an annual cycle that includes reproduction, molt, dispersal and/or migration, and winter maintenance. How food and energy requirements vary with stage of the annual cycle, and which stage (if any) constitutes an energy bottleneck, are poorly known, but two alternative hypotheses have generally been recognized (Masman et al. 1989). The "reallocation hypothesis" holds that abundant food and moderate temperatures during the breeding season result in decreased thermoregulatory and foraging costs, which allows energy to be reallocated to breeding. This hypothesis predicts little seasonal variation in field metabolic rate (FMR). The "increased-demand hypothesis" holds that breeding results in a substantial increase in the energy demand of adults. By breeding during the season with maximum food availability, parent birds are able to meet their increased energy demands. This hypothesis predicts that FMR should reach a seasonal maximum during the breeding season. Early attempts to deduce the annual cycle in FMR by extrapolating laboratory metabolic measurements to the field produced conflicting patterns. Kendeigh (1973) derived a monthly energy budget for central Illinois House Sparrows (*Passer domesticus*) in which FMR attained an annual maximum of 117 kJ day^{-1} in January and February and then gradually decreased to an annual nadir of 83 kJ day^{-1} in August. The seasonal change in FMR in Kendeigh's analysis was driven largely by seasonal variation in basal metabolic rate and thermostatic costs. In contrast, Farner (1980) derived an annual energy budget for a migratory race of White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) in which FMR was 100 kJ day^{-1} during the winter and breeding seasons. Subsequent studies that estimated FMR using more direct techniques revealed a diversity of patterns (see Weathers and Sullivan 1993), with some species following the House Sparrow model and others showing little seasonal change in FMR. Which pattern is followed appears to be related to diet in that FMR increases little during the breeding season in species with energetically economical foraging modes, whereas FMR of species that feed on mobile animal prey is higher during the breeding season than during winter (Weathers and

Sullivan 1993). Further studies are needed, however, to evaluate these hypotheses.

We used the doubly labeled water (DLW) technique (Nagy 1983) to examine seasonal variation in FMR of a resident coastal population of White-crowned Sparrow (*Z. l. nuttalli*) located at the southern end of Point Reyes National Seashore, Marin County, California (37°56'N, 122°45'W). This population occupies coastal scrub dominated by coyote bush (*Baccharis pilularis*), bush monkey flower (*Mimulus aurantiacus*), and poison oak (*Rhus diversiloba*) interspersed with patches of introduced annual grasses (*Avena, Holcus, Phalaris*) and widely scattered Douglas fir (*Pseudotsuga menziesii*) trees up to 3 m high. The site experiences a warm Mediterranean-type climate with moderate to strong onshore winds and frequent fog, especially in summer. Mean monthly air temperature at the site ranges from around 6°C in winter to 13°C in summer (Mewaldt and King 1977). We postulated that this coastal population of sparrows would exhibit little seasonal change in FMR because (1) the thermal regime is relatively stable seasonally; (2) this species employs an energetically economical foraging method; and (3) its reproductive effort is spread over a 5-month breeding season, during which pairs produce two or three clutches of two to three eggs each (Mewaldt and King 1977).

Methods.—We measured CO_2 production and water flux of free-living sparrows using either the single- or double-sample DLW method (Webster and Weathers 1989). Winter measurements were made in 1993 between 22 January and 11 February and between 20 and 30 December. Summer DLW measurements of adults incubating eggs or feeding nestlings were made between 6 June to 19 July 1995. We captured birds in mist nets or Potter-style traps, banded them, weighed them to the nearest 0.1 g with an electronic balance or spring scale, and then injected them intramuscularly with 60 to 70 μL of water containing 97 atoms-percent ^{18}O and about 0.7 to 0.8 MBq ^3H. After this treatment, birds were either released immediately (single-sample method) or held for 1 h for isotope equilibration and subsequent blood sampling (double-sample method). Approximately one or two days later, the birds were recaptured, reweighed, and a first or second blood sample obtained.

For the single-sample method, we estimated initial

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TABLE 1. Recapture interval as fraction of 24 h, mean air temperature, and fraction of the field metabolic rate measurement interval that was daylight. Values are $\bar{x} \pm$ SD.

Parameter	Winter ($n = 21$)	Summer ($n = 26$)	t	P
Recapture interval	0.970 ± 0.073	0.993 ± 0.089	0.94	0.35
Mean air temperature (°C)	7.9 ± 2.2[a]	15.5 ± 1.5	13.31	<0.001
Daylight fraction (mean)	0.436 ± 0.060	0.649 ± 0.026	8.65	<0.001
Daylight fraction (range)	0.279–0.505	0.593–0.747		

[a] $n = 19$.

isotope level and fraction of body water based on 1-h equilibration values determined on 22 double-sample birds (11 from each season). Blood samples were refrigerated in sealed glass tubes until they were micro-distilled (Nagy 1983) to obtain pure water that was assayed for tritium activity by liquid-scintillation spectrometry (duplicate 5-µL samples, toluene-Triton X100-PPO scintillation cocktail). Oxygen-18 content of triplicate samples was determined by cyclotron-generated proton-activation analysis at the University of California, Davis (Wood et al. 1975). Body-water volumes, rates of carbon dioxide production, and water efflux were calculated using the equations of Nagy (1980, 1983) and Nagy and Costa (1980). We calculated FMR from CO_2 production assuming energy equivalents of 22.5 kJ L^{-1} CO_2 in winter and 23.3 kJ L^{-1} CO_2 in summer; these values were based on the seasonal change in diet from seeds in winter to a mixture of seeds and insects in summer (Martin et al. 1951). In validations of our DLW method, CO_2 production of individual birds measured by DLW differed from values determined simultaneously by the Haldane technique by less than 9%, whereas mean errors for groups of nine birds were less than 2% (Buttemer et al. 1986, Webster and Weathers 1989).

Concurrent with our DLW measurements, we monitored the thermal environment at a meteorological station placed in a clearing near the banding station. Parameters measured 1 m above ground level were (1) air temperature (T_a; shaded 36-gauge type-T thermocouple), (2) operative temperature (T_e; 3.5-cm diameter metal sphere thermometer painted flat gray; Bakken et al. 1985, Walsberg and Weathers 1986), and (3) wind speed (u; Thornthwaite Model 901 cup anemometer). We also measured T_e 5 cm above ground and in the center of a coyote bush. Sensor outputs were monitored at 10-s intervals, averaged every 10 or 30 min, and recorded with a Campbell Scientific 21× microdata logger. Thermocouples were calibrated against a National Bureau of Standards certified mercury thermometer; the cup anemometer was factory-calibrated.

We evaluated the effect of environmental factors on winter FMR using simple multiple regression models as well as models for the analysis of covariance that included continuous variables for days since winter solstice, mean air temperature, and day

length. In addition, by including a discrete variable for the presence or absence of rain on the day that FMR was measured, we evaluated several models that fit separate regression coefficients for explanatory variables for days with or without rain (separate-slopes models; Searle 1971). All analyses were conducted by calculating type III sums of squares using SAS Proc GLM (SAS 1996). Models in which the effects of interest were not significant ($P > 0.05$) were excluded. Within models that had significant contributory effects (temperature, day length, etc.) we selected the model with the smallest mean squared error (MSE).

Results.—We recaptured 21 sparrows in winter and 26 in summer. We tried to recapture birds as close as possible to 24 or 48 h after their initial release, so that our FMR measurements would represent daily energy expenditure. Recapture intervals in winter ranged from 0.776 to 2.040 days, with 16 of 21 birds recaptured within 2 h of either 24 or 48 h. In summer, 20 of 26 sparrows were recaptured within 2 h of either 24 or 48 h, and recapture intervals ranged from 0.844 to 1.976 days. The mean deviation from a 24-h or 48-h recapture interval was 1.2 ± SD of 1.2 h (range 0 to 4.3) in winter and 1.4 ± 1.7 h (range 0 to 8.9) in summer. Mean recapture intervals (expressed as a fraction of a day) did not differ by season (Table 1).

In winter, sparrows weighed 8% more than in summer and were fatter, as indicated by their lower body-water content (Table 2). During both seasons, most birds ate enough during the measurement interval to maintain their body mass. Mass change per day during measurements averaged 0.2% in summer and −1.2% in winter, a nonsignificant difference (Table 2).

Characterizing a bird's thermal environment requires knowledge of the operative temperature and wind speed encountered (Bakken 1980, 1990). Our efforts to assess the thermal environment met with limited success because our cup anemometer worked only intermittently and because the birds proved difficult to observe continuously. During both seasons, sparrows were often hidden from view within the dense brush canopy, which shielded them from the wind. Winter birds often foraged on the ground either beneath bushes or in small openings between bushes. We estimated T_e encountered by birds rest-

TABLE 2. Seasonal variation in body mass, field metabolic rate, and water efflux of White-crowned Sparrows from Point Reyes peninsula, Marin County, California. Values are $\bar{x}$ ± SD.

Parameter	Winter ($n = 21$)	Summer ($n = 26$)	t	P
Mean body mass (g)	31.1 ± 1.7	28.9 ± 1.6	4.3	<0.001
Body-mass change (% day^{-1})[a]	−1.2 ± 3.6	0.2 ± 2.1	1.6	0.110
CO_2 production (mL g^{-1} h^{-1})	5.98 ± 1.69	5.29 ± 0.57	1.9	0.061
Field metabolic rate (kJ day^{-1})	100.4 ± 28.7	85.5 ± 10.1	2.4	0.019
Water efflux (mL kg^{-1} day^{-1})	608 ± 264	467 ± 84	2.5	0.015
Body-water fraction	0.652 ± 0.036[b]	0.691 ± 0.011[b]	3.3	0.004

[a] Change in body mass during field metabolic rate measurement.
[b] $n = 11$.

ing within a coyote bush and while on the ground in the open. During winter FMR measurements, T_e inside the bush averaged 2.5 ± 2.2°C ($n = 251$) higher than T_a during the day and 0.5 ± 0.4°C ($n = 303$) lower than T_a at night. Overall, T_e within the bush averaged 0.8 ± 2.2°C ($n = 554$) higher than T_a; T_e on the ground averaged 6.8 ± 5.8°C ($n = 132$) higher than T_a during the daytime. Given that sparrows were usually shielded from the wind and that T_e generally was close to T_a, we believe that T_a provides a reasonable estimate of the birds' thermal environment in this study.

Both day length and air temperature varied seasonally. Mean T_a was lower in winter than in summer, although as expected the seasonal variation in T_a was fairly modest at our coastal study site (Table 1). The fraction of the FMR measurement interval that was daylight varied between individual birds, both because of the seasonal change in day length and because recapture intervals were seldom exactly one day. The proportion of the FMR measurement interval that was daylight was significantly higher in summer than in winter (Table 1). The relative amount of daylight encountered was more variable in winter, however, ranging 1.8-fold versus 1.3-fold in summer (Table 1).

CO_2 production tended to be higher in winter than in summer, but not significantly so. Because seasonal differences in diet altered the energy equivalent of CO_2, however, FMR expressed in kJ day^{-1} was significantly higher during winter (Table 2). Water efflux also was significantly higher during winter (Table 2).

Discussion.—The effort that parent birds invest in reproduction represents an evolutionary solution to the problem of maximizing fitness. To maintain a reserve for periods of stringency, parents may not work as hard as they are physiologically capable (Weathers and Sullivan 1989), but parental effort should constitute a relative maximum. Accordingly, FMR during the breeding season should equal or exceed that at other times of the year, as postulated by the reallocation and the increased-demand hypotheses. Each of the eight bird species in which FMR previously has been measured during winter and the breeding

season conforms to one of these two hypotheses (Weathers and Sullivan 1993), but the White-crowned Sparrow does not. Its FMR is 17% higher during winter than during the breeding season (Table 2). Because the high winter FMR in these sparrows represents a sustainable metabolic rate (individuals were in mass balance), this finding begs the question, why didn't breeding White-crowned Sparrows work harder? The obvious answer is that the fitness consequences of a given level of energy expenditure differ in winter and summer. Why this should be so is unclear, but many possibilities exist. For example, if the predation rate experienced while foraging is lower in winter than in summer, winter birds could forage longer before incurring the same level of predation risk and thus be able to support a higher FMR. Whatever the explanation, FMR does not attain an annual maximum during the breeding season in White-crowned Sparrows, in contrast to other species that have been studied (Weathers and Sullivan 1993).

In summer, sparrows exhibited relatively little variation among individuals in FMR (CV = 10%; Table 2). All breeding birds apparently worked equally hard, implying that they were functioning at a relative metabolic ceiling, as postulated by Drent and Daan (1980). In contrast, variation in FMR among individuals was three times higher in winter than in summer (CV = 29%; Table 2). Greater variability in winter FMR could be attributable to greater variation in the physical environment during winter (Table 1). For example, potential day length (civil twilight included) varied less in summer (14.5 to 14.8 h) than in winter (9.6 to 10.7 h).

To investigate the link between physical environment and winter FMR, we examined the effect of four environmental factors on winter FMR (1) calendar date (days since winter solstice), (2) minutes of daylight encountered during the measurement interval, (3) air temperature, and (4) rainfall (Figs. 1A-D). We did not quantify rainfall during the FMR measurements and thus included rain as a categorical variable in our analysis. Our field notes and precipitation data for three locations 13 to 19 km from our study site indicated that rain fell during 10 of the
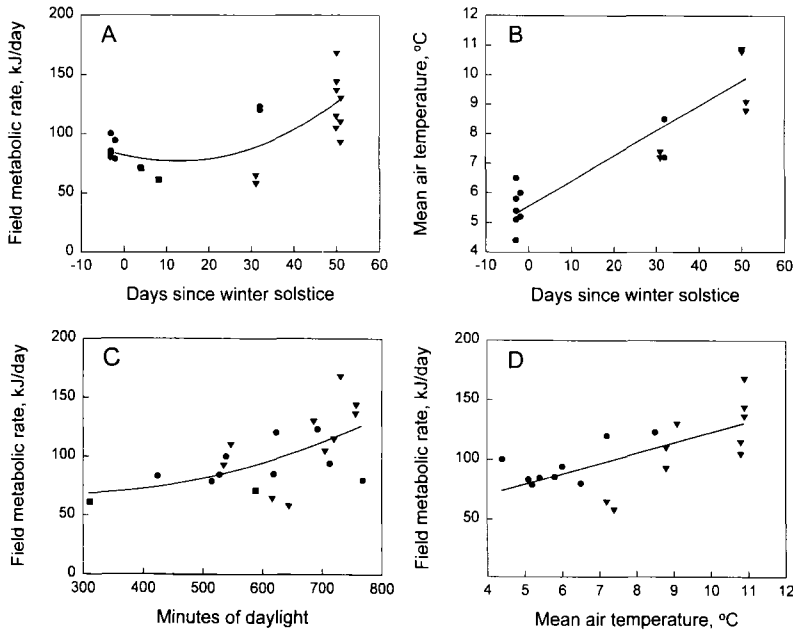
FIG. 1.   Relationship between field metabolic rate (FMR) of wintering White-crowned Sparrows and (A) calendar date, expressed as days since the winter solstice; (C) minutes of daylight per day during the FMR measurement interval; and (D) mean air temperature. The relationship between mean air temperature during the FMR measurement interval and calendar date is depicted in (B). Shaded boxes in (A) denote unusually warm days. Shaded diamonds denote measurement intervals during which rain fell.

21 days that we measured FMR in winter in amounts that ranged from 13 to 18 mm.

The continuous explanatory variables (days since the winter solstice, day length, and air temperature) are positively correlated with one another (Table 3). Consequently, using all of them in the same model to describe FMR will yield statistically unstable results because of multicollinearity. Accordingly, we employed simple multiple regression models as well as models for the analysis of covariance that included continuous variables for days since winter solstice, mean air temperature, and day length to evaluate the effect of environmental factors on FMR. In addition, by including a discrete variable for the presence or absence of rain on the day that FMR was measured,

TABLE 3.   Simple correlations (P in parentheses) among days since the winter solstice (days), minutes of daylight during the measurement interval (light), mean air temperature (temp), and field metabolic rate (FMR).

	Days	Light	Temp	FMR
Days	—	0.42 (0.072)	0.92 (0.001)	0.60 (0.007)
Light		—	0.64 (0.003)	0.50 (0.031)
Temp			—	0.70 (0.001)
FMR				—

we evaluated several models that fit separate regression coefficients for explanatory variables for days with or without rain (separate-slopes models; Searle 1971).

The two models that best describe variation in FMR include the presence or absence of rain on the day FMR was measured. In the model with the smallest mean squared error in which the relevant variables were significant ($P < 0.05$), FMR was a function of rain and days since the winter solstice (DAYS) and can be represented (with standard errors) as:

$$FMR = intercept - 0.19 \ (\pm \ 0.77) \times DAYS + 0.04$$
$$(\pm \ 0.2) \times DAYS^2 \qquad (1)$$

The intercept was 29.48 ($\pm$ 18.34) for days when it rained and 85.66 ($\pm$ 6.3) for days without rain. The mean squared error for this model was 326.2. Interestingly, this model was slightly better than one that makes use of average air temperature (MSE = 330.7), despite temperature having a higher correlation with FMR than days since the winter solstice (Table 3). Because both DAYS and temperature are strongly positively correlated, either one provides sufficient information to evaluate FMR. Yet, neither variable is able to accurately predict FMR without a variable for the presence or absence of rain included in the model. Models without rain as a factor either had nonsig-

TABLE 4. Field metabolic rate (FMR), water efflux, and body-mass change of White-crowned Sparrows in winter during measurement periods with and without rainfall. Values are $\bar{x} \pm$ SD.

Parameter	Rain	No rain	t^a	P
FMR (kJ day⁻¹)	112.7 ± 32.7	89.2 ± 18.2	1.96	0.062
Water efflux (mL kg⁻¹ day⁻¹)	792 ± 209	440 ± 185	3.89	0.001
Body-mass change (% day⁻¹)	-0.74 ± 3.39	-1.63 ± 3.78	0.54	0.600
Mean air temperature (°C)	9.6 ± 1.4	6.0 ± 1.2	5.59	<0.001
Daylight (min)[b]	670 ± 77	575 ± 126	1.97	0.061

[a] t-test with 19 df.

[b] Minutes of daylight birds encountered during FMR measurement period.

nificant explanatory terms, or mean squared errors so large that the accuracy of their predictions cannot be considered reliable. Other models had similar mean squared errors, and in several cases even smaller mean squared errors, yet failed to provide satisfactory predictions of FMR. Furthermore, it is important to note that models that included terms for both temperature and days from the winter solstice did not have the smallest mean squared error, nor were the regression coefficients for these explanatory variables significantly different from zero.

Although we do not know exactly how much rain individual birds encountered, FMR tended to be higher on rainy days by an average of 24 kJ day⁻¹ (Table 4). Water efflux was significantly higher on rainy days; 792 versus 440 mL kg⁻¹ day⁻¹ (Table 4). If data for rainy days are excluded, FMR was similar in winter and summer (89 vs. 86 kJ day⁻¹, respectively), as was mean water efflux (440 vs. 467 mL kg⁻¹ day⁻¹, respectively). In winter, the combination of rainfall and generally low T_a dramatically affected the sparrows' thermal environment, even reversing the usual dependency of FMR on temperature (Fig. 1D). Despite the colder winter conditions, sparrows maintained mass balance on rainy days, indicating that they are physiologically well equipped to handle such weather.

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Confirmation of Infanticide in the Communally Breeding Guira Cuckoo

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The killing of conspecific infants may be common (Hrdy 1979, Sherman 1981, Hrdy and Hausfater 1984, Parmigiani and Vom Saal 1994) but is reported infrequently because the behavior occurs rapidly. In several species of mammals, infanticide has been linked with mate takeover or cases where a new dominant male comes into contact with infants sired by the harem's previous male (Hausfater et al. 1982, Sommer 1994). In birds, infanticide usually has been reported in the context of sibling rivalry (Mock 1984, Fujioka 1985, Drummond et al. 1986, Mock and Forbes 1994), although evidence suggests that the killing of infants also may increase the perpetrator's fitness by decreasing a competitor's reproductive success or enhancing access to a potential mate (Trail et al. 1981, Stephens 1982, Stacey and Edwards 1983, Fujioka 1986).

Guira Cuckoos (*Guira guira*) occur in groups of as many as 26 individuals (Gallardo 1984) and are classified by Brown (1987) as plural breeders with joint nests. During reproductive periods, groups are smaller but still may include as many as 13 adults. Throughout the egg-laying and incubation periods, eggs are commonly tossed out of the nest by group members (Macedo 1992). After chicks hatch, group members do not participate equitably in nestling feeding or nest guarding (Macedo 1994). DNA analysis has shed light on several aspects of group dy-

namics. For example, despite the appearance of social monogamy, the Guira Cuckoo mating system includes polyandry and polygyny (Quinn et al. 1994). Additionally, breeding opportunities may be limited because some group members are excluded from reproduction. Circumstantial evidence has suggested that the killing of newly hatched chicks is a common occurrence and that high chick mortality probably results from infanticide by conspecifics (Macedo and Bianchi 1997b). In this paper, we confirm that infanticide is indeed an important cause of mortality for Guira Cuckoo nestlings, and we speculate about its function as a reproductive strategy.

Methods.—The study was conducted in a suburban area of Brasilia, Brazil (15°47′S, 47°56′W; elevation = 1,158 m), from September 1995 to March 1996 and September 1997 to February 1998; these periods coincide with the rainy season in this region. Further description of the study site and vegetation can be found in Macedo (1992). Each active nest was visited daily to check for new eggs, and the ground beneath the nesting tree was searched for vestiges of any eggs or chicks not in the nest. On the first or second days posthatching, each chick received temporary colored leg bands made out of plastic drinking straws, or colored dye marks. Continuous periods of nest observations were conducted primarily during the first week after chicks hatched (the period when nestling disappearance is most prevalent). Group size was estimated by counting the adults around the nest at

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