

Altitudinal variation in parental energy expenditure by white-crowned sparrows

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Summary

We used the doubly labeled water technique to measure daily energy expenditure (DEE) during the incubation and feeding nestling stages in two populations of white-crowned sparrows (*Zonotrichia leucophrys*) – one montane and migratory, the other coastal and sedentary – that differ in thermal environment and clutch size. We assessed the birds' thermal environment by continuously monitoring (among other variables) operative temperature and wind speed both in the open and within bushes and willow thickets occupied by sparrows. From these measurements, we derived several estimates of the birds' thermal environment, including standard operative temperature (T_{es}). Shade air temperature and T_{es} averaged 6.6 and 10.3°C lower, respectively, at the montane study site during DEE measurements. The montane population's DEE averaged 24% higher than that of the sea-level population (103.6±12.2 versus 83.7±9.6 kJ day⁻¹; means ± s.d., $N=31$ and 22, respectively), reflecting both its larger brood size (3.7 versus 2.9) and the colder environment. The DEE:BMR

ratio was lowest in the sea-level population (2.1 versus 2.6), but neither population worked to their physiological capacity to produce young. DEE was significantly correlated with temperature across populations, with T_{es} explaining 42% of the variation in DEE. Statistically removing the effect of temperature by adjusting DEE to a common temperature reduced the difference in DEE between populations by 34% to 87.7 and 100.8 kJ day⁻¹, respectively, for sea-level and montane populations. Basal and resting metabolic rates were similar in both populations, implying that greater activity in the montane population accounted for its higher temperature-adjusted DEE. Our results indicate that the thermal context within which behavior occurs can significantly affect interindividual variation in DEE. Attempts to assess reproductive effort by measuring DEE should therefore account explicitly for the effect of temperature.

Key words: field metabolic rate, reproductive effort, parental effort, white-crowned sparrow, *Zonotrichia leucophrys*.

Introduction

If parental working capacity is the primary determinant of reproductive effort (RE) (*sensu* Hirshfield and Tinkle, 1975), then variation in daily energy expenditure (DEE) may denote variation in fitness and thus be useful for studying life history evolution. Among birds, intraspecific variation in parental DEE has generally been assumed to result primarily from differences in behavior and thus to reflect variation in RE (Bryant, 1989, 1997; Bryant and Tatner, 1991; Tatner and Bryant, 1993). Both intraspecific (Bryant and Tatner, 1991) and interspecific (Bryant, 1997) analyses have emphasized the importance of body size and activity as determinants of the considerable interindividual variation in DEE typically seen in small birds. These and earlier analyses concluded that the thermal environment is an unimportant source of variation in DEE (Bryant, 1989). Recently, Bryant (1997) found that body mass, day length and air temperature explained 72% of the interspecific variation in DEE of 58 bird species weighing less

than 150 g. But when time spent in flight was incorporated into the analysis, it proved to be a better predictor than the two environmental variables, which became non-significant under the stepwise procedure used.

Most DEE studies in which temperature seemed unimportant used air temperature data obtained from meteorological stations located 8–50 km from the study site (e.g. Bryant et al., 1985; Bryant and Westerterp, 1980, 1983; Bryant and Tatner, 1988; Moreno, 1989; Tatner, 1990; Deerenberg et al., 1995). Given that environmental temperature can vary by 10°C with minor changes in location or posture (Mahoney, 1976; Mugaas and King, 1981), finding a weak (or no) correlation between DEE and remotely measured air temperature seems inconclusive. In addition, air temperature alone may provide an inadequate index of the thermal potential driving heat exchange (Campbell and Norman, 1998). Standard operative temperature (T_{es}), which

incorporates wind and radiation effects on endotherm heat transfer (Bakken, 1980, 1990), should usually provide a more reliable assessment of a bird's actual thermal environment (Piersma and Morrison, 1994), yet it has seldom been measured in DEE studies.

In this study, we measured DEE during the incubation and nestling stages in two subspecies of white-crowned sparrow (*Zonotrichia leucophrys*) that encounter very different thermal environments. One subspecies, Nuttall's white-crowned sparrow (*Z. l. nuttalli*), is a permanent resident of California's narrow coastal fog-zone between approximately 34 and 40°N latitude. It inhabits characteristically low, wind-swept terrain, often on sea-facing hillsides dominated by California sage (*Artemisia californica*) and coyote bush (*Baccharis pilularis*). The other subspecies, the mountain white-crowned sparrow (*Z. l. oriantha*), is an intracontinent migrant that breeds in the high mountains of the western United States and winters from the extreme southwestern United States and Baja California south as far as the Mexican states of Michoacan and Tamaulipas (American Ornithologist's Union, 1998). Compared with the climatically mild coastal environment of *Z. l. nuttalli*, the high-altitude, montane habitat of *Z. l. oriantha* is harsh and unpredictable. Late spring snowstorms often delay, disrupt or devastate the breeding attempts of *Z. l. oriantha*, with both adults and young often exposed to freezing temperatures, especially at night. We assessed each population's thermal environment concurrently with our DEE measurements, and used the field temperature assessments together with laboratory measurements of resting metabolic rate to evaluate DEE.

Materials and methods

Study sites and populations

We compared the energetics of *Z. l. nuttalli* breeding at Point Reyes Bird Observatory (PRBO), Marin County, California with that of *Z. l. oriantha* breeding at Tioga Pass Meadow (TPM) in California's central Sierra Nevada Mountains, Inyo County. The PRBO population has been the subject of a long-term study started in 1966 by L. Richard Mewaldt, and its general biology, behavior, breeding ecology and demography are well-documented (Blanchard, 1941; DeWolfe, 1968; Baker et al., 1981). Similarly, the TPM population has been under intensive study since 1968 by Morton and his students (Morton, 1976, 1977, 2002; Morton et al., 1972a,b, 1973, 1990, 1991).

These populations occur at the same latitude (approximately 38°N), breed about the same time of year (although *Z. l. nuttalli* usually starts approximately a month earlier than *Z. l. oriantha*), but differ somewhat in the details of their breeding effort. Single brooding is the rule in *Z. l. oriantha* (Morton, 1976), whereas *Z. l. nuttalli* at PRBO are commonly double-brooded, individuals averaging 2.0 clutches per season (Mewaldt and King, 1977; Baker et al., 1981). Clutch size averages 18% higher at TPM (3.86, $N=1154$; Morton, 2002) than at PRBO (3.27, $N=170$; N. Nur, G. Geupel and D.

DeSante, in preparation). The difference in clutch size implies higher instantaneous reproductive effort among *Z. l. oriantha*; the difference in brood number suggests greater cumulative reproductive effort in *Z. l. nuttalli*. Finally, male *Z. l. nuttalli* do not regularly begin to assist the female in feeding the young until they are approximately 4 days old (Blanchard, 1941), whereas male *Z. l. oriantha* usually begin to assist on the day of hatch, but do not feed as often as the female until the young are 3 days old (Morton et al., 1972a). During the incubation stage, male white-crowned sparrows sing, engage in other territorial behaviors and may accompany the female while she forages, but they do not incubate the eggs. Accordingly, all references to 'incubating males' refer to the stage of the breeding cycle, not the male's specific activity.

Doubly labeled water

We measured rates of CO₂ production and water flux of adult sparrows incubating eggs or feeding 5- to 7-day-old nestlings using either the single- or double-sample doubly labeled water (DLW) method (Webster and Weathers, 1989). Measurements at TPM were made between 29 June and 15 July 1993 (day of year=186±6; mean ± s.d.) and at PRBO between 8 June and 19 July 1995 (day of year=182±11). These mean day-of-year dates do not differ ($t_{51}=1.49$, $P=0.14$). We captured birds on their territories with mist nets or Potter-style traps, banded them, weighed them to the nearest 0.1 g with either a K-tron electronic balance or Pesola spring balance and gave them an intramuscular injection of 60–70 µl of water containing 97 atoms % ¹⁸O and approximately 0.7–0.8 MBq of ³H. The birds were then either released immediately (single-sample method) or held for 1 h for isotope equilibration and subsequent blood sampling (double-sample method). Approximately 1–2 days later, the birds were recaptured, reweighed and a first or second blood sample was obtained.

For the single-sample method, we estimated initial isotope level and body water fraction based on 1-h equilibration values determined on 8–11 double-sample birds from each population. Blood samples were kept in refrigerated sealed glass tubes until they were micro-distilled (Nagy, 1983) to obtain pure water, which was assayed for tritium activity by liquid scintillation spectrometry (duplicate 5 µl samples, toluene/Triton X-100/PPO scintillation cocktail). The ¹⁸O content of triplicate samples was determined by cyclotron-generated proton-activation analysis (Wood et al., 1975) at the University of California, Davis.

Body water volumes, rates of CO₂ production and water efflux were calculated using the equations of Nagy (1980, 1983) and Nagy and Costa (1980). We calculated daily energy expenditure (DEE) from rates of CO₂ production assuming an energy equivalent of 23.3 kJ l⁻¹ CO₂, based on a diet containing a mixture of seeds and insects (Martin et al., 1951). Maximum errors in validations of our DLW method were less than 9% for individual birds and less than 2% for groups of nine birds for both the double-sample (Buttemer et al., 1986) and single-sample (Webster and Weathers, 1989) techniques.

Environmental temperature

We assessed the birds' thermal environment during DLW measurements at both TPM and PRBO with centrally placed meteorological stations. At each site, we determined the following variables in the open 1 m above ground: air temperature (T_a) (shaded 36-gauge type-T thermocouple), operative temperature (T_e) [3.5 cm diameter metal-sphere thermometer painted flat gray (Bakken et al., 1985; Walsberg and Weathers, 1986)] and wind speed (u) (Thorntwaite model 901 cup anemometer). We also determined ground-level T_e and solar radiation (LiCor model 200 pyranometer) at the open site and T_e and wind speed (hotball anemometer; Roer and Kjölsvik, 1973) 0.5 m above ground inside bushes or shrubs. Sensor outputs were assessed at 10-s intervals, averaged every 10 or 30 min and recorded with Campbell Scientific 21X data loggers. The cup-anemometers and pyranometers were factory-calibrated. The various thermocouples were calibrated against a National Bureau of Standards certified mercury thermometer. We calibrated the hotball anemometers in a large laminar-flow wind tunnel at the UC Davis hydraulics laboratory against a HanDar two-dimensional sonic anemometer and a Campbell CSAT three-dimensional anemometer (both previously calibrated against primary standards).

The goal of our meteorology measurements was to estimate the standard operative temperature (T_{es}) that birds encountered during DLW measurements using the following equation (Bakken, 1990):

$$T_{es} = T_b - (1 + 0.26u^{0.5})(T_b - T_e),$$

where u is wind speed (m s^{-1}), T_e is operative temperature and T_b is body temperature (assumed to be 42°C). Calculating a realistic T_{es} requires knowledge of (i) the proportion of time the birds spend in various microhabitats (sun *versus* shade, in the open *versus* inside bushes, on the ground *versus* perched above ground, etc.) and (ii) the wind speed and T_e in each microhabitat at the time the bird occupies it. Unfortunately, sparrows proved impossible to observe continuously at both study sites. Birds were visible when males perched atop bushes and sang (more so in the morning) and when they foraged on open ground, but for much of the day both sexes remained hidden from view inside dense clumps of willow (*Salix lemmonii*) (TPM) or coyote bush (*Baccharis pilularis*) (PRBO). Accordingly, we sought correlations between DEE and various measures of the thermal environment including (i) mean shade T_a , (ii) mean T_{es} measured 1 m above ground in the open and (iii) weighted mean ambient temperature. The latter, which represents our best *a priori* guess as to the birds' effective thermal environment, is the mean temperature weighted for proportion of daylight and night-time hours, calculated from the mean daytime T_{es} (measured inside willow clumps or coyote bushes) and mean night-time air temperature. Both daytime T_{es} measured inside willow clumps or coyote bushes and night-time T_a were almost always below the birds' lower critical temperature.

Oxygen consumption

We determined resting metabolic rates (RMRs) of fasted adult white-crowned sparrows by measuring their rate of oxygen consumption ($\dot{V}O_2$) while they rested in the dark. We measured six TPM adults during June 1994 and six PRBO adults between late July and early August 1995. The PRBO birds' plumage was visibly more worn than that of TPM birds and, although they had begun the postnuptial molt, very few feathers were in sheaths. The birds used in RMR determinations were collected with seed-baited Potter traps, transported to Davis by automobile and housed in individual wire cages on a 15 h:9 h L:D photoperiod. They were provided with water, oyster shell grit and a commercially available mixed finch-seed diet supplemented daily with waxworm larvae (*Galleria* sp.) *ad libitum*. Sparrows were allowed 2 weeks to adjust to captivity before metabolic measurements began. Body mass was measured daily with a calibrated electronic balance. Most birds maintained their original capture body mass ($\pm 2\%$); one individual exhibited a 4% mass gain.

$\dot{V}O_2$ was determined with a positive-pressure open-circuit respiratory system similar to that of Weathers et al. (1980). Each bird was fasted for a minimum of 3 h and placed inside a metal metabolism chamber (volume 4 l) that was painted flat-black inside. The chamber was placed inside a controlled temperature cabinet ($\pm 0.5^\circ\text{C}$) and measurements were made at approximately 0, 15 and 30°C during the bird's subjective day (10:30–15:00 h) and night (17:30–22:00 h). Air temperature within the chamber was measured with a thermocouple suspended approximately 5 cm above the bird. Before beginning $\dot{V}O_2$ measurements, birds were allowed to equilibrate to chamber temperature for 1 h while dry, CO_2 -free air flowed through the chamber at approximately 800 ml min^{-1} . Flow rate was measured with Gilmont rotameters calibrated ($\pm 0.8\%$) with a bubble meter (Levy, 1964). Atmospheric pressure during the respirometry measurements and calibrations was measured with a mercury manometer. The fractional O_2 content of dry, CO_2 -free influx and efflux air was measured with an Applied Electrochemistry S3-A analyzer and recorded with Sable Systems software. The O_2 analyzer was calibrated using a metered flow of nitrogen (Fedak et al., 1981). Chamber efflux O_2 concentration was monitored for at least 20 min, and resting metabolic rate was calculated from the minimal stable O_2 concentration maintained for at least 3 min using equation 2 of Hill (1974). Values were corrected to STPD and converted to energy units assuming that 1 ml of O_2 is equivalent to 20.1 J of metabolic heat.

Authorizations

White-crowned sparrows were captured and maintained in captivity under authority of US Department of Interior Fish & Wildlife Service Permits Nos 9316 and 8400 and University of California Animal Use and Care Protocol Nos 3607. Field metabolic rate measurements using tritiated water were authorized by University of California Radiation Use Authorization No. 0942, State of California Department of Health Services Radioactive Material License No. 1334-57 and

US Forest Service Special Use Permit No. 2720, Inyo National Forest.

Values are presented as means \pm s.d.

Results

Meteorological measurements during DEE determinations confirm that Tioga Pass is both colder and windier than Point Reyes (Fig. 1). Both habitats exhibited a diurnal rhythm in temperature and wind speed, but the daily temperature fluctuation was greater at Tioga Pass. Solar radiation was more intense at the montane site, owing in part to generally clearer skies. Mean solar radiation between 11:00 and 13:00 h during DEE determinations was $1067 \pm 21 \text{ W m}^{-2}$ at TPM ($N=31$ days) and $618 \pm 221 \text{ W m}^{-2}$ at PRBO ($N=22$ days). Generally clear night-time skies at Tioga Pass contributed to a precipitous drop in night-time T_{es} , which averaged $-13.4 \pm 1.0^\circ\text{C}$ between midnight and 06:00 h. Over the same time period, T_a averaged $4.5 \pm 0.5^\circ\text{C}$ at TPM *versus* $11.0 \pm 0.4^\circ\text{C}$ at PRBO. Overall, mean T_{es} was 10.3°C lower and T_a 6.6°C lower at TPM than at PRBO (Table 1).

Daily energy expenditure and water flux

We injected 47 TPM sparrows with doubly-labeled water (DLW) and recaptured 25 of them within 0.91–1.09 days (0.97 ± 0.05 days) and six within 1.95–2.09 days (1.99 ± 0.05 days). We injected 39 PRBO sparrows and recaptured 16 within 0.84–1.07 days (0.99 ± 0.05) and six within 1.86–1.98 days (1.91 ± 0.05). With one exception, we recaptured all birds within $\pm 10\%$ of either a 1- or 2-day measurement interval. Thus, our DLW measurements approximate daily energy expenditure for most birds of both populations. We recaptured an additional four PRBO sparrows, but excluded them from our analyses because we were uncertain whether they were incubating eggs or feeding nestlings. Brood size (number of nestlings fed) averaged 2.9 ± 0.7 at PRBO and 3.7 ± 0.8 at TPM ($t_{19}=2.38$, $P=0.03$).

Fig. 2 summarizes the doubly-labeled water results, presenting mean values for male and female sparrows arranged

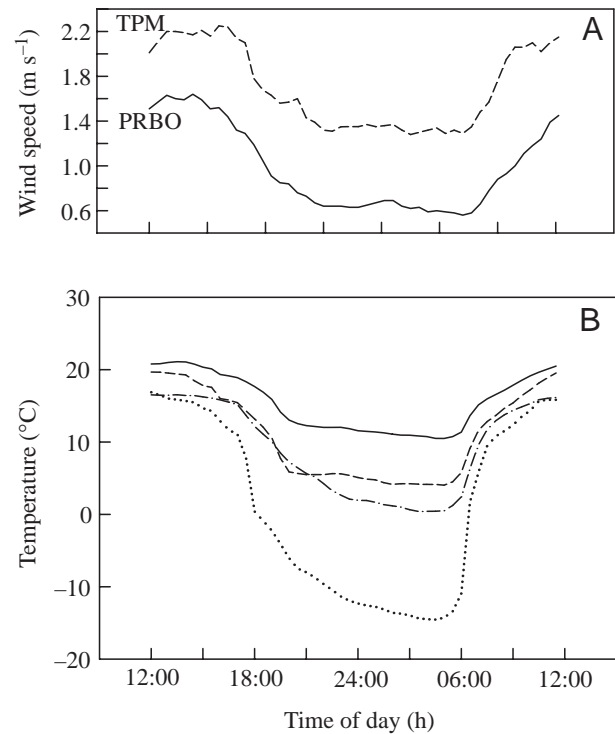


Fig. 1. Mean wind speed (A) at the montane (dashed line) and sea-level (solid line) study sites during measurements of daily energy expenditure. Mean air temperature (B) at the montane (dot-dashed line) and sea-level (solid line) sites and mean standard operative temperature at the montane (dotted line) and sea-level (dashed line) sites. Means were determined from measurements made at 10- or 30-min intervals over 31 days at Tioga Pass Meadow (TPM) and 22 days at Point Reyes Bird Observatory (PRBO).

by population and stage of the breeding cycle. Pooling data for each population (Table 1) reveals no difference in body mass during DEE measurements, but shows that mass-specific rate of CO_2 production and water efflux averaged 26% and 27% higher, respectively, at Tioga Pass Meadow.

Table 1. Mean physiological and meteorological variables during doubly labeled water measurements of white-crowned sparrows breeding at Point Reyes Bird Observatory (sea level) and Tioga Pass Meadow (montane) sites

Variable	Population		t_{51} (P)*
	Sea level (N=22)	Montane (N=31)	
Body mass (g)	28.2 \pm 1.7	28.3 \pm 1.7	1.03 (0.31)
Mass change (%)	0.02 \pm 2.02	-1.27 \pm 1.94	2.33 (0.02)
Rate of CO_2 production ($\text{ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	5.20 \pm 0.56	6.56 \pm 0.86	6.49 (<0.001)
Daily energy expenditure (kJ day^{-1})	83.7 \pm 9.6	103.6 \pm 12.2	6.33 (<0.001)
Water efflux ($\text{ml H}_2\text{O kg}^{-1} \text{ day}^{-1}$)	450 \pm 78	572 \pm 172	3.05 (0.004)
Shade air temperature ($^\circ\text{C}$)	15.6 \pm 1.6	9.0 \pm 2.6	10.8 (<0.001)
Standard operative temperature ($^\circ\text{C}$)	11.4 \pm 2.9	1.1 \pm 3.9	10.6 (<0.001)
Wind speed (m s^{-1})	0.98 \pm 0.38	1.70 \pm 0.37	9.45 (<0.001)

Values are means \pm s.d.

*Student's t value with probability in parentheses.

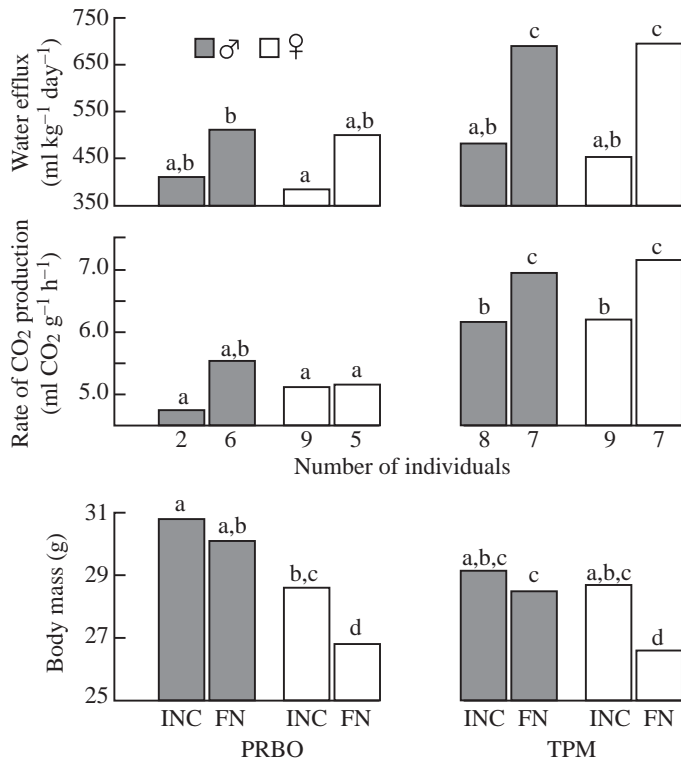


Fig. 2. Physiological variables of white-crowned sparrows during the incubation (INC) and feeding nestling (FN) breeding stages for the montane (TPM) and sea-level (PRBO) populations. Within variables, columns sharing the same letter are not significantly different.

Although the pooled body mass of the two populations did not differ (Table 1), there were significant sex differences in body mass within and between populations (Fig. 2). In both populations, the transition from incubating to feeding nestlings was accompanied by a decrease in body mass that was statistically significant only for females. Each of these conclusions was drawn from the results of several analyses. Specifically, the fully parameterized models included terms for the effect of population, sex and a covariate for the potential contribution of temperature. Additional models that provided for a different temperature regression coefficient for each population were also considered. Computations made use of the general linear model (GLM) procedure of SAS (2000), following typical techniques for linear models (e.g. McCulloch and Searle, 2000). Effects where the levels were found not to be significantly different from one another were deleted from later analyses.

PRBO females averaged 1.9 g (6%) lighter when feeding nestlings (26.6 ± 0.9 versus 28.5 ± 1.3 g); TPM females were 2.1 g (7%) lighter (26.6 ± 0.9 versus 28.7 ± 1.2 g). PRBO males feeding nestlings weighed significantly more than TPM males feeding nestlings (30.1 ± 1.0 versus 28.5 ± 1.6 g). Body mass change during the DEE measurement interval averaged 0% (range -3.7 to 4.2%) at PRBO versus -1.3% (range -5.6 to 3.4%) at TPM (Table 1). Neither mean differs significantly from zero mass change.

Mass-specific rate of CO₂ production was significantly higher at TPM than at PRBO for both sexes and reproductive stages (Fig. 2), averaging 26% higher overall. Combining data for males and females, the transition from incubation to feeding nestlings resulted in a significant increase in CO₂ production at TPM (6.16 ± 0.48 versus 7.02 ± 0.997 ml CO₂ g⁻¹ h⁻¹; $t_{29}=3.23$, $P=0.003$) but not at PRBO (5.04 ± 0.55 versus 5.36 ± 0.55 ml CO₂ g⁻¹ h⁻¹; $t_{20}=1.35$, $P=0.19$).

Daily energy expenditure (DEE, kJ day⁻¹) calculated from CO₂ production averaged 24% higher at TPM (Table 1). White-crowned sparrows at TPM worked harder than PRBO sparrows, as judged by their DEE/BMR ratios (2.6 versus 2.1 ; $t_{51}=6.42$, $P<0.001$).

There was no significant correlation between DEE and any measure of environmental temperature for either population considered separately, although the correlation between DEE at TPM and T_{es} measured in willow thickets during the day approached significance (Table 2). When data for the two populations were pooled, however, DEE correlated significantly with every measurement of temperature (Table 2). Again, a variety of linear models (with and without a temperature covariate) were fitted to these data, such that pooling was only considered across levels of effects that did not differ significantly. For the pooled data, the highest correlation was between DEE and T_{es} measured 1 m above ground (Fig. 3; $r^2=0.422$), but none of the five measures of temperature differed significantly.

Water efflux differed by population (Table 1) but not by sex within populations for the same breeding stage (Fig. 2). Combining data for males and females, incubation stage water efflux averaged 20% higher at TPM than at PRBO (391 ± 51 versus 470 ± 94 ml kg⁻¹ h⁻¹; $t_{26}=2.55$, $P=0.02$). Water efflux when feeding nestlings was 37% higher at TPM (509 ± 51 versus 696 ± 172 ml kg⁻¹ h⁻¹; $t_{23}=3.46$, $P=0.002$). Again, using combined data for males and females, water efflux of both populations was significantly lower when incubating than when feeding nestlings: for PRBO, 391 ± 51 versus 509 ± 51 ml kg⁻¹ h⁻¹ ($t_{20}=5.45$, $P<0.001$); for TPM, 470 ± 94 versus 696 ± 172 ml kg⁻¹ h⁻¹ ($t_{29}=4.64$, $P<0.001$).

Resting metabolic rate

Because the white-crowned sparrow's thermal neutral zone is approximately 23–37°C (King, 1964; Maxwell and King, 1976), our limited RMR measurements adequately describe the birds' thermoregulatory profile (*sensu* Scholander et al., 1950). Mean daytime and night-time body masses and basal metabolic rates (BMRs) of TPM and PRBO sparrows differed by less than 3% (all $P>0.53$, t -tests). During BMR measurements, pooled body mass averaged 25.3 ± 2.0 g ($N=12$). Pooled BMR ($N=12$) averaged 3.34 ± 0.23 ml O₂ g⁻¹ h⁻¹ during the daytime and 2.91 ± 0.31 ml O₂ g⁻¹ h⁻¹ at night (paired $t_{11}=3.33$, $P=0.007$). These values are 91% and 108%, respectively, of those predicted for passerine birds (Aschoff and Pohl, 1970). Daytime BMR averaged 115% of night-time BMR.

Repeated-measures analysis of covariance (ANCOVA) revealed that during the day the subthermoneutral RMR of the

Table 2. Correlation (r) between daily energy expenditure of white-crowned sparrows breeding at Point Reyes Bird Observatory (PRBO) and Tioga Pass Meadow (TPM) and various measures of environmental temperature

Temperature*	PRBO (N=22)			TPM (N=31)			Both (N=53)		
	Range [†]	r	P	Range	r	P	Range	r	P
Mean T_{es}	9.8	-0.119	0.60	15.7	-0.290	0.11	26.4	-0.650	<0.001
Mean T_a	5.3	-0.006	0.93	11.8	-0.275	0.13	17.3	-0.637	<0.001
T_{es} bush, day	11.2	-0.047	0.82	14.0	-0.322	0.07	23.7	-0.608	<0.001
Night T_a	6.0	-0.148	0.52	12.0	-0.064	0.73	20.5	-0.596	<0.001
Ambient temperature	6.9	-0.006	0.93	13.2	-0.275	0.13	21.5	-0.644	<0.001

T_a , ambient temperature; T_{es} , standard operative temperature.
 *See Materials and methods for descriptions of temperature measurements.
 †Temperature range during daily energy expenditure measurements.

two populations (Fig. 4) differed neither in slope ($F_{1,10}=0.02$, $P=0.90$) nor elevation ($F_{1,10}=0.36$, $P=0.56$). Night-time measurements (Fig. 4) differed significantly in elevation ($F_{1,10}=13.39$, $P=0.004$), but not in slope ($F_{1,10}=1.50$, $P=0.25$). Effects attributable to individual sparrows were significant for both daytime ($F_{1,10}=6.23$, $P<0.01$) and night-time ($F_{1,10}=3.83$, $P=0.02$) measurements. We derived the following equations for subthermoneutral RMR ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) using a pooled-slopes model: daytime RMR= $6.58-0.139T_a$ ($s_{yx}=0.69$, $s_b=0.021$, $r^2=0.66$, $N=24$); night-time RMR at PRBO= $6.25-0.127T_a$ ($s_{yx}=0.13$, $s_b=0.011$, $r^2=0.84$, $N=12$); night-time RMR at TPM= $5.57-0.127T_a$ ($s_{yx}=0.14$, $s_b=0.011$, $r^2=0.82$, $N=12$), where s_{yx} and s_b are, respectively, the standard errors of the estimated intercept and slope.

The higher night-time RMR in PRBO birds probably resulted from their sparser plumage. Because the PRBO birds' plumage was sparser, one would expect the slope of their metabolic rate/temperature relationships to be steeper. Indeed,

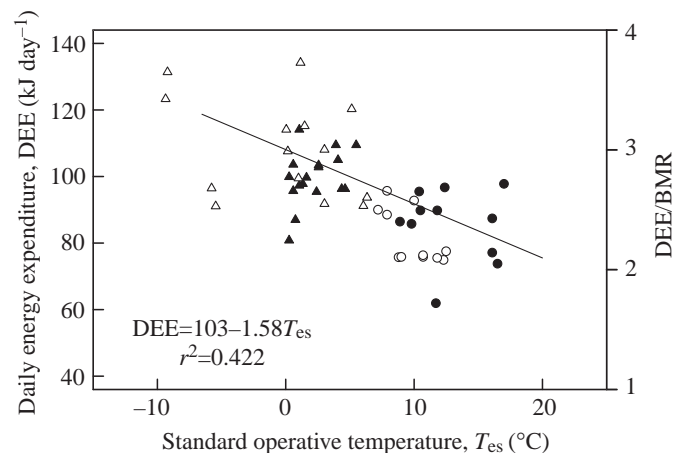


Fig. 3. Relationship between daily energy expenditure and standard operative temperature measured 1 m above ground in the open during the incubation (shaded symbols) and feeding nestling (open symbols) breeding stages for montane (triangles) and sea-level (circles) sparrow populations. BMR, basal metabolic rate.

their slopes were steeper for both daytime (0.148 versus $0.122 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and night-time (0.141 versus $0.110 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) $\dot{V}O_2$ measurements, but neither difference was statistically significant (see F values above). We presumably lack the statistical power to detect the differences because the sample sizes for these measurements were small. The night-time RMR of Gambel's white-crowned sparrow (*Z. l. gambelii*) measured during the autumn (King, 1964) is similar to that of our TPM birds and is described by the equation: night-time RMR= $5.27-0.125T_a$.

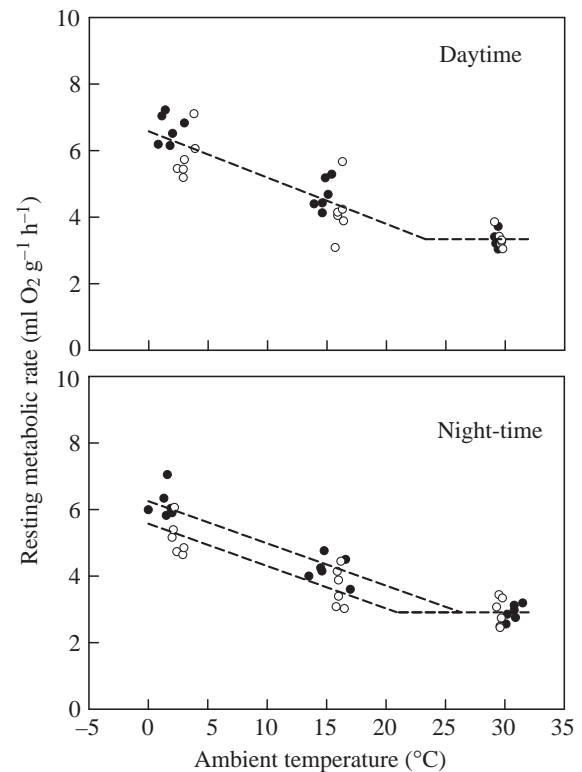


Fig. 4. Relationship between resting, fasted rate of O_2 consumption (resting metabolic rate) and ambient temperature for montane (open circles) and sea-level (shaded circles) white-crowned sparrow populations. See text for details of the slopes.

Table 3. Doubly labeled water studies in which temperature explained a significant fraction of interindividual variation in daily energy expenditure, denoted by the coefficient of determination (r^2)

Species	Mass (g)	Temperature		r^2	N	Source
		Measured*	Range			
House martin <i>Delichon urbica</i>	18.8	Min T_a	–	0.13	78	Bryant and Westerterp (1980)
House martin <i>Delichon urbica</i>	18.8	Min T_a	–	0.08	55	Bryant and Westerterp (1983)
Sand martin <i>Riparia riparia</i>	14.3	T_a	–	0.29	10	Westerterp and Bryant (1984)
Loggerheaded shrike <i>Lanius ludovicianus</i>	45.5	T_e	7.2	0.52	8	Weathers et al. (1984)
Budgerigar <i>Melopsittacus undulatus</i>	35.4	T_e	19.1	0.46	16	Buttemer et al. (1986)
European dipper <i>Cinclus cinclus</i>	63.1	T_a	–	0.05	77	Bryant and Tatner (1988)
Northern wheatear <i>Oenanthe oenanthe</i>	24.3	T_a	–	0.20	19	Moreno (1989)
Northern wheatear <i>Oenanthe oenanthe</i>	24.3	T_a	13	0.20	24	Tatner (1990)
Verdin <i>Auriparus flaviceps</i>	6.5	T_{es}	16.4	0.21	34	Webster and Weathers (1990)
Western bluebird <i>Sialia mexicana</i>	27.5	Max T_a	–	0.30	31	Mock (1991)
House wren <i>Troglodytes aedon</i>	10.5	Min T_a	10.2	0.20	30	Dykstra and Karasov (1993)
Orange-breasted sunbird <i>Nectarinia violacea</i>	9.5	T_e	7	0.62	8	Williams (1993)
Great tit <i>Parus major</i>	17.7	T_a	12.8	0.23	32	Tinbergen and Dietz (1994)
Ruddy turnstone <i>Arenaria interpres</i>	108	T_{es}	15.3	0.55	11	Piersma and Morrison (1994)
New Holland honeyeater <i>Phylidonyris novaehollandiae</i>	17.3	T_{es}	9.0	0.52	12	Weathers et al. (1996)
Great tit <i>Parus major</i>	21.8	Min T_a	10.2	0.34	22	Bryan and Bryant (1999)
White-crowned sparrow <i>Zonotrichia leucophrys</i>	31.1	T_a	6.5	0.49	21	Weathers et al. (1999)
Great tit <i>Parus major</i>	≈18	T_a	14	0.29	38	Tinbergen and Dietz (2000)
Verdin <i>Auriparus flaviceps</i>	6.5	T_{es}	26.6	0.85	21	Webster and Weathers (2000)
Great tit <i>Parus major</i>	≈17.7	T_a	13	0.29	44	Sanz et al. (2000)
White-crowned sparrow <i>Zonotrichia leucophrys</i>	28.5	T_{es}	26.4	0.42	53	This study

* T_a , air temperature; T_e , operative temperature; T_{es} , standard operative temperature; Min, minimum; Max, maximum.

Discussion

Bryant (1989) concluded that ‘the impact of thermoregulatory demands on energy expenditure of small birds is often likely to be obscured by the effects of more important factors’. In his view, interindividual differences in DEE result primarily from differences in activity and, thus, provide reliable indicators of reproductive effort (RE). If, however, thermoregulatory demands have a major impact on DEE, then interindividual differences in DEE partly represent ‘noise’ from which the RE signal may be difficult to extract. Bryant’s conclusion rests on air temperature (T_a) measurements made 8–50 km from the various study sites. Remotely measured T_a may not reflect the actual temperature encountered during DEE measurements, however, and several studies suggest that thermoregulatory demands may be significant. For example, Mock (1991) found that in western bluebirds (*Sialia mexicana*) weather was the greatest source of variation in DEE (coefficient of variation 42% for thermoregulatory costs versus 18% for activity). Similarly, in northern wheatears (*Oenanthe oenanthe*) (Moreno, 1989), metabolic intensity (DEE/BMR) was more closely correlated with mean T_a ($r^2=0.86$) than with nestling feeding rate ($r^2=0.61$), even though T_a was obtained from a site 40 km distant.

A literature review revealed 21 studies in which temperature significantly affected DEE (Table 3), accounting for up to 85% of the variation in DEE. Clearly, temperature can be a principal

determinant of DEE variation under some circumstances, yet measuring temperature accurately can be extremely difficult. In the studies presented in Table 3, T_{es} or operative temperature (T_e) generally explained more variation in DEE than T_a ; $r^2=0.53$ (range 0.21–0.85) versus $r^2=0.24$ (range 0.05–0.46) ($t_{20}=4.40$, $P<0.001$). In our study, however, T_{es} was only slightly more effective at explaining interindividual variation in DEE than T_a , implying that we were unable to reliably assess the actual temperature encountered. Furthermore, within white-crowned sparrow populations, DEE was not significantly correlated with any measure of environmental temperature (Table 2). The absence of a significant correlation between DEE and temperature within sparrow populations may derive in part from the limited range in temperatures encountered. Temperatures were less variable and higher at PRBO than at TPM, and the correlations between DEE and temperature at PRBO were generally lower (Table 2). Some correlations approached significance at TPM, where the temperature range was greater, and across sparrow populations T_{es} explained 42% of the variation in DEE (Table 2).

An alternative to quantifying temperature is to use a paired experimental design in which the DEE of an experimental bird (e.g. brood manipulation) and a control bird are determined on the same day (e.g. Dickinson and Weathers, 1999). Yet, even if both birds in such a paired design encounter the same temperature, inferring RE from their DEE may be confounded. For example, bluebirds that feed enlarged broods have DEEs

equal to those feeding smaller broods, yet they perch in the sun more often, which reduces the thermoregulatory component of their DEE and thus masks the energy cost of greater provisioning (Mock, 1991). Even in the absence of such behavioral compensation, the prospects of gaining meaningful insights into RE through DEE are hampered because the net energy cost of activity is itself temperature-dependent. When ambient temperature is below the thermal neutral zone, the heat produced as a by-product of activity can substitute for the heat required for thermoregulation, effectively reducing the energy cost of activity (Paladino and King, 1984; Webster and Weathers, 1990). As an extreme example of this phenomenon, the rate of energy expenditure of white-crowned sparrows at -10°C is the same whether they are perched in a bush shivering or hopping on the ground (Paladino and King, 1984). At this low temperature, activity has no net energy cost. Clearly, studies that hope to gain insight into RE by measuring DEE need to consider the thermal context within which behavior occurs.

Two alternative explanations exist for observed patterns of parental investment by altricial birds. The energy limitation hypothesis holds that food and/or adult working capacity are limited (Lack, 1954, 1968; Drent and Daan, 1980; Martin, 1987; Roff, 1992) and that increasing parental effort increases the relative success of a brood, but simultaneously decreases the parent's survival and/or future reproductive success (cost of reproduction: Williams, 1966; Lessells, 1991; Stearns, 1992). The alternative view, the predation limitation hypothesis (Skutch, 1949), holds that constraints due to predation risk limit adult activity at the nest, thereby limiting clutch size and consequently parental effort. In the latter hypothesis, parent birds may have substantial reserve physiological capacity but be prevented from working harder by predation pressure. In support of this hypothesis, both nest visitation rate and nest predation rate have been shown to decrease with increasing brood size in open-nesting species, once effects of nest site on predation risk are accounted for (Martin et al., 2000a,b). These two hypotheses lead to differing predictions about the relationship between reproductive effort, brood size and parental survival. If parental investment is primarily limited by nest predation, then parental DEE could be submaximal and unrelated to either adult survival or future reproductive success. In this scenario, one might find substantial variation in DEE between years or populations. Alternatively, if parental investment is limited primarily by parental working capacity, then DEE should be maximal, invariant and correlate with adult survival and/or future reproductive success.

Doubly labeled water measurements of parental effort in altricial birds provide inconclusive support for (or even contradict) the energy limitation hypothesis (Bryant, 1988, 1997). In many species, DEE is well below the maximal sustainable level of approximately 5–6 times BMR (Masman et al., 1989; Weathers and Sullivan, 1989; Bryant, 1997), yet it is often unrelated to manipulated brood size (Bryant and Westerterp, 1983; Ricklefs and Williams, 1984; Williams,

1987; Moreno, 1989; Moreno et al., 1995; Deerenberg et al., 1995), implying a 'ceiling' on parental effort. Moreover, DEE is consistent across populations in some species but variable in others. There is no difference in DEE among populations of least auklet (*Aethia pusilla*; Obst et al., 1995), but DEE differs by up to 60% among populations of Leach's storm petrel (*Oceanodroma leucorhoa*; Montevecchi et al., 1992) and by up to 43% among great tit populations (*Parus major*; Sanz et al., 2000). Similarly, in female great tits tending manipulated broods, maximal DEE varies by as much as 38% between years (Tinbergen and Verhulst, 2000). Such disparity in results implies that the primary limit on reproductive effort may be energy in some species but predation risk in others.

In our white-crowned sparrows, DEE was submaximal in both populations (2.1 ± 0.2 times BMR at PRBO versus 2.6 ± 0.3 times BMR at TPM; $t_{51} = 6.48$, $P < 0.001$), suggesting that neither energy availability nor parental working capacity is the primary limit on reproductive effort in this species. Interestingly, the two populations' nesting success (expressed as the proportion of nests fledging at least one young) is not significantly different; averaging 47.3% for 1331 *Z. l. oriantha* nests over 22 years (Morton, 2002) and 53.7% for 255 *Z. l. nuttalli* nests (N. Nur, G. Geupel and D. DeSante, unpublished observations) ($\chi^2 = 1.89$, $P > 0.05$, d.f. = 1). Presumably, equivalent nesting success in the two populations is attained by greater nest predation at PRBO offsetting greater weather-induced nest failure at TPM.

If nest predation is the principal limit on white-crowned sparrow reproduction, then adult survival should be unrelated to DEE. There is some support for this notion. Late in the breeding season, TPM females often feed nestlings and fledglings by themselves while in molt and, although molt is delayed somewhat in these 'hard-working' females, they are able to catch up by shortening the molting period. Furthermore, this cohort of females returns to the study area the following year at the same rate as females that raise their young early in the season, have continuous help from their mates and molt at a slower pace (Morton, 2002). This observation suggests that adult survival in white-crowned sparrows may be only weakly related to DEE if at all.

Although there is some support for a link between DEE and fitness traits, as required if DEE is to denote the cost of reproduction (Bryant, 1988; Deerenberg et al., 1995; Golet et al., 2000), the results here are also inconsistent. Female yellow-eyed juncos (*Junco phaeotus*) with a relatively low DEE reneest faster and are more likely to breed in multiple years (Sullivan et al., 1999), providing a link between DEE and a fitness trait. Yet, in black-legged kittiwakes (*Rissa tridactyla*), DEE is the same in Alaska (61°N) and Norway (70°N), although adult mortality is 2.3 times higher in Norway (Golet et al., 2000). Clearly, more studies that explicitly evaluate the relationship between DEE and survival are needed to determine the utility of DEE as a fitness index.

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References

- American Ornithologist's Union** (1998). *Checklist of North American Birds*, 7th edition. Washington, DC: American Ornithologist's Union.
- Aschoff, J. and Pohl, H.** (1970). Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* **111**, 38-47.
- Baker, M. C., Mewaldt, L. R. and Stewart, R. M.** (1981). Demography of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *Ecology* **62**, 636-644.
- Bakken, G. S.** (1980). The use of standard operative temperature in the study of the thermal energetics of birds. *Physiol. Zool.* **53**, 108-199.
- Bakken, G. S.** (1990). Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* **107**, 587-594.
- Bakken, G. S., Santee, W. R. and Erskine, D. J.** (1985). Operative and standard operative temperature: tools for thermal energetics studies. *Am. Zool.* **25**, 933-943.
- Blanchard, B. D.** (1941). The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.* **46**, 1-178.
- Bryan, S. M. and Bryant, D. M.** (1999). Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proc. R. Soc. Lond. B* **266**, 157-162.
- Bryant, D. M.** (1988). Energy expenditure and body mass changes as measures of reproductive costs in birds. *Funct. Ecol.* **2**, 23-34.
- Bryant, D. M.** (1989). Determination of respiration rates of free-living animals by the double-labelling technique. In *Toward a More Exact Ecology*, vol. 30 (ed. P. J. Grubb and J. B. Whittaker), pp. 85-109. Oxford: Blackwell.
- Bryant, D. M.** (1997). Energy expenditure in wild birds. *Proc. Nutr. Soc.* **56**, 1025-1039.
- Bryant, D. M., Hails, C. J. and Prys-Jones, R.** (1985). Energy expenditure by free-living dippers (*Cinclus cinclus*) in winter. *Condor* **87**, 177-186.
- Bryant, D. M. and Tatner, P.** (1988). Energetics of the annual cycle of dippers *Cinclus cinclus*. *Ibis* **130**, 17-38.
- Bryant, D. M. and Tatner, P.** (1991). Intraspecific variation in avian energy expenditure: correlates and constraints. *Ibis* **133**, 236-245.
- Bryant, D. M. and Westerterp, K. R.** (1980). The energy budget of the house martin *Delichon urbica*. *Ardea* **68**, 91-102.
- Bryant, D. M. and Westerterp, K. R.** (1983). Short-term variability in energy turnover by breeding house martins (*Delichon urbica*): a study using doubly labelled water. *J. Anim. Ecol.* **52**, 524-544.
- Buttemer, W. A., Hayworth, A. M., Weathers, W. W. and Nagy, K. A.** (1986). Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* **59**, 131-149.
- Campbell, G. S. and Norman, J. M.** (1998). *An Introduction to Environmental Biophysics*, 2nd edition. New York: Springer-Verlag.
- Deerenberg, C., Pen, I., Dijkstra, C., Arkies, B., Visser, G. H. and Daan, S.** (1995). Parental energy expenditure in relation to manipulated brood size in the European kestrel *Falco tinnunculus*. *Zool. Anal. Complex Syst.* **99**, 38-47.
- DeWolfe, B. B.** (1968). *Zonotrichia leucophrys oriantha* mountain white-crowned sparrow. In *Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows and Allies* (ed. A. C. Bent), pp. 1338-1344. US Natural History Museum Bulletin **237**, part 3.
- Dickinson, J. L. and Weathers, W. W.** (1999). Replacement males in the western bluebird: opportunity for paternity, chick-feeding rules, and fitness consequences of male paternal care. *Behav. Ecol. Sociobiol.* **45**, 201-209.
- Drent, R. H. and Daan, S.** (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**, 225-252.
- Dykstra, C. R. and Karasov, W. H.** (1993). Nesting energetics of house wrens (*Troglodytes aedon*) in relation to maximal rates of energy flow. *Auk* **110**, 481-491.
- Fedak, M. A., Rome, L. and Seeherman, H. J.** (1981). One-step N₂-dilution technique for calibrating open-circuit respirometry systems. *J. Appl. Physiol. Respir. Environ. Exer. Physiol.* **51**, 772-776.
- Golet, G. H., Irons, D. B. and Costa, D. P.** (2000). Energy costs of chick rearing in Black-legged Kittiwakes (*Rissa tridactyla*). *Can. J. Zool.* **78**, 982-991.
- Hill, R. W.** (1974). Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. Appl. Physiol.* **33**, 261-263.
- Hirshfield, M. F. and Tinkle, D.** (1975). Natural selection and the evolution of reproductive effort. *Proc. Natl. Acad. Sci. USA* **72**, 2227-2231.
- King, J. R.** (1964). Oxygen consumption and body temperature in relation to ambient temperature in the white-crowned sparrow. *Comp. Biochem. Physiol.* **12**, 13-24.
- Lack, D.** (1954). *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.
- Lack, D.** (1968). *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Lessells, C. M.** (1991). The evolution of life histories. In *Behavioural Ecology: An Evolutionary Approach*, 3rd edition (ed. J. R. Krebs and N. B. Davies), pp. 32-68. Oxford: Blackwell.
- Levy, A.** (1964). The accuracy of the bubble meter method for gas flow measurements. *J. Sci. Instrum.* **41**, 449-453.
- Mahoney, S. A.** (1976). Thermal and ecological energetics of the white-crowned sparrow (*Zonotrichia leucophrys*) using the equivalent black-body temperature. PhD thesis, Washington State University.
- Martin, A. C., Zim, H. S. and Nelson, A. L.** (1951). *American Wildlife and Plants*. New York: McGraw-Hill.
- Martin, T. E.** (1987). Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Systematics* **18**, 453-487.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. and Fontaine, J. J.** (2000a). Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482-1485.
- Martin, T. E., Scott, J. and Menge, C.** (2000b). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond. B* **267**, 2287-2294.
- Masman, D., Dijkstra, C., Daan, S. and Bult, A.** (1989). Energetic limitation of avian parental effort: field experiments in the kestrel (*Falco tinnunculus*). *J. Evol. Biol.* **2**, 435-455.
- Maxwell, C. S. and King, J. R.** (1976). The oxygen consumption of the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) in relation to air temperature. *Condor* **78**, 569-570.
- Mewaldt, R. L. and King, J. R.** (1977). The annual cycle of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) in coastal California. *Condor* **79**, 445-455.
- McCulloch, C. E. and Searle, S. R.** (2000). *Generalized, Linear and Mixed Models*. New York: J. Wiley and Sons, Inc.
- Mock, P. J.** (1991). Daily allocation of time and energy of western bluebirds feeding nestlings. *Condor* **93**, 598-611.
- Montevocchi, W. A., Birt-Friesen, V. L. and Cairns, D. K.** (1992). Reproductive energetics and prey harvest of Leach's storm-petrels in the Northwest Atlantic. *Ecology* **73**, 823-832.
- Moreno, J.** (1989). Variation in daily energy expenditure in nesting northern wheatears (*Oenanthe oenanthe*). *Auk* **106**, 18-25.
- Moreno, J., Cowie, R. J., Sanz, J. J. and Williams, R. S. R.** (1995). Differential response by males and females to brood manipulations in the pied flycatcher: energy expenditure and nestling diet. *J. Anim. Ecol.* **64**, 721-732.
- Morton, M. L.** (1976). Adaptive strategies of *Zonotrichia* breeding at high latitude or high altitude. In *Proceedings of the 16th International Ornithological Congress (Canberra)* (ed. H. J. Frith and J. H. Calaby), pp. 322-336. Canberra: Australian Academy of Science.
- Morton, M. L.** (1977). Relationship of reproductive cycle to environmental conditions and energy stores in white-crowned sparrows at high altitude. *Proc. Am. Phil. Soc.* **121**, 377-382.
- Morton, M. L.** (2002). The mountain white-crowned sparrow: migration and reproduction at high altitude. *Studies Avian Biol.* **24**, 1-273.
- Morton, M. L., Horstmann, J. and Carey, C.** (1973). Body weights and lipids of summering mountain white-crowned sparrows in California. *Auk* **90**, 83-93.
- Morton, M. L., Horstmann, J. and Osborn, J.** (1972a). Reproductive cycle and nesting success of the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. *Condor* **74**, 152-163.
- Morton, M. L., Orejuela, J. and Budd, S.** (1972b). The biology of immature mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) on the breeding ground. *Condor* **74**, 423-430.
- Morton, M. L., Peterson, L. E., Burns, D. M. and Allan, N.** (1990). Seasonal and age-related changes in plasma testosterone levels in mountain white-crowned sparrows. *Condor* **92**, 166-173.
- Morton, M. L., Wakamatsu, W. M., Pereyra, M. E. and Morton, G. A.** (1991). Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scand.* **22**, 98-106.
- Mugaas, J. N. and King, J. R.** (1981). Annual variation of daily energy

- expenditure by the black-billed magpie: a study of thermal and behavioral energetics. *Studies Avian Biol.* **5**, 1-78.
- Nagy, K. A.** (1980). CO₂ production in animals: Analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**, R466-R473.
- Nagy, K. A.** (1983). *The Doubly Labeled Water (³HH¹⁸O) Method: A Guide to its Use*. Publication No. 12-1417. Los Angeles: University of California.
- Nagy, K. A. and Costa, D. P.** (1980). Water flux in animals: Analysis of potential errors in the tritiated water method. *Am. J. Physiol.* **238**, R454-R465.
- Obst, B. S., Russell, R. W., Hunt, G. L., Eppley, Z. A. and Harrison, N. M.** (1995). Foraging radii and energetics of least auklets (*Aethia pusillia*) breeding on three Bering Sea islands. *Physiol. Zool.* **68**, 647-672.
- Paladino, F. and King, J. R.** (1984). Thermoregulation and oxygen consumption during terrestrial locomotion by white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Physiol. Zool.* **57**, 226-236.
- Piersma, T. and Morrison, R. I. G.** (1994). Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high arctic climatic conditions. *Auk* **111**, 366-376.
- Ricklefs, R. E. and Williams, J. B.** (1984). Daily energy expenditure and water-turnover rate of adult European starlings *Sturnus vulgaris* during the nesting cycle. *Auk* **101**, 707-716.
- Roff, D.** (1992). *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman and Hall.
- Roer, P. and Kjølsvik, M.** (1973). Equipment for measuring low air velocity. *Agric. Meteorol.* **12**, 281-296.
- Sanz, J. J., Tinbergen, J. M., Moreno, J., Ordell, M. and Verhulst, S.** (2000). Latitudinal variation in parental energy expenditure during brood rearing in the great tit. *Oecologia* **122**, 149-154.
- SAS** (2000). *SAS/STAT User's Guide*. Version 8.01. Cary: SAS Institute Inc.
- Scholander, P. F., Hock, R., Walters, V., Johnson, F. and Irving, L.** (1950). Heat regulation in some arctic and tropical birds and mammals. *Biol. Bull.* **99**, 237-258.
- Skutch, A. F.** (1949). Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430-455.
- Stearns, S. C.** (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Sullivan, K. A., Roper, J. J. and Weathers, W. W.** (1999). Individual variation in reneating internals, daily energy expenditure and reproductive success in passerines. In *Proceedings of the 22nd International Ornithological Congress* (ed. N. J. Adams and R. H. Slotow), pp. 401-411. Johannesburg: Bird Life South Africa.
- Tatner, P.** (1990). Energetic demands during brood rearing in the wheatear *Oenanthe oenanthe*. *Ibis* **132**, 423-435.
- Tatner, P. and Bryant, D. M.** (1993). Interspecific variation in daily energy expenditure during avian incubation. *J. Zool., Lond.* **231**, 215-232.
- Tinbergen, J. M. and Dietz, M. W.** (1994). Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **8**, 563-572.
- Tinbergen, J. M. and Verhulst, S.** (2000). A fixed energetic ceiling to parental effort in the great tit? *J. Anim. Ecol.* **69**, 323-334.
- Walsberg, G. E. and Weathers, W. W.** (1986). A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* **11**, 67-72.
- Weathers, W. W., Buttemer, W. A., Hayworth, A. M. and Nagy, K. A.** (1984). An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* **101**, 459-472.
- Weathers, W. W., Olson, C. R., Siegel, R. B. and Famula, T. R.** (1999). Winter and breeding-season energetics of non-migratory white-crowned sparrows. *Auk* **116**, 842-847.
- Weathers, W. W., Paton, D. C. and Seymour, R. S.** (1996). Field metabolic rate and water flux of nectarivorous honeyeaters. *Aust. J. Zool.* **44**, 445-460.
- Weathers, W. W., Shapiro, C. J. and Astheimer, L. B.** (1980). Metabolic responses of Cassin's finches (*Carpodacus cassinii*) to temperature. *Comp. Biochem. Physiol.* **65A**, 235-238.
- Weathers, W. W. and Sullivan, K. A.** (1989). Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.* **59**, 223-246.
- Webster, M. D. and Weathers, W. W.** (1989). Validation of single-sample doubly labeled water method. *Am. J. Physiol.* **256**, R572-R576.
- Webster, M. D. and Weathers, W. W.** (1990). Heat produced as a by-product of foraging activity contributes to avian thermoregulation. *Physiol. Zool.* **63**, 777-794.
- Webster, M. D. and Weathers, W. W.** (2000). Seasonal changes in energy and water use by verdins, *Auriparus flaviceps*. *J. Exp. Biol.* **203**, 3333-3344.
- Westerterp, K. and Bryant, D. M.** (1984). Energetics of free existence in swallows and martins (Hirundinidae) during breeding: a comparative study using doubly labeled water. *Oecologia* **62**, 376-381.
- Williams, G. C.** (1966). Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**, 687-690.
- Williams, J. B.** (1987). Field metabolism and food consumption of savannah sparrows during the breeding season. *Auk* **104**, 277-289.
- Williams, J. B.** (1993). Energetics of incubation in free-living orange-breasted sunbirds in South Africa. *Condor* **95**, 115-126.
- Wood, R. A., Nagy, K. A., MacDonald, S., Wakakuwa, S. T., Beckman, R. J. and Kaaz, H.** (1975). Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Anal. Chem.* **47**, 646-650.