SEASONAL CHANGES IN ENERGY AND WATER USE BY VERDINS, *AURIPARUS FLAVICEPS*

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Summary

We used the doubly labeled water (*DLW*) method to measure field metabolic rate (*FMR*) and water turnover during winter and summer in a very small (6.5 g) insectivorous desert passerine bird, the verdin (*Auriparus flaviceps*). Concurrently, we monitored weather conditions and used time–activity budget data of free-living birds and laboratory data on resting metabolic rate to construct time–activity laboratory (*TAL*) estimates of daily energy expenditure (*DEE*) and to partition the verdins' energy budget into thermoregulatory, activity and basal components. The *FMR* of adult verdins was $33.6\pm0.9\,\mathrm{kJ\,day^{-1}}$ (mean ± S.E.M.; $N{=}14$) in winter and $22.8\pm0.45\,\mathrm{kJ\,day^{-1}}$ ($N{=}7$) in summer. *FMR* correlated negatively with the mean standard operative environmental temperature (T_{es}) prevailing during the measurement period. *TAL* analysis produced *DEE* estimates that corresponded on average to within $-0.9\pm2.4\,\%$ of our *DLW*-measured *FMR* values (range of individual values $-18.3\,\%$ to $+14.3\,\%$). Metabolic expeditures for cold defense were $19.5\pm2.1\,\%$ of *DEE* in winter (computed assuming substitution of exercise thermogenesis for thermoregulatory costs in active birds). In the summer, thermoregulatory costs amounted to $9.0\pm0.4\,\%$ of *DEE* for keeping warm and $1.0\pm0.1\,\%$ of *DEE* for keeping cool in the heat. Activity costs were $21.0\pm0.5\,\%$ of *DEE* in winter and $17.5\pm0.1\,\%$ of *DEE* in summer. The water efflux of nonbreeding adult verdins was $3.9\pm0.2\,\mathrm{ml\,day^{-1}}$ ($624\pm22\,\mathrm{ml\,kg^{-1}\,day^{-1}}$) in summer ($N{=}5$) and $3.4\pm0.2\,\mathrm{ml\,day^{-1}}$ ($498\pm26\,\mathrm{ml\,kg^{-1}\,day^{-1}}$) in winter ($N{=}14$). The water economy index (*WEI*; water efflux per unit *FMR*) of verdins was higher in summer ($0.17\pm0.01\,\mathrm{ml\,kJ^{-1}}$) than in winter ($0.10\pm0.01\,\mathrm{ml\,kJ^{-1}}$) and correlated negatively with mean T_{es}.

Key words: doubly labeled water, field metabolic rate, seasonality, time budget, standard operative temperature, Passeriformes, water flux, verdin, *Auriparus flaviceps*.

Introduction

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' is poorly understood because energy requirements at different seasons have been studied for fewer than 10 bird species (Dawson and O'Connor, 1996). High thermoregulatory costs and low food availability during winter are assumed to increase energy demands during that season (King and Murphy, 1971), yet the breeding period can also be a period of high energy demand (King, 1974).

Comparisons between winter and breeding-season field metabolic rate (*FMR*) in eight bird species indicate little seasonal change in species with energetically economical foraging modes, but a substantially higher *FMR* during the breeding season in species with expensive foraging modes (Weathers and Sullivan, 1993). Additional studies involving nonbreeding summer birds are needed to assess more fully how seasonal changes in weather affect *FMR*.

In the present study, we sought to assess the effects of weather on the water and energy requirements of a very small, desert passerine bird by monitoring *FMR* in winter and summer in nonbreeding adult birds and to partition seasonal water and energy budgets into their component parts. We predicted that the *FMR* of nonbreeding birds should be higher in winter than summer as a result of higher thermoregulatory costs. The high prevailing summertime temperatures in California's Colorado desert, where we worked, probably require high rates of water use for cooling by evaporation and we hypothesize that water turnover should be higher in summer than in winter.

We investigated these questions in the verdin (*Auriparus flaviceps*) – a tiny (approximately 6.5 g) insectivorous passerine native to desert regions of the southwestern United States. Verdins are non-migratory and reside year-round in desert scrub or riparian wash habitat that includes palo verde

(*Cercidium floridum*), mesquite (*Prosopis nectaracea*), acacia (*Acacia* spp.) or smoketree (*Dalea spinosa*) among the dominant vegetation (Webster, 1999). They occur from south-central California to southern Sonora, Mexico, east to southern Utah and Nevada and west Texas and south to Sinaloa, Mexico (Webster, 1999).

We selected this species (i) because its small size should favor tight coupling to meteorological conditions and therefore reveal weather-dependent changes in energy and water use, (ii) because its habit of roosting year-round in enclosed nests (Taylor, 1971) allowed us to recapture isotopically labeled birds reliably, and (iii) because our previous studies of this species provide critical background information (Webster and Weathers, 1988, 1989, 1990).

Materials and methods
Study area and animals

We studied verdins *Auriparus flaviceps* (Sundevall) in the Colorado Desert (a branch of the Sonoran Desert) near Palm Desert, Riverside County, California, USA, during the winters of 1986–1988 (between December and the first week of March) and in summer 1988 (6–10 July). Our study area was a dry alluvial plain with a plant community dominated by palo verde, smoketree and cheesebush (*Hymenoclea salsosa*). During the winter portion of our study, verdins were not molting or breeding, although in February and March some males did sing from exposed perches, suggesting that territorial advertisement had begun (Taylor, 1971). Summer measurements involved five post-breeding adults (three of which had begun molt), two adults with dependent young, five dependent fledglings and two independent juveniles.

Doubly labeled water measurements

We measured the rates of CO_2 production ($\dot{V}_{CO_2}$) of free-ranging verdins using the doubly labeled water (*DLW*) method (Speakman, 1997). Verdins were captured by hand or mist net at or near their roost-nests in the late afternoon or early evening, weighed immediately to the nearest 0.05 g (K-Tron DS10 portable electronic balance), banded with a unique combination of plastic, colored leg bands (a maximum of two bands) and injected intramuscularly with 25 µl of water containing 0.28 MBq of ^3H and >95 atoms % ^{18}O using a previously calibrated Hamilton microliter syringe. Most of the birds were released near the capture site immediately after injection, but 23 (out of 54 experimental birds) were held in a darkened enclosure for an hour, reweighed and a 50–70 µl blood sample taken from the brachial vein before they were released. Initial samples from these birds (plus those from an additional 10 birds that were not released) served as controls for the single-sample *DLW* method. We also took blood samples from five uninjected birds to assess the population background level of ^{18}O, which averaged 0.2068 atoms %.

Verdin captured at their roost-nest in the evening were returned to their nest after labeling with *DLW*, and the nest entrance was temporarily plugged with cotton to prevent their escape. The birds settled down rapidly judging from the lack of struggling noises, and all were asleep when the cotton plug was removed approximately 1 h later. We recaptured birds approximately 24 h later, re-weighed them and took a 50–70 µl blood sample. Blood samples were flame-sealed in heparinized glass capillary tubes and kept under refrigeration until micro-distilled under vacuum to obtain pure water. We determined the ^{18}O content of triplicate 8 µl subsamples of the pure water by proton activation and subsequent counting of the ^{18}F thus produced (Packard model 5210 gamma counter). Analyses were performed either under the direction of Ken Nagy at the Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, USA, or by us at the Crocker Nuclear Laboratory, University of California, Davis, USA. Coefficients of variation in ^{18}O standards were less than 1 % and did not differ between analyses at Davis or UCLA. We measured the ^3H activity of the samples by liquid scintillation using toluene–PPO (2,5-diphenyloxazole) cocktail and a Searle Mark III counter.

We computed the CO_2 production of the doubly sampled birds using the equations of Lifson and McClintock (1966), as modified by Nagy (1975, 1983). Isotope turnover data from verdins that we did not initially bleed were analyzed using the single-sample approach (Nagy et al., 1984; Webster and Weathers, 1989). For this latter procedure, we computed CO_2 production using equation 1 of Webster and Weathers (1989; their method SS1) using the mean body water fraction (determined by ^{18}O dilution) and the logarithm of the initial isotope ratio from the control birds (*N*=11 in winter 1986–1987, *N*=13 in winter 1987–1988, *N*=8 in summer 1988). We computed the CO_2 production of the 12 recaptured double-sample verdins using both the double-sample and the single-sample *DLW* methods to evaluate the reliability of the single-sample method. Single-sample CO_2 values averaged 4.5 % higher (range −6.5 % to +14.6 %) than calculations based on both initial and final isotope levels. The difference was not statistically significant, however (paired t_{11}=2.16, $P>0.05$), and the values were highly correlated (r=0.85, $P<0.001$). From this, we infer that the single-sample and double-sample methods yield equivalent results for this species, as has been demonstrated previously (Webster and Weathers, 1989).

On the basis of our behavioral observations, stomach content analyses and the data of Taylor (1971), we estimated that the verdins' diet, by weight, consisted of 95 % arthropods and 5 % nectar (principally from *Beloperone californica*). Accordingly, we calculated *FMR* assuming 25.93 kJ of metabolized energy per ml of CO_2 produced (diet respiratory quotient=0.77). This value is similar to factors used previously for insectivores (Nagy et al., 1984; Weathers and Sullivan, 1989).

The CO_2 production of verdins that lost mass during the release period was corrected following the procedures of Weathers and Sullivan (1989, 1993) in which the CO_2 produced by metabolic oxidation of body fat is estimated by subtracting lost water (from the turnover of tritium) from the lost body mass. When we estimated metabolizable energy intake and food consumption, we omitted this source of CO_2 production.

Time budgets

In the winter, we quantified the activity patterns of free-living verdins by following focal individuals opportunistically and using a Radio Shack TRS100 microcomputer to record the occurrence and duration of the following activities: sitting, eating, preening, singing, aggressive interactions, foraging and flight. Flights of less than 1 m were included with the perch-hopping, pecking and foliage-gleaning activities that constitute foraging by verdins. Sitting was defined as any motionless period exceeding 5 s. Because we were unable to obtain complete time budgets for individual experimental birds, we used population mean activity records to develop our time-budget model (see below). Summer activity budgets were taken from Austin (1978), who recorded data similar to our own for verdins near Phoenix, Arizona, USA, in July.

Time–activity laboratory estimates of daily energy expenditure

We estimated daily energy expenditure (*DEE*) for comparison with the *DLW* measurements of *FMR* using a time–activity laboratory (*TAL*) model that incorporated laboratory metabolic rate measurements, behavioral data and information about the bird's microclimate. The approach was similar to that of Weathers et al. (1984) and Buttemer et al. (1986) and used the assumptions and values listed below and in Tables 1 and 2. Briefly, we used laboratory data on the metabolic responses of verdins to air temperature and wind along with field time–activity and thermal environment data to estimate *DEE*. Our *TAL* calculations were based on laboratory-determined thermal resistances of verdins in still air and wind (Webster and Weathers, 1988) coupled with 10 min average values of field air temperature, operative temperature (T_e; Bakken et al., 1985) and wind speed and incremental activity energy costs used in previous applications of the *TAL* approach (Weathers et al., 1984; Buttemer et al., 1986; Bakken, 1990; Webster and Weathers, 1989). We used two *TAL* models for our calculations: the 'additive model' assumed that the heat increment of feeding and exercise thermogenesis added arithmetically to maintenance metabolic rate [fasted, thermoneutral basal metabolic rate (*BMR*) plus thermostatic requirements; Walsberg, 1983]; the 'substitutive model' assumed that activity and specific dynamic action (*SDA*) heat

Table 1. *Measured values, predictive equations and assumptions of the time–activity laboratory model*

Variable	Winter	Summer	Source
Body mass (g)	6.7	6.5	Webster (1999); present study
BMR			
$\quad$(W m^{-2})	54.0	51.4	Wolf and Walsberg (1996)
$\quad$(kJ h^{-1})	0.544	0.506	Buttemer et al. (1987)
RMR$_\alpha$			
$\quad$(W m^{-2})	108.0	102.8	Webster (1999)
$\quad$(kJ h^{-1})	1.087	1.016	Wolf and Walsberg (1996)
r_b (s m^{-1})			
$\quad$Day	147.3	146.5 for $T_e<33\,°C$	Wolf and Walsberg (1996)
		60 if $T_e>44\,°C$	Webster and Weathers (1990)
		$426-9T_e$ if $T_e=33–44\,°C$	
$\quad$Night	$247.3-1.7T_e$	$140-1.1T_e$	Wolf and Walsberg (1996)
			Buttemer et al. (1987)
$r_b{'}$ (s m^{-1})			
$\quad$Day	$147.3-14.7u^{0.5}$	$r_b-0.1r_b\,u^{0.5}$	Buttemer et al. (1986, 1987)
$\quad$Night	r_b	r_b	
r_{nest} (s m^{-1})	126	84	Buttemer et al. (1987)
r_T (s m^{-1})			
$\quad$Day	196.6	196 if $T_e<33\,°C$	Webster and Weathers (1990)
		or $313-4.85T_e$ if $T_e>33\,°C$	Wolf and Walsberg (1996)
$\quad$Night	r_b+r_{nest}	r_b+r_{nest}	
$r_T{'}$ (s m^{-1})			
$\quad$Day	$196.6-19.7u^{0.5}$	$165-5.9u^{0.5}$	Wolf and Walsberg (1996);
			Webster and Weathers (1988)
$\quad$Night	r_b+r_{nest}	r_b+r_{nest}	Buttemer et al. (1986, 1987)

BMR, basal metabolic rate; *RMR*$_\alpha$, metabolic rate of fasted birds nesting in the dark during the active phase; r_T, total thermal resistance in free convection conditions; T_e, operative temperature; r_b, whole-body thermal resistance in free connection conditions; r_{nest}, nest thermal resistance; $r_T{'}$, total thermal resistance estimated for field wind conditions; u, wind speed; $r_b{'}$, whole-body thermal resistance estimated for field wind conditions.

Table 2. *Time–activity budgets of verdins and metabolic cost assignments used in the time–activity laboratory models of energy expenditure*

Activity	Time per day (h)	% of active period	Energy cost (×*BMR*)
Winter			
Roosting	14.1	–	1.0
Foraging	8.7	88.8	3.0
Perching	0.7	7.4	2.0
Flying	0.3	3.0	10.0
Other	0.1	0.8	2.3
All activities	9.9		
Summer			
Roosting	12.5	–	1.0
Foraging	5.7	49.5	3.0
Perching	5.1	44.5	2.0
Flying	0.2	1.7	10.0
Other	0.5	4.3	2.3
All activities	11.5		

Winter time–activity data are for Deep Canyon, Riverside County, California (Webster and Weathers, 1990). Summer time–activity data are for Maricopa County, Arizona (Austin, 1978).

BMR, basal metabolic rate.

(i.e. the heat increment resulting from feeding) substituted for otherwise necessary thermostatic requirements.

The *TAL* model is generally described by the equation:

$$DEE = (t_\rho BMR) + (t_\alpha RMR_\alpha + SDA) + (H_h + H_c + H_{act}), \quad (1)$$

where t_ρ and t_α are the duration of the rest and active phases of the daily cycle, *BMR* is basal metabolic rate, *SDA* is the heat increment of feeding (in this study, $0.17RMR_\alpha$), RMR_α is the metabolic rate of fasted birds resting in the dark during the active phase, H_h is the energy cost of thermoregulation during heat defense, H_c is the energy cost of thermoregulation during cold defense and H_{act} is the energy cost of activity. Each additive component of the right-hand term represents a time-weighted, weather-adjusted, cost of thermoregulation or activity. Daily time budgets and activity cost assignments determined previously (Table 2; Weathers et al., 1984; Buttemer et al., 1986; Webster and Weathers, 1990) were used to estimate daily energy cost increments associated with activity.

We computed standard operative environmental temperature (T_{es}) of verdins in the field from our T_e and wind-speed data and used T_{es} to calculate the temperature-dependence of *FMR* using the formulations of Bakken et al. (1985), Bakken (1990), Buttemer et al. (1986) and Weathers and Webster (1990) as expressed by the following equation (Robinson et al., 1976; Webster and Weathers, 1988):

$$T_{es} = T_b - \{[(r_b' + r_e')/(r_b + r_e)](T_b - T_e)\}. \quad (2)$$

We weighted the T_e measurements for time spent in the sun and shade by free-living verdins in the winter (83 % sun, 17 %

shade; *N*=274 observations of 5 min) and summer (25 % sun, 75 % partial sun between 06:00 and 11:00 h; 25 % shade, 75 % partial sun for the remainder of the day; B. O. Wolf, personal communication).

Our T_{es} calculations assumed that the daytime body temperature (T_b) of active verdins was 41.6 °C in winter (Webster and Weathers, 1988, 1990). For our summer *DEE* calculations, we assumed that daytime T_b was 42 °C when T_e was <40 °C and 42.5 °C when T_e was >40 °C (Wolf and Walsberg, 1996). Night-time T_b was assumed to be 35.7 °C (Buttemer et al., 1987) in winter; in summer, T_b was taken as 40 °C when T_e was >25 °C and 38 °C when T_e was <25 °C.

We used data from the literature on the temperature-dependence of verdin thermal resistance to estimate resistance values for the *TAL* models (Webster and Weathers, 1988, 1990; Wolf and Walsberg, 1996). Linear regression equations or fixed values were used, depending on the prevailing field weather conditions. Total (r_T'), whole-body (r_b') and equivalent (r_e') thermal resistances of verdins in the field were estimated by applying corrections for the effect of wind (Webster and Weathers, 1988, 1990).

For verdins sleeping in their roost-nests at night, we estimated body and nest thermal resistances (r_b and r_{nest}) from Buttemer et al. (1987) and Wolf and Walsberg (1996). Roost-nest thermal resistance was estimated to be 126 s m^{-1} in winter (computed from the data of Buttemer et al., 1987). In summer, our model used an arbitrary value one-third lower than the winter value (r_{nest}=84 s m^{-1}) on the basis of our observation that summer nests were smaller and had thinner walls than winter nests. Our estimates of night-time T_{es} and *DEE* assumed that wind did not penetrate the roost-nest (so that r_b=r_b') and that nest thermal insulation did not decrease with wind (Buttemer et al., 1987).

Meteorological measurements

Air temperatures (T_a) at our study site were monitored with shaded 0.25 mm (30 gauge) copper–constantan thermocouples positioned 1 and 3 m above the ground. We measured wind speed at 3 m using hotball anemometers previously calibrated to within ±0.1 m s^{-1} against a certified Gill propellor anemometer in a laminar-flow wind tunnel. In 1987–1988, factory-calibrated Thornthwaite cup anemometers (model 901-LED; stall speed 0.1 m s^{-1}) were also used to measure wind speed at 3 m. We measured T_e with 2 cm sphere thermometers (Walsberg and Weathers, 1986) painted flat gray. Three spheres were used: one was shaded, one was exposed to full sunlight and the third was placed in the outer foliage of a palo verde tree, which is where verdins typically forage. Except for the latter sphere, all the sensors were fixed to a 3.5 m pole placed in the open. Sensor outputs were recorded at 60 s intervals with a Campbell Scientific CR21X datalogger and averaged every 10 min.

Statistical analyses

We used least-squares linear regression and linear correlation to examine relationships among the data. We tested

hypotheses about our results and the regression equations using two-tailed Student's *t*-tests and considered that two values differed significantly when the probability of error was less than 5%. All values are given as means ± standard error of the mean (S.E.M.).

Results

Weather

No rain or snow occurred on the days on which we conducted our measurements. On winter *FMR* measurement days (*N*=10), air temperature (T_a, 3 m above the ground) ranged from overnight lows of 1.4–12.4°C (mean minimum T_a=6.8°C) to daytime highs of 15.9–31.4°C (mean maximum T_a=25.9°C). In summer, we conducted experiments on two days on which the daytime high T_a was 43.8 and 46.7°C and night-time lows were 21.8 and 23.3°C. The extremes of standard operative temperature during our experiments ranged from 0.2°C in winter to 45.0°C in summer (Fig. 1).

Field metabolic rate

In winter, we injected 25 birds and recaptured 17 of them; data from three individuals recaptured after periods longer than 24 h were not analyzed. Of those captured in roost-nests, all were roosting alone. All the winter birds had the distinctive yellow head and breast of adult verdins. None was molting. We released the winter verdins at approximately 19:30 h (Pacific standard time; range 17:45–21:10 h) and recaptured them at approximately 19:40 h (range 17:30–21:51 h). The *DLW* release period thus averaged 23.9±0.2 h (range 22.4–24.9 h).

In winter, verdin $\dot{V}_{CO_2}$ averaged 8.35±0.24 ml g^{-1} h^{-1} in eight males and six females (Table 3). The body mass of winter birds averaged 6.7±0.1 g upon capture; they lost 0.3±0.05 g during the release period following *DLW* injection (−5.1%; range −12% to −0.4%).

In summer, we injected 29 verdins. Fourteen birds were recaptured, including seven adults and seven juveniles. Of the recaptured adults, four were molting. We sexed the birds by noting the intensity of yellow coloration on the head and breast and by examining them for brood patches. Three young
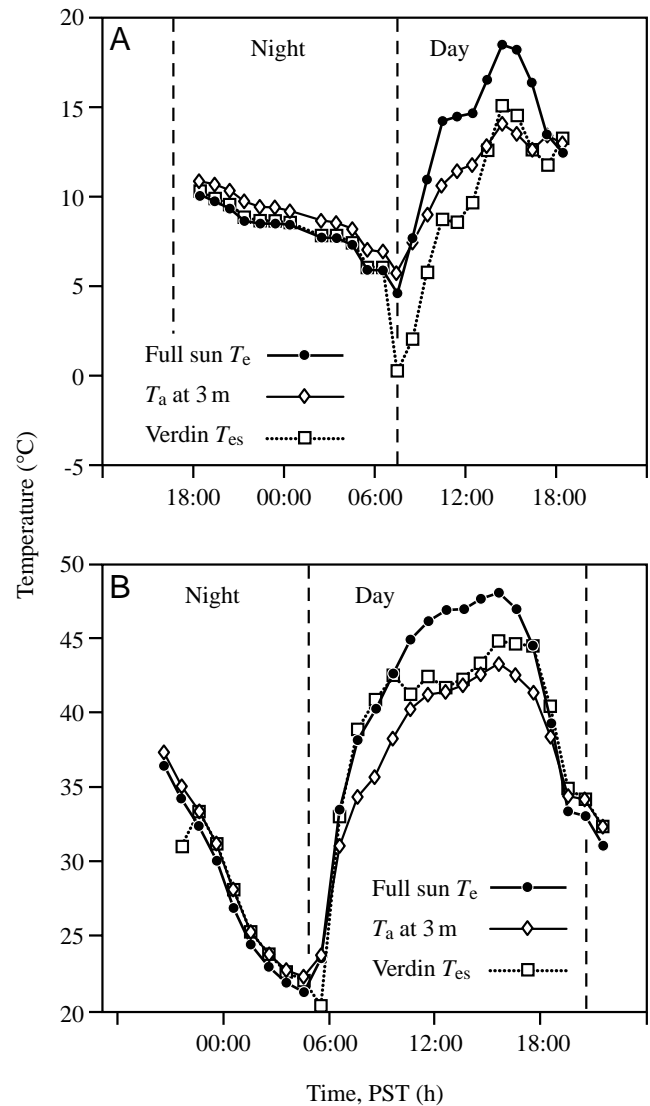

Fig. 1. Air temperature (T_a) at 3 m, operative temperature in the sun (T_e) and standard operative temperature (T_{es}) for verdins at Deep Canyon, CA, USA, throughout the winter day with the lowest average temperature (13–14 December 1987) (A) and the hottest summer day (7–8 July 1988) (B) on which we measured field metabolic rate. PST, Pacific standard time.

Table 3. *Body mass, $\dot{V}_{CO_2}$, field metabolic rate and field/basal metabolic rate ratio of verdins in winter and summer*

		Summer		
	Winter (*N*=14)	Adults (*N*=7)	Juveniles (*N*=2)	Dependent fledglings (*N*=5)
$\dot{V}_{CO_2}$ (ml g^{-1} h^{-1})	8.35±0.24 (6.8–9.8)	5.94±0.1 (5.45–6.25)	6.57, 6.64	5.1±0.2 (4.5–5.8)
FMR (kJ day^{-1})	33.6±0.91 (27.7–38.3)	22.8±0.45 (21.8–24.9)	25.8, 25.9	18.1±0.9 (15.8–20.9)
Predicted *FMR* (kJ day^{-1})	21.0	20.6		
FMR (kJ g$^{-0.63}$ day^{-1})	10.1±0.3 (8.3–11.8)	7.0±0.15 (6.6–7.6)	7.9, 7.8	5.9±0.3 (5.3–6.7)
Body mass (g)	6.7±0.1 (6.25–7.35)	6.33±0.4 (5.45–6.8)	6.6, 6.7	5.9±0.1 (5.45–6.4)
FMR/BMR	2.57	1.88	−	−

Summer adult data are pooled for two breeding adults and five post-breeding adults, three of which were molting.

Values are means ± S.E.M., with the range given in parentheses.

Predicted field metabolic rate (*FMR*) was calculated from log*FMR*=0.741+0.704logM_b (Williams and Tieleman, 2000).

BMR, basal metabolic rate; M_b, body mass; $\dot{V}_{CO_2}$, rate of CO_2 production.

birds (identified by their yellow bills, entirely gray heads and sprigs of downy juvenile plumage) were captured roosting with an adult female. This adult and two of her young were recaptured the next night in a different nest approximately 20 m distant. Another female and two dependent juveniles were recaptured together at their original roost-nest. On the basis of their size and plumage, we estimate that these young verdins were 18–21 days old (Taylor, 1971). Because of the date, these were probably young from a second brood for the season. Two young birds were captured roosting alone; we assumed that these were independent juveniles because of their black bills and the lack of yellow plumage on the head. We released the summer-captured birds at approximately 22:15 h (Pacific daylight savings time; range 21:08–00:08 h) and recaptured them at approximately 22:05 h (range 21:04–23:30 h). The release period averaged 23.8±0.2 h (range 23.4–25.7 h).

Summer $\dot{V}_{CO_2}$ did not differ between adult verdins captured with dependent young and those roosting alone (and presumed to be post-breeding), so we pooled the data (Table 3). Adult verdins in summer (without dependent young, $N=5$) averaged 6.49±0.10 g in body mass. During the release period following *DLW* injection, they lost 0.22±0.04 g (−3.4 % of initial mass; range −0.8 to 5.1 %). Summer adults with dependent young averaged 5.9 g in initial mass and lost 2.0 % of their mass during the release period.

Independent juveniles ($N=2$) had a higher body mass than adults (but not significantly higher when compared using a pooled t-test with $P>0.05$; Table 3) and lost more mass during the release period (−7.3 % of initial mass on average). Dependent juveniles ($N=5$), those with yellow bills captured in the company of an adult, had a signficantly lower initial body mass (pooled t-test; $P<0.05$) and lower $\dot{V}_{CO_2}$ than adults

(pooled t-test; $P<0.05$), but lost approximately the same amount of body mass during the release period (0.22±0.06 g; range 0–0.4 g).

Adult verdin *FMR* (winter and summer combined) correlated negatively with mean standard operative temperature (T_{es}) during the release period (Fig. 2). A linear regression equation with T_{es} as the independent variable explained 85 % of the variance in *FMR*. *FMR* was not significantly correlated with body mass, with mass loss during the release period or with the duration of the release period.

Water turnover

Total body water (^{18}O dilution space) of nonbreeding adult verdins was 4.49±0.07 ml in winter ($N=14$) and 4.41±0.07 ml in summer ($N=5$). Body water as a percentage of initial mass was 66.5±0.5 % in winter and 68.0±0.4 % in summer. Water efflux of adult verdins without dependent young was 623.5±21.6 ml kg^{-1} day^{-1} in summer and 498.2± 26.1 ml kg^{-1} day^{-1} in winter. These values correspond to the loss of 3.4±0.2 ml H_2O day^{-1} in winter and 3.9±0.2 ml H_2O day^{-1} in summer. Water efflux correlated positively with mean T_{es} ($r^2=0.30$, $P<0.05$) during the release period (Fig. 3), although there was wide variation so that a linear regression equation with T_{es} as the independent variable explained only 30 % of the variance in water efflux.

The water economy index (*WEI*; Nagy and Peterson, 1987; ml H_2O kJ^{-1}) of verdins differed significantly between seasons (0.17±0.01 ml kJ^{-1} in summer *versus* 0.10±0.01 ml kJ^{-1} in winter; $P<0.01$) and correlated positively with mean T_{es} during the release period (Fig. 4). Mean release period T_{es} explained 77 % of the variance in *WEI*.
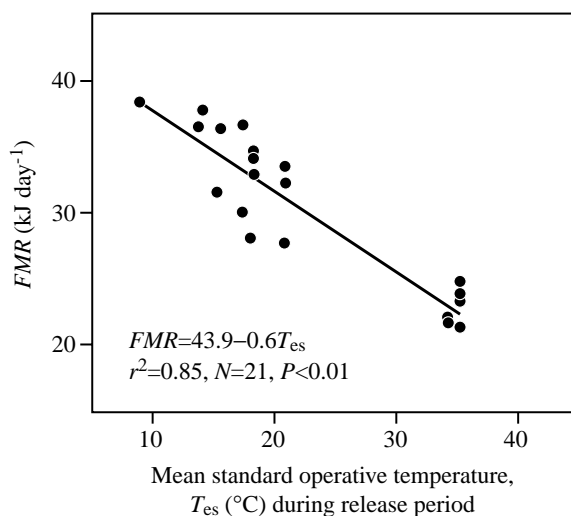

Fig. 2. Field metabolic rate (*FMR*, kJ day^{-1}; measured using doubly labeled water) as a function of mean daytime standard operative temperature (T_{es}, °C). The cluster of points near a mean T_{es} of 35 °C depicts data collected on 7–8 July 1988 and 9–10 July 1988 when the field metabolic rates of several birds were measured simultaneously.
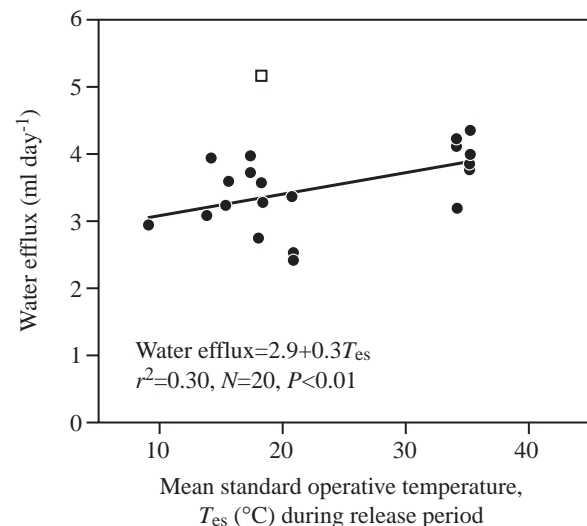

Fig. 3. Rate of water efflux (ml day^{-1}) of free-living verdins, measured using the doubly labeled water method, plotted as a function of mean standard operative temperature (T_{es}) during the release period. The linear regression equation shown was computed ignoring the outlier data point (square), which was more than 7 S.E.M. from the mean winter rate of water efflux.
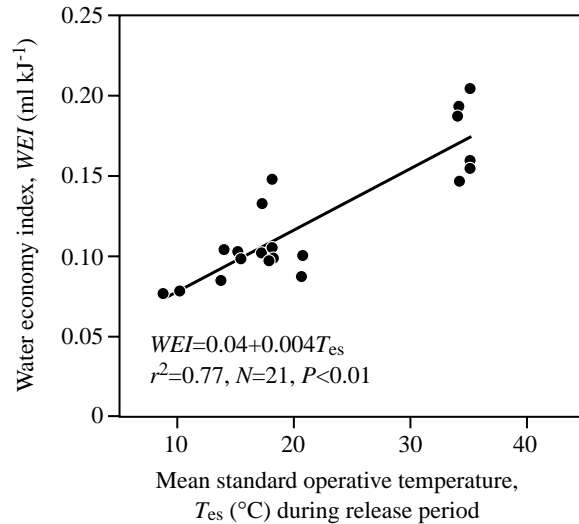
Fig. 4. Water economy index (*WEI*, the ratio of water efflux to field metabolic rate; ml kJ^{-1}) of verdins in winter and summer plotted as a function of mean standard operative temperature (T_{es}) during the release period.

Time–activity laboratory estimates of field metabolic rate

The *TAL* model that we used to estimate verdin *DEE* extrapolated laboratory data to a field setting. It depended heavily on predictive equations for various biophysical variables and utilized population mean values for time–activity data. Nevertheless, our *TAL* model yielded *DEE* estimates that approximated *DLW* measurements of *FMR* (Table 4). The additive model produced *FMR* estimates that were on average 9.3±2.0% higher than the *DLW* measurements [range −3.5 to +31.2%; computed as 100(*DEE*−*FMR*)/*FMR*]. The

substitutive model, in which activity heat subsumed the thermostatic costs of keeping warm when T_{es} was below the lower critical temperature (T_{lc}; the temperature below which energy must be expended in thermoregulation), was in closer agreement overall (average −0.9±2.4% lower than *DLW*) but also had *DEE* values that ranged widely around the *DLW*-measured data (range −18.3 to +14.3%). *DEE* estimates did not differ significantly from the corresponding *FMR* values (paired *t*-test, *P*<0.01).

Discussion

Verdins are among the smallest of passerine birds and might therefore be expected to show a high degree of weather-related variability in their *FMR*. Indeed, the close correlation between mean T_{es} and *FMR* in verdins (Fig. 2) reflects their low thermal inertia and the close coupling of very small birds to their physical environment (cf. Calder and King, 1974). Our *TAL* model allowed us to examine further the dependence of *FMR* on T_{es} and to estimate how the verdin's thermoregulatory requirements change seasonally. Our data revealed significant energy costs of thermoregulation not only in winter, but during summer as well.

Our *TAL* estimates of daily energy expenditure corresponded fairly well with our estimates derived from *DLW*, but did not accurately match individual *FMR* values [*FMR*/*DEE* linear correlation coefficients (r^2) were 0.71–0.78 for the two *TAL* models]. Like *TAL* estimates of *DEE* for the kestrel (*Falco tinnunculus*; Masman et al., 1988) and yellow-eyed junco (*Junco phaeonotus*; Weathers and Sullivan, 1989, 1993), our additive model predicted a higher *FMR* than we measured. Altering the model to include the assumption that

Table 4. *Time–activity laboratory estimates of verdin daily energy expenditure in winter and summer*

	Winter	Summer
DLW-measured *FMR*	33.6±0.9 (27.7–38.3)	22.8±0.5 (21.4–24.9)
Additive *TAL* model		
DEE	36.4±0.9 (32.9–42.9)	25.0±0.1 (24.3–25.5)
Resting metabolic rate	19.0±0.2 (17.8–19.8)	17.9±0.1 (17.7–18.2)
Cold defense, H_c	10.9±0.9 (7.2–18.8)	2.6±0.1 (2.0–3.0)
Heat defense, H_h	−	0.25±0.03 (0.16–0.35)
Activity cost	6.6±0.1 (6.2–7.5)	4.3±0.01 (4.3–4.4)
Substitutive *TAL* model		
DEE	31.4±0.7 (28.8–36.6)	24.8±0.1 (24.2–25.3)
Resting metabolic rate	19.0±0.2 (17.8–19.8)	17.9±0.1 (17.7–18.2)
Cold defense, H_c	6.3±0.8 (3.5–12.6)	2.2±0.1 (1.7–2.6)
Heat defense, H_h	−	0.25±0.03 (0.16–0.35)
Activity costs	6.6±0.1 (6.2–7.5)	4.3±0.01 (4.3–4.4)

See text for details of models used.

All data are reported in kJ day^{-1}, as means ± S.E.M. (with the range in parentheses).

Resting metabolic rate as used here is basal metabolic rate minus the minimal cost of daytime existence (fed, alert, perching metabolic rate) in the absence of thermoregulatory or activity costs.

DLW, doubly labeled water; *FMR*, field metabolic rate; *TAL*, time–activity laboratory; H_c, energy cost of cold defense; H_h, energy cost of heat defense; *DEE*, daily energy expenditure.

activity-generated heat substitutes for thermoregulatory requirements when T_{es} is less than T_{lc} did not improve the correspondence of individual values (r^2=0.71) but did produce population mean *DEE* estimates that were slightly closer to the measured *FMR* (Table 4). We take this as further evidence that exercise thermogenesis substitutes for thermostatic costs in small birds (e.g. Paladino and King, 1984; Webster and Weathers, 1990) and thus emphasize in our analyses thermoregulatory cost estimates based on the substitutive *TAL* model.

Energy cost of thermoregulation

In winter, when activity and cold stress were coincident, thermoregulatory requirements for cold defense (H_c) made up between 10.4 and 37.5 % of *DEE* (19.5±2.1 %). By using activity-generated heat to replace otherwise necessary H_c (Table 4), verdins apparently reduce the energy cost of thermoregulation by 42 %, from a predicted 10.9 kJ day^{-1} (in the additive model) to 6.3 kJ day^{-1} (Table 4).

Thermoregulatory costs would have been even higher were it not for the verdin's unusual habit of building and using roost-nests year-round. Winter roost-nests, shown by Buttemer et al. (1987) to reduce significantly overnight energy expenditure,

also offer verdins protection from extreme daytime weather. Several periods of inclement weather – high winds, rain or sleet and temperatures near freezing – allowed us to observe verdin behavior during storms. On two such occasions, we found verdins in their roost-nests in the middle of the day. Moore (1965) reported finding a female verdin in a roost-nest during a sleet storm which coated the nest with ice. W. K. Taylor (personal communication) observed verdins in Arizona entering their nests upon the onset of a summer thunderstorm. We rarely saw verdins actively foraging in the rain or when winds were high, but even on cold days they became active again as soon as the weather improved.

Summer roost-nests are less substantial than winter nests, but nevertheless serve to reduce the verdins' energy cost for cold defense. Summertime temperatures in the Colorado desert are high during the day (Fig. 1B), but at night they typically fall below the verdin's lower critical temperature (T_{lc}) of 28 °C (Buttemer et al., 1987), necessitating expenditure of energy for thermoregulation. Summertime thermoregulatory costs for cold defense (H_c) make up 9.0±0.4 % of *DEE*. Because summer T_{es} rarely was below T_{lc} (28 °C) during the verdins' active phase, savings from activity heat substitution were estimated to be only approximately 0.2±0.03 kJ day^{-1}, or

Table 5. *Avian field metabolic rate measured in winter and summer from studies that have examined seasonal changes*

Species	Field metabolic rate, *FMR* (kJ day^{-1})		Stage[a]	Difference (%)[b]	Reference
	Winter	Summer			
Little penguin *Eudyptula minor*[c]	1207	1788	B	48.1	Gales and Green (1990)
Long-eared owl *Asio otus*[d]	211	301	B	42.4	Wijnandts (1984)
Eurasian kestrel *Falco tinnunculus*[e]	♂ 267 (2.8)	261 (2.4)	BM	−2.2	Masman et al. (1988)
	♀ 322 (2.9)	297 (3.2)	BM	−7.8	
Chukar *Alectoris chukar*[f]	356 (2.1)	232 (1.6)		−34.8	Kam et al. (1987)
Sand partridge *Ammoperdix heyi*[g]	188 (2.0)	119 (1.5)		−36.7	Kam et al. (1987)
Dipper *Cinclus cinclus*	♂ 257 (3.9)	219 (3.1)	M	−14.6	Bryant and Tatner (1988)
	♀ 199 (3.4)	174 (2.9)	M	−12.6	
Black-billed magpie *Pica pica*[h]	♂ 298 (2.2)	258 (1.9)	M	−13.4	Mugaas and King (1981)
	♀ 266 (1.8)	228 (1.5)	M	−16.7	
Verdin *Auriparus flaviceps*	33.6 (2.6)	22.8 (1.9)	M	−31.8	This study
Dark-eyed junco *Junco hyemalis*[i]	70.5 (2.3)	70.7 (2.3)	B	0.3	Weathers and Sullivan (1993)
Yellow-eyed junco *Junco phaeonotus*	70.5 (2.4)	70.7 (2.3)	B	0.3	Weathers and Sullivan (1993)
White-crowned sparrow *Zonotrichia leucophrys*	100.4 (2.2)	85.5 (1.8)	B	−10.1	Weathers et al. (1999)

All data are in kJ day^{-1}; the value in parentheses is the multiple of *BMR* (night-time basal metabolic rate) at that season.

Except where noted, summer data are for adults in the post-breeding phase of the annual cycle.

If not measured during the study, *BMR* was estimated from the equations of Aschoff and Pohl (1970).

[a]Stage indicates condition of summer birds: B, breeding; M, molting.

[b]Per cent difference computed as (100[summer−winter]/winter). A positive value indicates that *FMR* increased during summer.

[c]Data are for non-breeding birds in July (winter) and for breeding birds during the mid chick-rearing phase. During the measurements, penguins foraged at sea and spent some time on land. *BMR* multiples are omitted because of widely varying estimates of resting metabolism.

[d]Males and females averaged.

[e]Time–activity laboratory (*TAL*) estimates for nonbreeding adults in January and adults that were either feeding nestlings or molting in August.

[f]Winter value is the average of pre- and post-rain periods.

[g]Winter value is for the pre-rain period only.

[h]These data are derived from *TAL* estimates for nonbreeding adult magpies in December and late July (during their postnuptial molt).

[i]Summer value is for breeding adults (males and females pooled); *BMR* was estimated from body mass and the data of Bakken et al. (1990).

0.4–0.8 % of *DEE*. These calculations show that, even with the added insulation of night-time roost-nests, verdins devote a significant fraction of their energy resources to maintaining their body temperature during summer.

The metabolic cost of heat defense (H_h) in the summer is much lower than H_c (Table 4). In summer, H_h averaged 0.25 ± 0.03 kJ day^{-1} and accounted for only 1.0 ± 0.1 % of *DEE*. This finding suggests that heat defense, by verdins and other desert birds, is not a significant metabolic burden and that any costs of defending against heat stress manifest themselves as water, rather than energy, requirements. Our results support the conclusion of Dawson and O'Connor (1996) that '...vigorous evaporative heat defense has only a minor impact on *FMR*'.

Seasonal changes in energy use

The energy requirements of nonbreeding adult verdin are considerably higher in winter than in summer. Our analysis of energy budget components and meteorological data supports our prediction that elevated thermoregulatory requirements increase *FMR* in winter. In Table 5 are assembled data from all studies to date that have measured seasonal changes in *FMR* or *DEE* in birds. These same data were reviewed by Dawson and O'Connor (1996) and Weathers and Sullivan (1993), but their emphasis was on the energy costs of reproduction (because breeding birds are more amenable to *DLW* methods). Bryant (1997) used data for 58 species in an allometric analysis of *FMR*, including all stages of the annual cycle. We selected from the available data those seasonal studies that demonstrate primarily weather, rather than behavior, effects on *FMR*.

In verdins, chukar (*Alectoris chukar*; Kam et al., 1987) and sand partridge (*Ammoperdix heyi*; Kam et al., 1987), a significant decrease in *FMR* occurs from winter to summer. A similar but less marked reduction in *FMR* was measured in black-billed magpies (*Pica pica*; Mugaas and King, 1981), kestrels (Masman et al., 1988) and dippers (*Cinclus cinclus*; Bryant and Tatner, 1988). Long-eared owls (*Asio otus*; Wijnandts, 1984) and little penguins (*Eudyptula minor*; Gales and Green, 1990) show a large increase in *FMR* from winter to summer, but these (summer) data were recorded from birds feeding nestlings.

Despite the uncertainties of extracting patterns from the breeding-to-nonbreeding variation in *FMR* that exists among bird species so far studied (Weathers and Sullivan, 1993; Dawson and O'Connor, 1996; Bryant, 1997), it seems clear that in most species nonbreeding adult *FMR* is higher during winter than in summer. We infer from this that there is indeed a significant daily cost of thermoregulation for cold season survival in temperate-wintering birds.

Food and water intake

We used our *FMR* data to estimate the food intake of verdins during summer and winter. In winter, verdins must procure approximately 5.4 g (fresh mass) of arthropods and 0.5 g of nectar daily to meet their energy needs. Assuming that our

Table 6. *Water budgets of verdins in winter and summer*

	Winter (*N*=14)	Summer (*N*=5)
Gains		
Water intake in food[a]	3.83	2.86
Metabolic water[b]	0.95	0.65
Drinking	–	??
Total estimated gains	4.78	3.51
DLW-measured influx	3.20	3.72
Estimated gains minus influx	+1.48	–0.21
Losses		
Evaporation	1.20	1.46
Excretory water loss[c]	2.22	2.41
DLW-measured efflux	3.42	3.87

Gains and losses were estimated from our doubly-labeled water (*DLW*) data, from measurements of the water content of nectar and insects, and by extrapolation of laboratory data on evaporative water loss (Wolf and Walsberg, 1996). We assumed that the verdins' diet consisted of 95 % insects and 5 % nectar in both seasons. Body mass was 6.7 g in winter and 6.5 g in summer.

[a]In the summer, insects we collected from foliage where verdins foraged contained 68 % water (eight vials of insects collected and dried at 50 °C had mean ± S.E.M. water content of 68.2±0.1 %). We assumed that insects had a similar water content in the winter. Nectar was assumed to be 80 % water (Bell, 1990).

[b]Metabolic water was estimated by multiplying food intake, derived from field metabolic rate (*FMR*) data and the caloric content of the diet, by 0.49 ml g^{-1} dry matter. This figure was derived from insect and nectar nutrient composition and the data of Schmidt-Nielsen (1990) on oxidative water produced by the metabolism of various foodstuffs.

[c]Excretory water loss was estimated from the difference between efflux and evaporative water loss.

sweep net samples yielded a representative population of insects and spiders, the average mass of one typical Colorado desert foliage-dwelling arthropod is approximately 10 mg. Verdins in winter must, therefore, find and eat 540 spiders, insects or larvae daily. In 8.7 h of foraging time, verdins in the winter must capture approximately one prey item per minute. Reduced thermoregulatory costs, higher insect abundance and longer days may reduce the intensity of foraging required for energy balance in summer. We estimate that, in the summer, verdin daily food intake includes approximately 3.8 g (fresh mass) of arthropods and 0.3 g of nectar. This corresponds to approximately 380 typical arthropods each day and a capture rate (assuming 5.7 h of foraging; Austin, 1978) of 1.1 insects per minute. Evidently, verdins are able to reduce foraging time in the summer, but their rate of energy intake from foraging does not differ greatly between the seasons (4.0 kJ h^{-1} in summer, 3.9 kJ h^{-1} in winter; based on data from Tables 2 and 3).

Taylor (1971) and Rosenberg et al. (1991) found that verdin stomachs contained mostly arthropods, mainly lepidopteran larvae and adult Homoptera and Coleoptera. Our foraging observations indicated that verdins found food mainly by gleaning the live foliage of palo verde trees (Webster and

Weathers, 1990). In winter, but not in summer, we occasionally saw verdins pecking at palm fruit (*Washingtonia* spp.) in the Living Desert Reserve arboretum located near our study area. We often saw verdins gleaning in and around flowers, especially of palo verde, in February and March. Plant material, including seed pods of mesquite, palo verde and ironwood (*Olnya tesota*), may comprise a greater proportion of the verdin diet in winter (Taylor, 1971). The stomachs of verdins that we collected in winter contained mostly Cercopidacae (spittle bug) larvae and the legs and elytra of adult curculionid weevils. Rosenberg et al. (1991) reported that verdins in the lower Colorado River valley ate mostly scale insects, aphids, caterpillars and jumping spiders together with some berries.

The *FMR* of two independent juveniles was higher (25.8 and 25.9 kJ day^{-1}) than that of adult verdins (Table 3). This is consistent with the data of Weathers and Sullivan (1989), who showed that juvenile yellow-eyed juncos had a higher *FMR* than adults because of their lower foraging proficiency. Dependent juveniles (*N*=5) that were captured with an adult female had a much lower *FMR* (18.1±0.85 kJ day^{-1}). This result, along with the observation that they lost only 3.7±1.1 % of their initial body mass, suggests that the dependent juveniles were less active than adults and that they were being provisioned by a parent.

Water turnover by free-living verdins was 16 % higher in summer than in winter (Table 6). Summer water influx measures were consistent with the assumption that verdin meet their summertime energy needs by consuming mainly arthopod prey containing 68 % water. Water influx was surprisingly low in winter (Table 6), however, indicating that verdins were probably eating drier foods (arthropods or plant material with less water) at that time of year. In neither season were influx rates high enough to indicate that verdins drank water, which they are not known to do (Miller and Stebbins, 1964; Taylor, 1971; Weathers, 1988).

The water economy index *WEI* (Nagy and Peterson, 1987) of verdins ranges from 0.08 to 0.21 ml kJ^{-1} (Fig. 4). Higher values for *WEI* occurred in summer, reflecting the lower *FMR* and relatively higher water efflux at that season. Nagy and Peterson (1987), who developed this index for use as a measure of animal water economy, suggest that desert birds have a lower *WEI* than birds inhabiting more mesic habitats. Our data support this hypothesis, as do the data of Williams et al. (1993) for ostriches (*Struthio camelus*). The correlation between *WEI* and T_{es} that we observed for verdins suggests adjustments of their water economy (i.e. reduced evaporative water loss, lowered metabolic rate, reduced excretory water loss; Webster, 1991) to accommodate the potentially dehydrating summer heat.

List of symbols

BMR   basal metabolic rate (kJ h^{-1}) of fasted birds resting in the dark at night at a thermally neutral temperature

DLW   doubly labeled water, $^3HH^{18}O$

DEE   total daily heat production (kJ day^{-1}) estimated by *TAL* analysis

FMR   field metabolic rate (kJ day^{-1}) of free-living birds, measured using *DLW*

H_{act} energy cost of activity, including all categories mentioned in Table 2

H_c energy cost of thermoregulation during cold defense

H_h energy cost of thermoregulation during heat defense

r_b whole-body (tissue plus coat) thermal resistance (s m^{-1}) in free convection conditions

r_b' whole-body thermal resistance (s m^{-1}) estimated for field wind conditions

r_e equivalent resistance (s m^{-1}) in still air, computed as the parallel sum of the radiative and boundary-layer resistances to heat loss

r_e' equivalent resistance (s m^{-1}) at field wind speed

r_{nest} nest thermal resistance

r_T total thermal resistance (s m^{-1}) in free convection conditions

r_T' total thermal resistance (s m^{-1}) estimated for field wind conditions

RMR_α metabolic rate (kJ h^{-1}) of fasted birds resting in the dark during the active phase

SDA   specific dynamic action or the heat increment of feeding

t_α duration of active phase of daily cycle

t_ρ duration of rest phase of daily cycle

TAL   time–activity laboratory model for computing DEE

T_a air temperature (°C)

T_b body temperature (°C)

T_e operative temperature (°C)

T_{es} standard operative temperature (°C)

T_{lc} lower critical temperature (°C)

u wind speed

$\dot{V}_{CO_2}$ rate of CO$_2$ production (ml g^{-1} h^{-1})

WEI   water economy index

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