

Seasonal daily, daytime and night-time field metabolic rates in Arabian babblers (*Turdoides squamiceps*)

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Summary

Arabian babblers (*Turdoides squamiceps*; mean adult body mass=72.5 g) inhabit extreme deserts of Israel. Previous studies have shown that their daily field metabolic rates are similar in winter and summer and that there is an increase during the breeding season. We hypothesized that the difference in seasonal daily field metabolic rate would be a consequence of differences in daytime metabolic rate, and that night-time metabolic rate would be similar during the three seasons. We used doubly labelled water to determine daily, daytime and night-time field metabolic and water-influx rates in breeding babblers in spring and nonbreeding babblers in winter and summer.

Daily and daytime energy expenditure rates were higher during the breeding season than during either summer or winter, but there was no difference among seasons in night-time energy expenditure rates. Thus, our hypothesis was supported. The daytime field metabolic rates in summer and winter nonbreeding babblers were 3.92× and 4.32× the resting metabolic rate (RMR), respectively, and in breeding babblers was 5.04× RMR, whereas the night-

time field metabolic rates ranged between 1.26× RMR and 1.35× RMR in the three seasons. Daily and daytime water-influx rates were highest in winter, intermediate during the breeding season and lowest in summer, but there was no difference among seasons in night-time water-influx rate. Daytime water-influx rate was greater than night-time water-influx rate by 2.5-fold in summer, 3.9-fold in the breeding season and 6.75-fold in winter.

Seasonal patterns of daily and daytime energy expenditure were similar, as were seasonal patterns of daily and daytime water influx. Daily and daytime energy expenditure and water-influx rates differed among seasons whereas night-time rates of both did not. Daily and daytime field metabolic rates of babblers were highest during the breeding season, whereas daily and daytime water-influx rates were highest in winter.

Key words: Arabian babbler, *Turdoides squamiceps*, doubly labelled water, daily field metabolic rate, daytime field metabolic rate, night-time field metabolic rate, water-influx rate.

Introduction

Feeding and the search for food are the predominant activities of most free-living animals (Rozin, 1976). Consequently, field metabolic rate, which reflects the costs and efficiencies of gathering food, has taken a central role in ecological and physiological studies (Nagy, 1987; Bryant, 1988). Field metabolic rate, often estimated using the doubly labelled water technique (Nagy, 1980; Speakman, 1997), integrates the total daily energy expenditure or heat production of an animal and can be used to calculate its food intake. Heat production includes metabolism of food and catabolism of body tissue (Kam and Degen, 1997a,b).

Dietary selection and food intake influence metabolic rates (McNab, 1988). Some small birds have to forage during the day in order to accumulate sufficient body energy reserves to survive the night (King, 1972; Chaplin, 1974; Blem, 1976).

Consequently, overnight energy demands of birds are important in assessing their ability to survive. Most previous studies monitored changes in body mass and used them as an indication of energy use (Webster, 1989; Chan, 1994). In some studies, time activity budgets were used to calculate time energy budgets, and basal or resting metabolic rates were assumed for night roosting (Carmi-Winkler et al., 1987).

In the present study, we determined the daily, daytime and night-time metabolic rates of free-living Arabian babblers (*Turdoides squamiceps* Cretzsch; Timaliidae; adult body mass=65–85 g) in summer and winter in nonbreeding adults and in spring in breeding adults. The Arabian babbler inhabits the Arava, part of the Great Rift, an extreme desert of Israel (Zahavi, 1990). This diurnal bird lives in groups of mixed sex, is terrestrial and is active throughout the day (Wright et al.,

2001). It is an omnivore that eats invertebrates and fruits and, at least at our study site, appears not to drink (Anava et al., 2000). In earlier studies, we found no difference in the daily field metabolic rate of nonbreeding babblers during winter and summer (Anava et al., 2000), but breeding babblers had higher daily metabolic rates than nonbreeding babblers (Anava et al., 2001a). We hypothesized that the daytime metabolic rate of breeding babblers would be higher than the summer and winter daytime metabolic rates of nonbreeding babblers, but that the night-time metabolic rate would be similar in the breeding, summer and winter seasons.

Materials and methods

The study was undertaken at the Shezaf Nature Reserve at Hatzeva (30°45'N; 35°15'E) in the Arava, approximately 30 km south of the Dead Sea. This site is in the northern part of the Arabian Sahara Desert and is characterized by long, hot, dry summers. It is extremely arid (UNESCO, 1977), averaging 9.6 days of rainfall each year, yielding a mean annual winter rainfall of 35 mm; total annual dew is <1 mm. There are, however, large annual variations in total rainfall and in its temporal and spatial distribution. Evaporation averages 3400 mm annually and, in summer, averages 14 mm daily. Average daily air temperature for the hottest (July–August) and coldest (January–February) months are 30°C and 15°C, respectively. Average maximum daily air temperature for July–August is 38°C, with temperatures reaching 47°C, and average minimum daily air temperature for January–February is 9°C, rarely dropping below 0°C (Stern et al., 1986). The soil is of the Hatzeva formation, which is known for its ability to hold water, and, as a result, the area has more vegetation than other deserts with similar rainfall. Vegetation is of the Sudan type and is dominated by a community of sparse shrubs, including *Anabasis articulata*, *Lycium shawii*, *Hammada scoparia*, *Zygophyllum simplex* and *Salsola baryosma* (Anava, 1998).

The study was carried out during 1997. There were approximately 13 h light and 11 h dark in summer, 11 h light and 13 h dark in winter and 12 h light and 12 h dark in spring (breeding period). There is a period of 10–20 min of dim light at sunrise and at sunset. The groups of babblers at the reserve have been observed continually for over 30 years (Zahavi, 1990; Wright et al., 2001) and there were more than 20 groups on the site at the time of the study. The legs of all babblers were colour banded, which allowed for quick individual identification. The birds foraged on their own in the wild; however, they were accustomed to the presence of observers within 2–3 m without showing signs of fear.

Doubly labelled water measurements

Measurements of field metabolic rate and water influx in Arabian babblers were made for nonbreeding adults in winter (January–February) and summer (July–August) and for breeding adults in spring (March–May). Tritiated-water space measurements (as an estimate of total body water volume) were made concomitantly but not on the same individuals that

were used for doubly labelled water measurements. In each season, 12 adult babblers (six males and six females) were captured using traps in which the doors were triggered shut when the birds walked in; mealworms were used as bait. For tritiated-water space measurements, the birds were weighed and then a 100–200 µl blood sample was taken by pricking the basilic vein, located on the ventral surface of the wing, and collecting blood with microhematocrit tubes. These samples were used to measure background radioactivity levels. Each bird was then injected intramuscularly with 0.5 ml of sterile isotonic avian saline containing 1.85 MBq of tritium. The birds were kept without food or water for 45–60 min to allow for equilibration of the isotope with body fluids (Degen et al., 1981), after which time they were weighed again and another 100–200 µl blood sample was collected. The mean of the two weighings was used in subsequent calculations. Blood samples were refrigerated and then micro-distilled to dryness to obtain pure water (Wood et al., 1975). The specific activity of tritium was determined in duplicate samples by liquid scintillation spectrometry (Kontron; Munchenstein, Switzerland) in which each sample contained 20 µl of distillate in 5 ml scintillation fluid (Amersham, UK). Samples were counted for 10 min, and counts were corrected for quenching using a series of quenched standards. Tritiated water space was estimated from the dilution of tritium in the body fluids (Nagy and Costa, 1980; Degen et al., 1981).

We developed a technique in which doubly labelled water measurements were made without touching the babblers (Anava et al., 2000). Birds were trained to walk onto a large platform balance (Moznei-Shekel, Kibbutz Keshet, Israel; model B-2-P, 104; –0.2 g), at which time they were weighed. Furthermore, isotopes were delivered to birds in a unique manner. 50 µl water containing 95 atoms % ¹⁸O (Yeda, Rehovot, Israel) and 4.625 MBq tritium (Nuclear Research Centre, Negev, Beer-Sheva, Israel) was injected into a cricket. The cricket was then fed to a babbler at between 09:00 h and 11:00 h, and the isotopes were allowed to equilibrate with body water, which usually occurred within an hour (Degen et al., 1981). The following morning, the babblers were observed, weighed and a fresh excreta sample from each babbler was collected from the ground into a glass vial immediately after the sample was excreted. Samples were also collected that evening and the following morning, at which time the birds were weighed.

Excreta samples were refrigerated and then micro-distilled under vacuum until dryness (Wood et al., 1975) to obtain pure water. Tritium levels were determined as above, except that 50 µl (rather than 20 µl) of distillate was analysed. Levels of ¹⁸O specific activity were measured in triplicate by an autogamma counting system (Packard, Downers Grove, IL, USA) after converting ¹⁸O to γ -emitting ¹⁸F by cyclotron-generated proton activation (Wood et al., 1975). Excreta samples from three non-injected birds were treated similarly to measure background levels of ¹⁸O and tritium.

Water fluxes were calculated from the decline in specific activity of tritium over time (Nagy and Costa, 1980; Degen et

Table 1. Daily, daytime and night-time energy expenditure rates of free-living adult breeding Arabian babblers in spring and nonbreeding adults in summer and winter

Season	N	Body mass (g)	Energy expenditure (J g ⁻¹ h ⁻¹)		
			Daytime	Night-time	Daily
Breeding	45	72.6±0.77 ^{a,b}	135.7±5.7 ^a	36.2±6.7 ^a	86.5±6.0 ^a
Summer	22	70.3±0.98 ^a	105.6±7.5 ^b	34.7±10.3 ^a	73.0±7.5 ^b
Winter	17	75.6±1.30 ^b	116.4±5.9 ^b	33.9±6.7 ^a	71.7±6.2 ^b

Columns containing values with different superscripts are significantly different from each other (analysis of covariance; $P < 0.05$).

al., 1981; Degen, 1997), and rates of CO₂ production were estimated from the decline in specific activity of tritium and ¹⁸O over time (Lifson and McClintock, 1966; Nagy, 1980). For calculation of water flux, we used equation 2 of Nagy (1980), which assumes that total body water changes linearly over the time of measurement. These calculations require knowledge of the total body water volume of the animal. For this, we used the mean value determined from the tritiated-water space measurements for each sex and within each season. The excreta samples were collected within 30 min of the babblers descending from the tree to start daytime activity and 30 min before they ascended the tree for roosting. The two morning samples allowed calculations of daily rates. The morning and evening samples allowed calculations of daytime rates, as both samples were taken during daytime activity. Total daytime rates were then calculated by multiplying hourly rates by the hours of daytime activity. The night-to-morning fluid samples included daytime activity at both ends and thus would overestimate night-time rates. As a result, total night-time rates were calculated as the total daily rate minus the total daytime rate. CO₂ production rate was converted to energy expenditure by assuming that 25.7 J of heat energy are produced for each ml of CO₂ (Anava et al., 2000).

For comparisons of field metabolic rate and water-influx rate among seasons, we used a two-way analysis of covariance (ANCOVA) using body mass as a covariate factor. We accepted $P < 0.05$ as the minimum level for significance. Values are presented as means ± S.E.M.

Results

Babblers in winter were heavier than in summer; breeding babblers were intermediate in body mass and did not differ from either winter or summer babblers (Table 1). However, during measurements within each season, the birds maintained body mass. There was no difference in energy expenditure rate or water-influx rate between sexes in each season and, therefore, data for males and females were pooled.

Daily and daytime energy expenditure rates during the breeding season were significantly higher than during either summer or winter, but there was no difference in night-time energy expenditure rate among seasons. Daytime energy expenditure rate was significantly greater than night-time energy expenditure rate: by 3.04-fold in summer, 3.43-fold in winter and 3.74-fold in the breeding season (Table 1).

Table 2. Daily, daytime and night-time water influx rates of free-living adult breeding Arabian babblers in spring and nonbreeding free-living adults in summer and winter

Season	Water influx rate (ml g ⁻¹ h ⁻¹)		
	Daytime	Night-time	Daily
Breeding	0.0290±0.0008 ^a	0.0074±0.0009 ^a	0.0182±0.0009 ^a
Summer	0.0164±0.0008 ^b	0.0066±0.0007 ^a	0.0118±0.0007 ^b
Winter	0.0459±0.0030 ^c	0.0068±0.0007 ^a	0.0247±0.0024 ^c

Columns containing values with different superscripts are significantly different from each other (analysis of covariance; $P < 0.05$).

Sample sizes and body masses of the babblers are presented in Table 1.

Daily and daytime water-influx rates were highest in winter, intermediate during the breeding season and lowest in summer, but there was no difference in night-time water-influx rates among seasons. Daytime water-influx rate was significantly greater than the night-time rate: by 2.5-fold in summer, 3.9-fold in the breeding season and 6.75-fold in winter (Table 2).

Discussion

Doubly labelled water method

Doubly labelled water has been used in a variety of animals to determine CO₂ production (a measure of field metabolic rate) and water-influx rates (Speakman, 1997). This method is attractive in that: (1) it allows measurements to be made under near-normal free-living conditions; (2) validation studies have shown that estimations are within 10% of actual measurements (Nagy, 1980; Williams, 1985; Speakman and Racey, 1988); and (3) it does not affect metabolic and behavioural responses of animals, at least in common poorwills (*Phalaenoptilus nuttallii*; Zurowski and Brigham, 1994) and mice (*Mus musculus*; Speakman et al., 1991).

The doubly labelled water method follows the decline over time in concentrations of oxygen and hydrogen isotopes after introducing the isotopes into an animal and allowing them to equilibrate with body fluids. The rate of decline of the hydrogen isotope estimates water flux, and the difference in decline of isotope concentrations is used to estimate CO₂ production rate (Lifson and McClintock, 1966; Kam and Degen, 1997a).

Fluid samples are required to measure the rate of decline of the isotopes; blood, urine, faeces, saliva and respiratory water have been used. All have proven to provide reliable and similar results. For example, following the administration of tritium in humans, the specific activity of water obtained from either urine or sweat was the same as that of body water (Pinson and Langham, 1957). Urine and blood were used in small mammals (Lifson et al., 1975), and urine and saliva were used in humans, with accurate results (Schoeller and van Santen, 1982). Calculations of CO₂ production rates using doubly labelled water gave similar results regardless of whether fluid was taken from blood or faeces in reindeer (*Rangifer tarandus tarandus*) (Gotaas et al., 1997). Furthermore, faecal samples collected off the ground were used to measure water flux in free-living blesbok (*Damaliscus dorcas phillipsi*) and impala (*Aepyceros melampus melampus*) (Fairall and Klein, 1984; Klein and Fairall, 1986).

In general, the weighing of animals and collection of fluid samples for doubly labelled water measurements entail their capture, placing them in bags and pricking their blood vessels for blood samples. However, these procedures can stress the animals and affect measurements of energy expenditure. The present study eliminated these stressful procedures. The method was tested on two babblers in the laboratory. Daily energy expenditure and water influx measured by the doubly labelled water method described above, were, on average, 4.0% and 4.6% higher, respectively, than the values obtained by the balance method (Anava, 1998). These differences in methods were acceptable and similar to others reported in validation studies for avian species (Nagy, 1980; Williams, 1985; Speakman and Racey, 1988), indicating that the method could be used to estimate metabolic rate and water flux in free-living birds. Furthermore, the delivery of isotopes orally and the use of urine for fluid samples, as adapted in this study, gave accurate results of energy expenditure in humans (Schoeller and van Santen, 1982).

Field metabolic rate and water influx

The daily energy expenditure of nonbreeding Arabian babblers in winter, 124.7 kJ day⁻¹, and in summer, 127.0 kJ day⁻¹, were similar, but daily energy expenditure of breeding babblers, 150.1 kJ day⁻¹ for a 72.5 g babbler, was significantly greater than the expenditure of nonbreeding adults. This is in agreement with a number of studies that have shown that the breeding season is the most costly in terms of energy expenditure in avian species (Tatner, 1990; Tinbergen and Dietz, 1994). However, the daily energy costs of the breeding babblers were relatively low when compared with other breeding passerines. Allometric equations of Masman et al. (1989) and Nagy (1987) predict that a 72.5 g breeding passerine bird should expend 219.9 kJ day⁻¹ and 195.9 kJ day⁻¹, respectively. In the present study, energy expenditure of breeding Arabian babblers was 68–77% of these values.

The resting metabolic rate (RMR) of Arabian babblers was reported as 26.9 J g⁻¹ h⁻¹ (Anava et al., 2001b), which, when

compared with the phylogenetically adjusted equation for basal metabolic rate (BMR) in birds, is only 73% of the value predicted for a bird of its body mass (Reynolds and Lee, 1966; Williams, 1999). Using this RMR value, the daily field metabolic rate of Arabian babblers ranged between 2.70× RMR in nonbreeding adults and 3.22× RMR in breeding adults. As BMR is lower than RMR (Degen, 1997), field metabolic rates as a multiple of BMR would be higher than as a multiple of RMR. It is likely, therefore, that for breeding birds it would fall somewhere between the predicted values of 3.2× BMR (Daan et al., 1991) and 4.0× BMR (Drent and Daan, 1980).

Night-time field metabolic rates per hour were similar between breeding and nonbreeding babblers, which supported our hypothesis, and ranged between 1.26× RMR and 1.35× RMR. Tinbergen and Dietz (1994) found that night-time field metabolic rate in the 17.7 g breeding great tit (*Parus major*) was 1.9× BMR. BMR is slightly lower than RMR, and therefore the ratio to BMR would be slightly lower than the ratio to RMR but, most likely, still higher than that for breeding Arabian babblers. The night-time field metabolic rate was 47% of the daily field metabolic rate for nonbreeding babblers in both summer and winter. The value during the breeding season was 42%, which was lower than the 62% reported for breeding great tits (Tinbergen and Dietz, 1994). Thus, the energy expended at night-time, as a percentage of total daily energy expenditure, was greater in the great tit than in the Arabian babblers. Daytime field metabolic rate was greater in breeding than nonbreeding babblers, which also supports our hypothesis. The daytime field metabolic rate in nonbreeding summer and winter babblers was 3.92× RMR and 4.32× RMR, respectively, and in breeding babblers was 5.04× RMR. Furthermore, daytime field metabolic rates were approximately 3.20× night-time field metabolic rates in nonbreeding babblers and 3.74× night-time field metabolic rates in breeding babblers.

Patterns of seasonal daily and daytime water-influx rates of the babblers differ from those of daily energy expenditure. Water-influx rate was highest in winter, intermediate during breeding and lowest in summer. These differences in water influx were associated mainly with preformed water of the diet and not energy intake, as the birds shifted diets among seasons. In winter, babblers consume more fruit and less insects than in summer (Anava et al., 2000). A higher water influx in avian species during winter than in summer owing to a dietary shift was also reported in Negev desert chukars (*Alectoris chukar*) and sand partridges (*Ammoperdix heyi*) (Alkon et al., 1985; Kam et al., 1987). The night-time water-influx rate was similar between breeding and nonbreeding babblers, approximately 0.0070 ml g⁻¹ h⁻¹, and ranged between 27% and 55% of the daily water-influx rate in nonbreeding winter and summer babblers, respectively. The water-influx rate during the daytime was higher than the night-time rate by 2.48× in summer, 3.92× in the breeding season and 6.75× in winter.

In summary, seasonal patterns of daily and daytime energy expenditure were similar, as were seasonal patterns of daily and daytime water influx. Daily and daytime energy

expenditure and water-influx rates differed among seasons, whereas night-time rates of both did not. Daily and daytime field metabolic rates of babblers were highest during the breeding season, whereas daily and daytime water-influx rates were highest in winter.

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