

THERMOREGULATORY RESPONSES OF BRIDLED AND JUNIPER TITMICE TO HIGH TEMPERATURE¹

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Abstract. Bridled Titmice (*Baeolophus wollweberi*) and Juniper Titmice (*B. ridgwayi*) occur sympatrically in southeastern Arizona, with Bridled Titmice preferring habitats that are more heavily vegetated, moister, and cooler than those occupied by Juniper Titmice. To assess whether these differences in habitat preference have physiological correlates, we measured the oxygen consumption, evaporative water loss, and body temperature of post-breeding titmice at ambient temperatures between 24–44°C. Bridled Titmice were less tolerant of heat than Juniper Titmice and had significantly higher rates of metabolic heat production and evaporative water loss, but not body temperature, at ambient temperatures above 40°C. These differences were entirely attributable to the Bridled Titmouse's smaller body size (10 versus 15 g), and the differences vanished when rates were expressed per unit metabolic mass (mass raised to either the 2/3 or 3/4 power). Within the thermoneutral zone, the rate of evaporative water loss (EWL) was significantly lower in Juniper Titmice than Bridled Titmice, even after accounting for the difference in body size. Reduced EWL is characteristic of species from hotter, drier habitats and suggests that physiology plays a role in these species' habitat preferences.

Key words: *Baeolophus ridgwayi*, *Baeolophus wollweberi*, energy metabolism, evaporative water loss, habitat selection, heat stress.

INTRODUCTION

Organisms are inextricably linked to their physical environment through a continuous and reciprocal exchange of matter and energy. Although this exchange is widely regarded as fundamental to the evolution of life histories (Fisher 1930, Bartholomew 1958, Dunham et al. 1989), its importance in influencing species distribution, abundance, and habitat choice remains poorly known (Root 1988a, 1988b). Studies of congeneric species provide mounting evidence for small but significant physiological differences having adaptive value in specific environments (e.g., Hinds and Calder 1973, Hayworth and Weathers 1984, Hinsley et al. 1993). Although these studies suggest that physiology may have a pervasive role in determining species distribution, they are based upon two-species comparisons, which have been criticized on statistical grounds (Garland and Adolph 1994). However, two-species studies remain valuable tools in physiological ecology because they provide unique insights into organismal performance. They can even be used to study adaptation (*sensu* evolutionary processes) by per-

forming meta-analyses on multiple two-species comparisons (Gurevitch et al. 1992). This latter approach is especially useful given that conclusions from multispecies comparisons based upon modern comparative methods may change when the underlying phylogeny is revised (Garland et al. 1991).

In this study, we compare physiological responses to high temperature in two congeners, the Bridled Titmouse (*Baeolophus wollweberi*) and the Juniper Titmouse (*B. ridgwayi*). Bridled Titmice weigh about one-third less than Juniper Titmice (Dunning 1984) and although their evolutionary relationship is unclear, both species presumably descended from a recent common ancestor (Gill et al. 1989). The Bridled Titmouse is typically found in mid-elevation, mesic juniper-pine woods throughout its more southerly distribution (Fig. 1) (Miller et al. 1957, R. Hutto, pers. comm.) and thus it may encounter generally cooler temperatures than those that prevail at the lower elevations preferred by the Juniper Titmouse (Cicero 1996). In the Chiricahua Mountains of southeastern Arizona where both species are common residents, Bridled Titmice generally breed at higher elevations than Juniper Titmice (1,500–2,300 versus 1,350–1,700 m) (E. Greene, pers. observ.) and thus experience markedly cooler temperatures. Even in the zone

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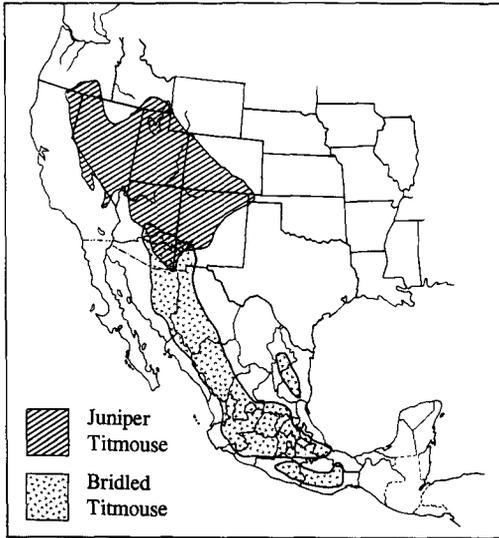


FIGURE 1. Ranges of Bridled Titmouse and Juniper Titmouse in North America (based upon Cicero 1996, and Ficken and Necedal, in press).

of elevational overlap, Bridled Titmouse prefer sites that are more heavily vegetated, moister, and average 3.3°C cooler than those occupied by Juniper Titmouse (Greene and Weathers, unpubl. data). These differences in habitat use were initially attributed to interspecific competition and interspecific territoriality (Dixon 1950, Marshall 1957). More recent studies indicate that direct contest competition does not appear to be important as these species can overlap during the breeding season without aggressive interactions (Gaddis 1987) and they do not respond to heterospecific song during territory establishment or during the breeding season (E. Greene, unpubl. data). In this study, we examine the possibility that differences in the species' physiological tolerance to heat and aridity may underlie their breeding habitat segregation in southeastern Arizona.

METHODS

We studied the thermoregulatory responses of postbreeding Bridled and Juniper Titmouse to temperature during July 1989 at the Southwestern Research Station (hereafter SWRS) located in the Chiricahua Mountains of southeastern Arizona near Portal, Arizona ($32^{\circ}0'N$, $109^{\circ}10'W$). During our study, shade air temperature at SWRS between 09:30–17:30 averaged $32.0 \pm 5.1^{\circ}\text{C}$ (range 26.4 – 39.8°C). Thus the birds we

measured were presumably heat acclimated. They had started to molt, but we did not quantify its intensity.

PHYSIOLOGICAL MEASUREMENTS

We determined metabolic heat production and evaporative heat loss of captive adult Bridled ($n = 11$) and Juniper ($n = 9$) Titmouse by measuring their oxygen consumption ($\dot{V}\text{O}_2$) and evaporative water loss (EWL) at stable air temperatures between 24 and 44°C . We captured birds with mist nets during the morning and transported them to the laboratory at SWRS where they were housed individually in 20-L glass terraria with live meal worms (*Tenebrio*) and wax worms (*Galleria*) provided ad libitum. Both species proved to be tame, readily ate the available food and, for the most part, maintained weight. Bridled Titmouse held in captivity more than one day exhibited a mean mass change of -0.03% (range -4.6 to 8.0%). The comparable value for Juniper Titmouse was -4.5% (range -10.5 to 0.0%).

We measured $\dot{V}\text{O}_2$ and EWL at night (21:00–02:00) on fasting birds (minimum of 4 hr post-prandial) that were resting in the dark. Measurements typically began the day of capture with individual birds being subjected to 2–3 different randomly selected temperatures per night over 1–3 nights. Individual birds were measured on average (mean \pm SD) 4.0 ± 1.8 times (range 1–6) for the Bridled Titmouse and 3.7 ± 1.2 times (range 2–5) for the Juniper Titmouse. The metabolism chamber consisted of a 1.5-L glass jar equipped with a wooden perch, mineral oil trap for urine and feces, a thermocouple for recording air temperature (T_a), and air inlet and outlet ports. Air temperature within the chamber was controlled to within $\pm 0.2^{\circ}\text{C}$ of the desired level by placing the chamber in a dark, temperature-controlled cabinet. The cabinet was equipped with a viewing port and light that allowed us to assess the bird's behavior at the end of the metabolism runs.

To measure metabolism, birds were weighed to the nearest 0.05 g with a calibrated electronic balance and placed in the respirometry chamber at a preset temperature. In most cases we allowed 1 hr to elapse after temperature within the metabolism chamber had stabilized before monitoring $\dot{V}\text{O}_2$ and EWL for at least 5 min. However, for measurements on Bridled Titmouse at $T_a > 41.5^{\circ}\text{C}$, the equilibration time was reduced to

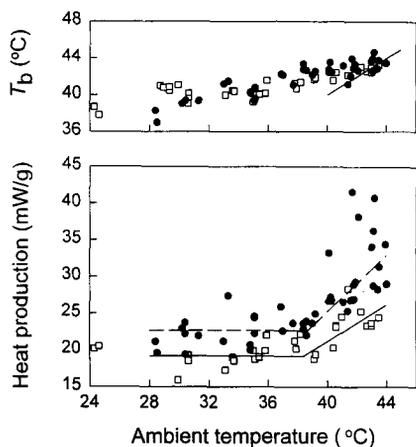


FIGURE 2. Relation of colonic body temperature (above) and metabolic heat production (below) to ambient temperature in Bridled Titmice (solid circles) and Juniper Titmice (open squares). Line of equality depicted in top panel. See text Equations 1–3 for regression statistics.

an average of 47 min (range 33–58 min) because these birds became severely stressed by longer exposures. At the end of each run, the light within the cabinet was turned on and the bird's behavior was simultaneously noted. The bird was then quickly removed from the chamber and its body temperature (T_b) measured within 30 sec by inserting a sheathed 40-gauge thermocouple into the colon such that no temperature drop occurred upon slight withdrawal. The bird was reweighed and the mean of the initial and final mass was used in calculations.

Dry, CO_2 -free air passed through a rotameter (calibrated with a bubble meter, Levy 1964) and into the metabolism chamber at between 0.4 to 0.75 L min^{-1} , which resulted in chamber air attaining 99% equilibrium in 9.2–17.3 min (Lasiewski et al. 1966). The dew point of outlet chamber air was determined to the nearest 0.1°C with a General Eastern model 1100DP dew point hygrometer. Evaporative heat loss was calculated from dew point (Bernstein et al. 1977), assuming that 2.43 kJ of heat were dissipated for each g of water evaporated. Because buildup of chamber humidity due to an animal's evaporative water loss can interfere with evaporative cooling at high temperatures (Lasiewski et al. 1966), we employed higher air-flow rates (mean = 0.63 L min^{-1}) at air temperatures $> 40^\circ\text{C}$. This maintained the chamber water vapor pressure at $0.97 \pm 0.25 \text{ kPa}$ (mean \pm SD) when T_a

$> 40^\circ\text{C}$, which is sufficiently low that evaporation should not have been impeded. (Above 40°C , relative humidity averaged $11.8 \pm 2.9\%$ and was unrelated to T_a ; $r = 0.14$, $P = 0.45$.) The fractional concentration of O_2 in inlet and outlet chamber air (both dry and CO_2 -free) was determined with an Applied Electrochemistry S3-A oxygen analyzer, and $\dot{V}\text{O}_2$ was calculated with Eq. 2 of Hill (1974). We corrected $\dot{V}\text{O}_2$ to STPD and calculated rates of metabolic heat production assuming 20.1 kJ of heat were produced per liter of O_2 consumed by fasted birds. We monitored temperature of the metabolism chamber with a 36-gauge thermocouple suspended about 5 cm above the bird and connected to a Bailey/Sensortek model Bat-12 thermocouple thermometer. Thermocouple calibration (both T_a and T_b) was against a mercury thermometer traceable to the National Bureau of Standards.

DATA ANALYSIS

Because we had only a limited number of birds available for study, we had to make multiple measurements on individuals in order to describe each species' physiological response to temperature. This pseudoreplication (Hurlbert 1984) is a virtually inevitable consequence of working with uncommon organisms. To assure complete sample independence for data plotted in Figures 2–4, we would have had to capture a total of 62 individual titmice, which was not possible at our study site. We accommodated the pseudoreplication by using repeated-measures

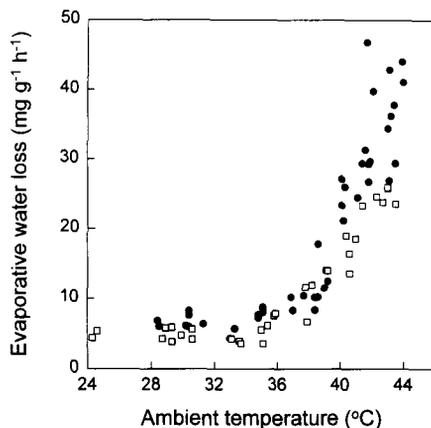


FIGURE 3. Relation of evaporative water loss to ambient temperature in Bridled Titmice (solid circles) and Juniper Titmice (open squares).

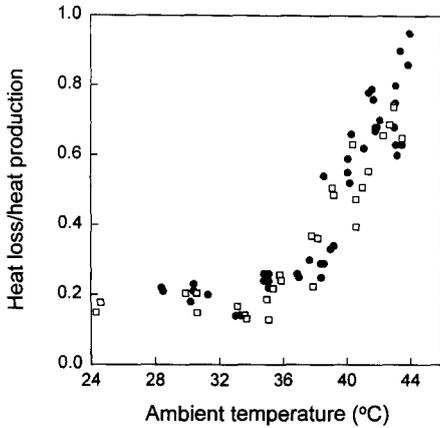


FIGURE 4. Ratio of heat lost by evaporation to metabolic heat production in Bridled Titmice (solid circles) and Juniper Titmice (open squares).

ANCOVA (SAS 1992) to compare least squares regressions describing the species' physiological responses to high temperature. These analyses revealed individual birds to be statistically equivalent (probabilities for individual effects were 0.14–0.69). Thus, no significant bias was introduced by repeatedly sampling the same individuals. Means reported for various parameters were calculated using average values for individual birds.

Comparing rates of metabolic heat production and evaporative water loss of species that differ in body size is somewhat problematic. Traditionally, mass independent values have been calculated by dividing physiological rates by body mass raised to the 0.75 power (Kleiber 1947), although an argument can be made for using an exponent of 0.67 (Heusner 1982). We avoided this controversy by adjusting rates using both exponents. The results were statistically equivalent.

Throughout the text, n denotes the number of individuals and N the number of measurements. For means, N and n are identical. Means are reported \pm SD.

RESULTS

BEHAVIORAL RESPONSES TO HIGH TEMPERATURE

Most individuals of both species were asleep at the end of metabolic runs conducted below 38°C. Birds slept either in an upright posture or with their heads tucked into their scapular feathers. Between 38–40.3°C, nearly all individuals

of both species were awake, but with their beaks closed and no visible signs of panting. At slightly higher temperatures the two species' responses diverged. At $T_a > 40.3^\circ\text{C}$, all Bridled Titmice were awake and panting vigorously with their wings held away from their bodies. Juniper Titmice, however, did not begin to pant until T_a exceeded 40.6°C, and even then they never drooped their wings as did Bridled Titmice. These behavioral observations are consistent with our physiological data and indicate that Bridled Titmice are more severely stressed by temperatures above 40°C than Juniper Titmice.

HEAT PRODUCTION

Metabolic heat production (\dot{H}_m) of most bird species is independent of T_a within the thermoneutral zone (TNZ) and increases linearly with T_a above the upper critical temperature (T_{uc}) (Weathers 1981). Both titmice species fit this pattern and we used linear relations to describe their \dot{H}_m versus T_a . We attempted to identify each species' T_{uc} objectively using a dual regression procedure similar to that of Yeager and Ultsch (1989). This proved unsuccessful, however, because regressions for both species at higher T_a s had negative slopes. Based upon the birds' behavior (see below) and visual inspection of the data (Fig. 2), the T_{uc} of both species appears to lie between 38–40°C. Accordingly, we fit regressions to data above 38°C, using weighted regression to compensate for the Bridled Titmouse's heteroscedastic data (Neter et al. 1990). The analyses yielded the following relations:

Bridled Titmouse:

$$\dot{H}_m (\text{mW g}^{-1}) = -53.2 + 2.04T_a \quad (1)$$

$$(r^2 = 0.420, s_{yx} = 4.23, s_b = 0.370, n = 11, N = 26)$$

Juniper Titmouse:

$$\dot{H}_m (\text{mW g}^{-1}) = -28.8 + 1.25T_a \quad (2)$$

$$(r^2 = 0.327, s_{yx} = 2.21, s_b = 0.582, n = 7, N = 12)$$

These equations differ neither in intercept (ANCOVA $F_{1,19} = 1.20, P > 0.2$) nor slope ($F_{1,19} = 1.78, P > 0.2$). However, lack of significant difference is attributable to the convergence of the data sets at lower temperatures. Above 40°C, mean \dot{H}_m of the two species is significantly different (Table 1). There is no significant difference in mean \dot{H}_m above 40°C, however, when

TABLE 1. Mean (SD) of measurements made at ambient temperatures exceeding 40°C for 11 Bridled and 6–7 Juniper Titmice.

Variable	Bridled Titmouse	Juniper Titmouse	t^a	P
Ambient temperature, °C	41.4 (0.4)	41.9 (0.5)	2.05	0.06
Body temperature, °C	43.1 (0.4)	42.7 (0.4)	2.05	0.06
Heat production, mW g ⁻¹	29.8 (4.4)	24.4 (1.9)	2.88	0.01
Heat production, mW g ^{-3/4}	53.0 (7.9)	47.8 (3.2)	1.56	0.14
Heat production, mW g ^{-2/3}	63.7 (9.9)	57.9 (3.8)	0.99	0.34
Evaporative water loss, mg g ⁻¹ hr ⁻¹	28.3 (7.1)	21.8 (2.3)	2.22	0.04
Evaporative water loss, mg g ^{-3/4} hr ⁻¹	50.4 (12.7)	42.7 (4.4)	1.19	0.16
Evaporative water loss, mg g ^{-2/3} hr ⁻¹	61.0 (15.3)	53.4 (5.5)	1.19	0.25
Heat loss/heat production	0.60 (0.09)	0.59 (0.10)	0.23	0.80

^a Two-tailed test, df = 15 or 16.

\dot{H}_m is expressed per unit metabolic mass, i.e., body mass raised to either the 2/3 or the 3/4 power (Table 1).

We calculated basal metabolic rate (BMR, mW⁻¹g) at thermoneutral temperatures (24–38°C) using mean values for individual birds. BMR was significantly higher in Bridled than in Juniper Titmice (Table 1), but the difference in BMR was insignificant when the difference in the species' body mass was taken into account (Table 2).

BODY TEMPERATURE

The body temperature (T_b) of both species increased linearly with ambient temperature (Fig. 2). Equations fit to data above 32°C for each species differed neither in slope ($F_{1,40} = 0.86$, $P > 0.3$) nor intercept ($F_{1,40} = 0.51$, $P > 0.4$). The common equation for pooled data above 32°C is:

$$T_b = 29.6 + 0.32T_a \quad (3)$$

$$(r^2 = 0.767, s_{yx} = 0.72, s_b = 0.023, n = 20,$$

$$N = 62)$$

Mean T_b calculated for measurements above 40°C also did not differ between species (Table 1).

EVAPORATIVE WATER LOSS

Mean evaporative water loss (EWL) measured at $T_{a,s}$ between 24–35°C was significantly higher in Bridled Titmice and the difference persisted when EWL was expressed on a mass independent basis (Table 2). Above 32°C, EWL of both species increased exponentially (Fig. 3), as is typical of homeotherms. At $T_{a,s}$ above 40°C, the mean EWL of Bridled Titmice was significantly higher than that of Juniper Titmice, but this difference vanished when EWL was expressed on a mass-independent basis (Table 1).

Regressions of \log_{10} mg g⁻¹ hr⁻¹ EWL versus T_a for data at $T_{a,s} > 32^\circ\text{C}$ did not differ significantly for the two species either in slope ($F_{1,38} = 0.32$, $P > 0.5$) or intercept ($F_{1,38} = 0.90$, $P > 0.3$). The common regression for the pooled data is:

$$\log_{10} \text{ EWL} = -2.4076 + 0.091T_a \quad (4)$$

$$(r^2 = 0.881, \log_{10} s_{yx} = 0.1117, s_b = 0.004,$$

TABLE 2. Mean (SD) body mass, basal metabolic rate, and evaporative water loss measured within the thermoneutral zone for 9 Bridled and 7 Juniper Titmice.

Variable	Bridled Titmouse	Juniper Titmouse	t^a	P
Body mass, g	10.0 (0.8)	14.8 (1.0)	10.52	0.001
Basal metabolic rate, mW g ⁻¹	22.4 (1.9)	19.3 (0.7)	3.95	0.002
Basal metabolic rate, mW g ^{-3/4}	39.9 (3.9)	37.8 (1.2)	1.27	0.22
Basal metabolic rate, mW g ^{-2/3}	47.9 (4.9)	47.3 (1.5)	0.30	0.76
Evaporative water loss, mg g ⁻¹ hr ⁻¹	7.4 (0.7)	5.2 (1.2)	4.26	0.001
Evaporative water loss, mg g ^{-3/4} hr ⁻¹	13.1 (1.3)	10.2 (2.3)	2.95	0.01
Evaporative water loss, mg g ^{-2/3} hr ⁻¹	15.8 (1.6)	12.8 (2.9)	2.50	0.02

^a Two-tailed test, df = 14.

$$n = 19, N = 60)$$

EVAPORATIVE HEAT LOSS

The ratio of heat lost by evaporation to metabolic heat production (\dot{H}_e/\dot{H}_m) provides an overall index of the response to heat. As is typical of birds generally, the \dot{H}_e/\dot{H}_m ratio of titmice increased exponentially at higher temperatures (Fig. 4). At $T_a > 32^\circ\text{C}$, there was no significant difference between the two species in either intercept ($F_{1,37} = 0.38, P > 0.5$) or slope ($F_{1,37} = 0.53, P > 0.5$). The combined data can be described as:

$$\log_{10} \dot{H}_e/\dot{H}_m = -3.2078 + 0.072T_a \quad (5)$$

$$(r^2 = 0.894, \log_{10} s_{yx} = 0.0824, s_b = 0.003,$$

$$n = 19, N = 60)$$

At T_a s above 40°C , the mean \dot{H}_e/\dot{H}_m ratio of both species was identical (Table 1).

DISCUSSION

We hypothesized that because Bridled Titmice prefer cooler habitats than those occupied by Juniper Titmice, they would be less heat tolerant. Our data support this hypothesis. Bridled Titmice exhibit greater increases in resting metabolic rate and evaporative water loss at ambient temperatures above 40°C than do Juniper Titmice, and behaviorally they appear more stressed by high temperature. Although significant, these differences are entirely attributable to the Bridled Titmouse's smaller body size. We found no evidence which would suggest that Juniper Titmice are better adapted to high temperature than Bridled Titmice, except by virtue of their larger size. Apparently, the high temperatures encountered by these species in southeastern Arizona can be accommodated fully by generic parid physiology. In contrast, our data suggest that aridity may help shape these species' microhabitat preferences.

Aridity is a significant selective force in the evolution of avian physiology as both basal metabolic rate (BMR) and evaporative water loss (EWL) within the thermoneutral zone are relatively low in desert species (Dawson and Bennett 1973, Dawson 1984, Williams 1996). Neither of the titmice we studied is a desert species and both had average or above average BMR and EWL. BMR of Bridled and Juniper Titmice averaged 116 and 119%, respectively, of that predicted allometrically (Aschoff and Pohl

1970), and EWL averaged 133 and 102%, respectively, of that predicted allometrically (Williams 1996). When the species' difference in body size is accounted for, however, BMRs were statistically equivalent, whereas EWL of Juniper Titmice averaged 20% lower than that of Bridled Titmice (Table 1). Juniper Titmice in Arizona's Chiricahua Mountains occupy habitats that are more xeric than those preferred by Bridled Titmice and this is reflected in their significantly lower EWL. Whether this is an evolved response is unclear, but it implies that for these species moisture is more important than temperature in establishing habitat preferences.

At high ambient temperatures, resting metabolic rate (RMR) increased more slowly in both species than expected for birds of their size. The slope of the line relating RMR to ambient temperature (i.e., the coefficient of heat strain, h_s) in Bridled Titmice averaged 69% of that predicted allometrically (Weathers 1981) and in Juniper Titmice only 50% of that predicted. This probably reflects the fact that the titmice were heat-acclimated prior to study, whereas the species in Weathers' (1981) allometric analysis were not. Heat acclimation reduces h_s (DeShazer et al. 1970, Marder et al. 1989), and measurements of titmice unacclimated to heat are needed to ascertain if these species' responses are unusual. Regardless of whether the titmice's low h_s is an evolved response, it has (general sense) adaptive value. The increase in RMR which occurs at temperatures above the upper critical temperature has two principal sources: the muscular effort involved in panting and elevated body temperature. Because metabolic heat production exacerbates heat stress by increasing the total heat load, reducing its magnitude may have adaptive value (Weathers 1981). The value of a relatively low rate of increase in RMR is apparent as Bridled Titmice must increase EWL at high temperatures much more than do Juniper Titmice in order to dissipate their extra heat production. Thus compared with Bridled Titmice, Juniper Titmice have the dual advantage of expending both less energy and water at high temperatures. Although these differences are entirely attributable to the Juniper Titmouse's larger size, they improve this species' physiological performance in its dryer and somewhat hotter preferred habitat.

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LITERATURE CITED

- ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 111:38-47.
- BARTHOLOMEW, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates, p. 81-95. *In* C. L. Hubbs [ed.], *Zoogeography*. Am. Assoc. Adv. Sci., Washington, DC.
- BERNSTEIN, M. H., D. M. HUDSON, J. M. STEARNS, AND R. W. HOYT. 1977. Measurement of evaporative water loss in small animals by dew-point hygrometry. *J. Appl. Physiol.: Resp., Environ., and Exercise Physiol.* 43:382-385.
- CICERO, C. 1996. Sibling species of titmice in the *Baeolophus inornatus* complex (Aves: Paridae). *Univ. Calif. Publ. Zool.* 128:1-127.
- DAWSON, W. R. 1984. Physiological studies of desert birds: present and future considerations. *J. Arid Environ.* 7:133-155.
- DAWSON, W. R., AND A. F. BENNETT. 1973. Roles of metabolic level and temperature regulation in the adjustment of western plumed pigeons (*Lophophaps ferruginea*) to desert conditions. *Comp. Biochem. Physiol.* 44A:249-266.
- DESHAZER, J. A., K. A. JORDON, AND C. W. SUGGS. 1970. Effect of acclimation on partitioning of heat loss by the laying hen. *Trans. Am. Soc. Agr. Eng.* 13:82-84.
- DIXON, K. L. 1950. Notes on the ecological distribution of the Juniper and Bridled Titmice in Arizona. *Condor* 52:140-141.
- DUNHAM, A. E., B. W. GRANT, AND K. L. OVERALL. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol. Zool.* 62:335-355.
- DUNNING, J. B. 1984. Body weights of 686 species of North American birds. *Western Bird Banding Assoc. Monogr.* 1. Eldon Publishing, Cave Creek, AZ.
- FICKEN, M. S., AND J. NECEDAL. *In press*. Bridled Titmouse (*Parus wollweberi*). *In* A. Poole and F. Gill [eds.], *The birds of North America*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- FISHER, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.
- GADDIS, P. K. 1987. Social interactions and habitat overlap between Juniper and Bridled Titmice. *Southwestern Nat.* 32:197-202.
- GARLAND, T., JR., AND S. C. ADOLPH. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* 67:797-828.
- GARLAND, T., JR., R. B. HUEY, AND A. F. BENNETT. 1991. Phylogeny and thermal physiology in lizards: a reanalysis. *Evolution* 45:1969-1975.
- GILL, F. B., D. H. FUNK, AND B. SILVERIN. 1989. Protein relationships among titmice (*Baeolophus*). *Wilson Bull.* 10:182-197.
- GUREVITCH, J. L., L. L. MORROW, A. WALLACE, AND J. S. WALSH. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* 140:539-572.
- HAYWORTH, A. M., AND W. W. WEATHERS. 1984. Temperature regulation and climatic adaptation in Black-billed and Yellow-billed Magpies. *Condor* 86:19-26.
- HEUSNER, A. A. 1982. Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? *Resp. Physiol.* 48:1-12.
- HILL, R. W. 1974. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. Appl. Physiol.* 33:261-263.
- HINDS, D. S., AND W. A. CALDER. 1973. Temperature regulation of the pyrrhuloxia and the Arizona cardinal. *Physiol. Zool.* 46:55-71.
- HINSLEY, S. A., P. N. FERNS, D. H. THOMAS, AND B. PINSHOW. 1993. Black-bellied Sandgrouse (*Pterocles orientalis*) and Pin-Tailed Sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiol. Zool.* 66:20-42.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field studies. *Ecol. Monogr.* 54:187-211.
- KLEIBER, M. 1947. Body size and metabolic rate. *Physiol. Rev.* 27:511-541.
- LASIEWSKI, R. C., A. L. ACOSTA, AND M. H. BERNSTEIN. 1966. Evaporative water loss in birds I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* 19:445-457.
- LEVY, A. 1964. The accuracy of the bubble meter method for gas flow measurements. *J. Scientific Instrum.* 41:449-453.
- MARDER, J., Y. ARIELI, AND J. BEN-ASHER. 1989. Defense strategies against environmental heat stress in birds. *Israel J. Zool.* 36:61-75.
- MARSHALL, J. T. 1957. Birds of pine-juniper woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna* 32.
- MILLER, A. H., H. FRIEDMAN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico, Part II. *Pacific Coast Avifauna* 33.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. *Applied linear statistical models*, 3rd ed. Irwin, Homewood, IL.
- ROOT, T. 1988a. Energy constraints on avian distributions and abundance. *Ecology* 69:330-339.
- ROOT, T. 1988b. Environmental factors associated with avian distributional boundaries. *J. Biogeography* 15:489-505.

- SAS INSTITUTE. 1992. SAS user's guide: statistics, Version 6.08. SAS Institute, Inc., Cary, NC.
- WEATHERS, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiol. Zool.* 54:345-361.
- WILLIAMS, J. B. 1996. A phylogenetic perspective of evaporative water loss in birds. *Auk* 113:457-472.
- YEAGER, D. P., AND G. R. ULTSCH. 1989. Physiological regulation and conformation: a BASIC program for the determination of critical points. *Physiol. Zool.* 62: 888-907.