

THE ENERGETIC SIGNIFICANCE OF HUDDLING BEHAVIOR IN COMMON BUSHTITS (*PSALTRIPARUS MINIMUS*)

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ABSTRACT.—The daily energetics of a very small passerine, the Common Bushtit (*Psaltriparus minimus*), were examined by measuring 24-h existence metabolism, activity, and nocturnal metabolic rate. Bushtits consumed 80% of their body mass (5.5 g) in mealworms per day at 20°C. A lower energy intake than this resulted in marked weight loss (0.5–0.8 g), slight hypothermia upon exposure to 10°C for 4 h ($T_b = 38.6^\circ\text{C}$), and a higher diurnal activity level than well-fed birds. Birds housed in pairs or larger groups spent portions of the day perching together and spent all of the nocturnal period huddled in a tight mass. These birds were also less active diurnally than isolated individuals and had lower nocturnal metabolism; the metabolism of paired birds was 79% of that of single individuals at 20°C. The energy savings gained by the gregarious nature of this diminutive species, reflected by the diminished cost to an individual of being a member of a flock, may be integral to its survival during periods of food scarcity or inclement weather. Received 10 August 1981, accepted 12 December 1981.

THE North American Common Bushtit [*Psaltriparus minimus* (Paridae)] is one of the smallest passerine species (5.5 g) in the world. It ranges from coastal southern British Columbia to northern México and may encounter subfreezing temperatures on winter nights in parts of its range (Bent 1946, Smith 1972). Bushtits' diminutive size and consequent high rate of heat loss make the maintenance of a constant body temperature on cold nights potentially energetically expensive. Some small (<15 g) parid species, such as the Black-capped Chickadee (*Parus atricapillus*) and Willow and Siberian tits (*P. montanus* and *P. cinctus*), conserve energy at low temperatures by nocturnal hypothermia (Haftorn 1972, Chaplin 1976, Grossman and West 1977). Other species, such as Long-tailed Tits (*Aegithalos caudatus*) and bushtits, which are ecological equivalents on different continents (Austin and Smith 1972), huddle together when exposed to cold (Miller 1921, Bent 1946, Lack and Lack 1958, Smith 1972). Bushtits are extremely gregarious during the nonbreeding season. They may travel in flocks of 20–70 birds in the daytime, and all enter the same tree to roost at night (Miller

1921, Bent 1946). Such gregarious behavior may be a strategy for ameliorating the roost microclimate. Thus, for bushtits, at least part of the solution to the problem of excessive heat loss in the cold may be found in their social behavior. The purposes of this study were: (1) to determine the energetic significance of the huddling behavior in bushtits, and (2) to measure the extent to which bushtits use nocturnal hypothermia or reduce their activity to limit their energy expenditures.

METHODS

Six bushtits were captured in mist nets during November 1974 and six more in June 1975 in a sycamore-oak grove outside the Moore Laboratory of Zoology at Occidental College, Los Angeles, California (34° latitude). They were weighed immediately after capture ($\bar{x} = 5.54 \text{ g} \pm 0.07 \text{ SE}$ in November and $\bar{x} = 5.51 \text{ g} \pm 0.04 \text{ SE}$ in June), color-banded for individual recognition, and placed in a 0.5-m³ wire screen cage supplied with perches and with cedar shavings on the floor. The birds were fed mealworm (*Tenebrio molitor*) larvae and pupae *ad libitum* and were supplied with drinking water (which they were never observed to use) from a dish on the cage floor. The cage was placed in a walk-in environmental chamber regulated at a constant $20 \pm 2^\circ\text{C}$ and a 12L:12D photoperiod. The chamber had a one-way view port through which the birds were observed at intervals during the day and at night with the aid of a low intensity red bulb near the cage.

In order to calculate the energy expenditures and

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energy intake of single and grouped individuals, I measured basal metabolism and cloacal body temperatures at night over a 10–30°C temperature range, amount of food eaten and feces produced per day, amount of activity during the light period, and body weight changes over a 24-h period. Nocturnal resting metabolism was measured by an open-flow system, utilizing a Gelman pump to push air through a column of drierite to the metabolism chamber (500 cc/min for one bird in the chamber, 700 cc/min for two birds). A 4-l double-lipped paint can with a wire screen floor over a layer of mineral oil was used as the metabolic chamber. Air exiting the chamber passed through a column of a drierite-ascarite mix (3:1) before entering the sample cell of a Beckman E-2 paramagnetic oxygen analyzer at 100 cc/min. Birds were taken from their cage at the beginning of the nocturnal period, weighed, and placed individually or in pairs in the metabolic chamber, which was then placed in a temperature-controlled incubator set at one of the test temperatures. Incubator and metabolic-chamber temperatures were monitored over the next 3–4 h with a YSI telethermometer. Readings of oxygen content of exit air were taken at 30-min intervals for the first 2–3 h of the experiment and at 10-min intervals during the last hour. Birds were then removed from the chamber, and cloacal or esophageal temperature was taken as quickly as possible (30–60 s) by inserting a 40-gauge YSI thermistor probe to a standard depth (0.7 cm into the cloaca or 2.0 cm into the esophagus). The bird was weighed again before being returned to the cage. The highest sustained reading of oxygen concentration of exit air (corrected to STP and for N₂ expansion after CO₂ and H₂O vapor removal) was used to calculate oxygen consumption in cc O₂ · g⁻¹ · h⁻¹ according to the appropriate formulae in Depocas and Hart (1957).

Activity of single and grouped birds ($n = 5$) was recorded continuously for 24 h at 20°C in a 0.25-m³ cage via a treadle-activated microswitch connected to an Esterline-Angus event recorder. When inactive, the birds tended to perch on the treadle rather than the side of the cage, causing a downward deflection in the record. Thus, one could calculate the number of minutes spent at rest from the activity record. The sum of minutes of pen markings (treadle movement) divided by the total 720-min light period gave the percentage of activity per day.

Diurnal metabolism was estimated from the activity record by using the assumptions that diurnal metabolism of resting birds is approximately 20% higher than nocturnal basal metabolism (Aschoff and Pohl 1970) and that diurnal metabolism of active birds is 1.70–2.0 times the nocturnal basal metabolism at a specific temperature (Brenner 1965, Hainsworth et al. 1977, Beuchat et al. 1979). *Bushtits* were very active throughout the day, but their activity consisted almost entirely of short-distance hops from one side of the cage to the other rather than flight or

hovering attempts. Active metabolism was estimated at 2.0 times BMR, because the birds were hopping around the cage about 50–75% of the time. In addition, it was assumed that birds were usually in an absorptive condition during the light period, because they were fed at frequent intervals and thus probably had an R.Q. of 1.0. Hence, the energy equivalent of metabolic expenditure during this period would be 21.31 joules/cc O₂ (Gordon 1977). Diurnal metabolic expenditure was then calculated as follows:

Diurnal Expenditure = Energy expended in activity + Energy expended at rest

$$\text{D.E. (joules)} = [\text{activity}(h) \cdot (MR_{T_a} \cdot 2.0) + \text{rest}(h) \cdot (MR_{T_a} \cdot 1.2)] \cdot 21.31.$$

Nocturnal metabolism was calculated from the MR_{T_a} regression curve as follows:

$$\text{Nocturnal Expenditure (joules)} = MR_{T_a} \cdot 12 \text{ h} \cdot 21.31.$$

Adding the diurnal and nocturnal expenditures then gives the total predicted daily expenditure at a particular temperature.

Ingestion and egestion of single birds were measured concurrently with activity and converted to energetic terms to give an estimate of daily energy expenditure by measurement of existence metabolism. Approximately 1.5 g of medium-sized mealworms were presented to a bird at regular intervals four times a day, and the feeding periods were noted on the activity record. Mealworms were weighed to the nearest 0.1 g before each feeding, and all mealworms and remnants remaining from the previous feeding were also weighed. The bird was weighed at the beginning of the feeding trial (0800) and again 24 h later. A large sheet of glassine paper placed in the bottom of the cage permitted easy removal of feces, which generally accumulated directly under the treadle perch. After removing feeding remnants (heads and exoskeletons), I placed the feces in a vacuum drying oven at 45°C and weighed them to the nearest 0.1 g after 24 h. The dessicating environment and small mass involved (<0.5 g) insured that the samples dried very rapidly and that there was no mass lost to bacterial decay.

The energy ingested and that remaining in the feces were determined in the following way. Three samples of 1.0 g of mealworms were weighed, dried to a constant mass, reweighed, and then ignited in a Parr adiabatic bomb calorimeter to determine the energy value of mealworms. The total mass of ingested mealworms multiplied by their percentage dry weight (32.3) and energy equivalent (25.87 kJ/g dry weight) yielded the total ingested energy. The total dry mass of feces multiplied by their energy equivalent (13.98–17.92 kJ/g dry weight) yielded the total egested energy. The difference of ingested and

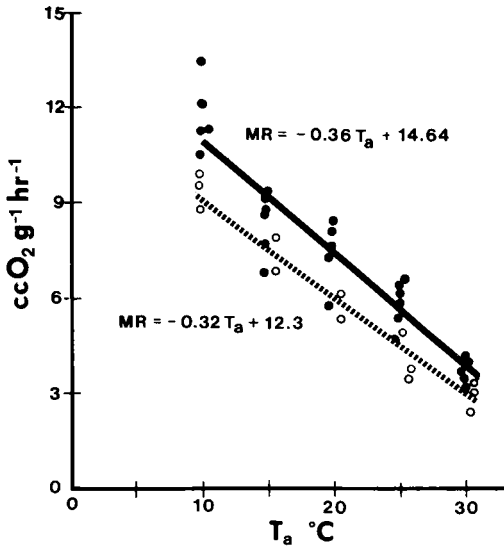


Fig. 1. Relationship of nocturnal metabolism, measured as oxygen consumption, and temperature in single (●) and paired (○) bushtits. The standard error of the regression ($s_{y,x}$) for the single bushtits was 0.18 and for paired bushtits was 0.11.

egested energy, metabolized energy, was compared with the predicted diurnal metabolic expenditure calculated as described above. If the results of these two calculations were similar, one could then examine the relative importance of each of the components of daily expenditure to the bird's energy budget and compare costs of daily maintenance for single, paired, or multiple-caged individuals.

RESULTS

Nocturnal metabolism.—The lowest rate of oxygen consumption of bushtits was $3.96 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at 30°C , which closely approximates the resting standard metabolism predicted for a 5.5-g bird ($4.14 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) by the Aschoff-Pohl metabolism-weight regression equation (Aschoff and Pohl 1970). It was assumed that metabolism at this temperature represented the basal rate, as 30°C is probably in the bushtit's thermoneutral zone based on similar findings in other species of this size living in roughly the same climate [e.g. Verdin (*Auriparus flaviceps*), Goldstein 1974; Anna's Hummingbird (*Calypte anna*), Lasiewski 1963].

There was no significant difference between the basal rates of metabolism or slopes of the $\text{MR}-T_a$ regression of birds captured in Novem-

ber and June. This might be expected, because the average monthly temperature in June was 18.9°C and that for November was 16.8°C (NOAA 1974–1975). Thus, the data were combined to give one linear regression of metabolism on temperature: $M = 0.36T_a + 14.64$. This regression extrapolates to 40.7°C at zero metabolism, which is approximately the body temperature measured after birds were exposed to 25 and 30°C : $\bar{x} = 40.2 \pm 0.8^\circ\text{C}$ SE ($n = 7$). Body temperature of bushtits exposed to 10°C for 4 h averaged $38.6 \pm 1.6^\circ\text{C}$ SE ($n = 8$) and was not significantly lower than that of birds at thermoneutrality.

Oxygen consumption of two bushtits in the same chamber was markedly lower than that of single bushtits, when compared on a per gram basis (Fig. 1). Attempts to measure metabolism of more than two birds in the same chamber always resulted in highly spurious results. The birds never settled down and certainly did not huddle, even after 3–4 h. At 10°C the metabolic rate of paired birds was significantly lower than that of isolated birds ($P < 0.05$, Mann-Whitney test). There were no significant differences at higher temperatures. The metabolism of a pair of birds as a function of ambient temperature was described by the equation: $M = 0.32T_a + 12.30$. Although the slope of the pair regression was less than that of single birds, the two regression lines were not significantly different by a t -test of slopes. Nevertheless, these results suggest that chemical thermogenesis (heat production) of a particular individual is less at all ambient temperatures when that individual is a member of a group than when it is alone. Thus, some degree of energy conservation is obtained by huddling.

Diurnal metabolism.—Bushtits, like their parid relatives chickadees and titmice, are constantly active in their natural environment. In captivity a bushtit kept singly in a cage large enough to permit flight made continuous short-distance hops around the cage, usually calling continuously as it moved. Only after feeding did the birds perch for any length of time. As a consequence of this behavior, five singly caged bushtits were active an average of $55\% (\pm 8\% \text{ SE})$ of the light period. Adding other birds to the cage seemed to calm this fervent searching behavior and reduce the activity time, even though the likelihood of acti-

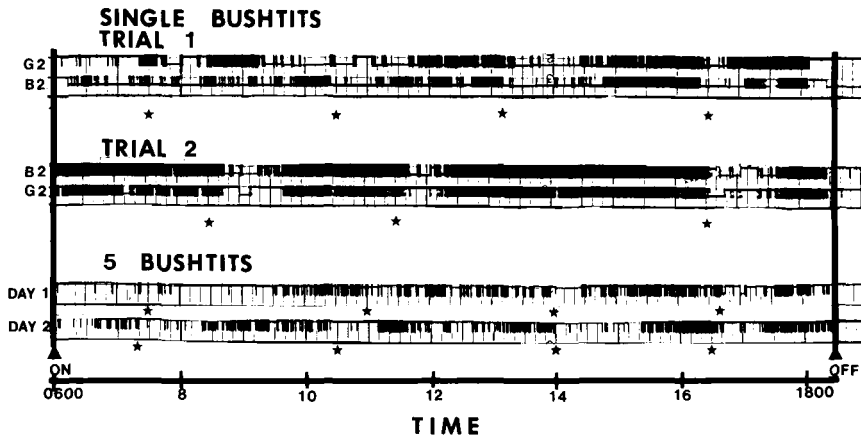


Fig. 2. Daily activity records of singly-housed and grouped bushtits. * indicates feeding times. ▲ indicates times of lights on and off in the environmental chamber. In Trial 1 for single bushtits, both individuals (G2 and B2) were given enough food for them to maintain their weight. In Trial 2 for the same birds, one feeding period was skipped, and the daily intake was inadequate to maintain weight.

vating the perch microswitch was increased with multiple birds per cage. Five birds in a cage together activated the perch only 43.5% ± 5.3 SE of the daytime (mean of 4 continuous days of recording). The most notable decrease in activity in grouped birds took place after feeding. Whereas single birds perched for 10–20 min after eating most of the mealworms introduced, grouped birds often perched for 30–50 min, especially during the middle of the light period (1200) (Fig. 2). In fact, even at the moderate temperature of the feeding experiment (20°C), the birds sat close together on the perch, and some exhibited a typical sleeping posture.

Daily energetics.—Bushtits kept at a constant 20°C consumed a mean of 35.17 kJ ± 1.26 SE mealworms per day and metabolized 31.40 kJ ± 1.26 SE of that intake. The six birds used

to calculate these data had a mean mass of 5.5 g and maintained that mass ±0.2 g over the next 24 h. The calculated daily metabolic expenditure for a single 5.5-g bird, 26.5 kJ (Table 1), based on the assumptions given in the methods, was less than the energy metabolized. Thus, the estimated metabolic expenditure may be too conservative but is still useful to predict the energetic consequences of temperature, food supply, or amount of activity on the individual's energy balance.

In four feeding trials insufficient food was (inadvertently) presented during the light period, and the birds lost 0.5–0.8 g. In two cases, the same birds maintained their weight during a feeding experiment 3–4 days earlier, and this serendipitous experiment provided an interesting comparison with the normal energy balance situation (Table 2). As a group, the four

TABLE 1. Estimated daily energy expenditures of birds housed singly vs. in pairs for individuals weighing 5.5 g kept under 12L:12D and 20°C conditions. See text for explanation of calculations.

	$M_{nocturnal}$		$M_{diurnal}$				Total energy expended (kJ)
	O_2 consumption (cc $O_2 \cdot g^{-1} \cdot h^{-1}$)	kJ	$M_{activity}$		$M_{inactivity}$		
			Time active (h)	kJ	Time inactive (h)	kJ	
Singly	7.44	9.88	6.50	11.05	5.50	5.61	26.50
Paired	5.90	7.83	5.50	7.41	6.50	5.32	20.56

TABLE 2. Metabolized energy compared with estimated daily expenditure for two birds fed an amount of food adequate to maintain weight (± 0.1 g) in one trial and an inadequate amount of food in another trial.

	Energy intake in kJ (measured)			Energy expenditure in kJ (calculated)			
	Food	Feces + urine	Metabolized	M_{noc}	M_{act}	M_{rest}	Total
Adequate food							
B-2 (5.3-5.2)	24.45	3.10	21.35	8.54	9.29	5.07	22.90
G-2 (5.7-5.8)	38.27	4.48	33.79	9.29	10.17	5.27	24.73
Inadequate food							
B-2 (5.5-5.0)	20.31	2.68	17.63	8.50	14.15	2.14	25.04
G-2 (5.8-5.0)	20.31	2.93	17.38	8.75	15.03	1.93	25.71

birds ingested and metabolized less energy than they required for daily maintenance, and some of them also expended more energy diurnally than those individuals fed an adequate amount by having a higher percentage of activity per day (79% vs. 55%) (Fig. 2). These two factors alone probably accounted for the large energy deficit and marked weight loss in these birds. The extent to which these individuals used nocturnal hypothermia and decreased metabolism to balance their energy budget was not tested. Body temperatures of birds exposed to 10°C, however, even of individuals weighing less than normal, were only 2-3°C lower than daytime body temperatures. Hence, decreased nocturnal metabolism seems to be a less important avenue of energy conservation in bushtits, at least during short-term cold exposure.

DISCUSSION

Communal roosting or decreased individual distance (*sensu* Hediger 1950) is not uncommon among small birds, especially during unseasonably cold weather (Löhrl 1955, Koskimies 1961, Grubb 1973, White et al. 1975, Meservy and Kraus 1976, Beal 1978, McNicholl 1979). The physiological, especially the energetic, advantage of this behavior, however, has been demonstrated only for Starlings (*Sturnus vulgaris*; Brenner 1965), which, at a body weight of 70-80 g, should be considered large passerines. Communal roosting enables bushtits to reduce both their nocturnal maintenance cost and their diurnal inactive cost. The nocturnal cost at 20°C for a member of a pair of bushtits is 79% of that of a single bird, and,

presumably, the cost further decreases as the rate of heat loss decreases in larger groups of huddling individuals. The diurnal costs for a member of a group might also be reduced below those of a single individual, perhaps by a reduction in activity time and by daytime huddling behavior. Although a single individual may be able to balance its energy budget under the conditions of adequate food or moderate temperatures used in this study, the real energetic advantage of this contact social behavior is to increase the survival time during periods of inclement or cold weather or low food availability. The two bushtits fed an inadequate amount of food (Table 2) metabolized only 17.6 and 17.4 kJ/day and lost 0.5-0.8 g but could have almost maintained their weight during that period by having just one other bird in the cage. Their expenditures would then have been approximately 20.6 kJ/day (Table 1), compared to the 25.0 and 25.7 kJ/day estimated from their daily activity record. Brenner (1965) found that the survival time of singly housed Starlings at 4°C was extended from 1 day to 3 by placing them in groups of four.

The gregarious behavior of a flock of bushtits is important not only for nocturnal energy conservation but perhaps for reduction of daytime expenditures and maximization of energy acquisition as well. Search intensity for food by an individual could be reduced by its being a member of a flock the individuals of which communicate information about the location and density of resources and the presence of predators (Murton 1971). Flock foraging is the typical mode of feeding among parid species who are often the leaders of mixed insectivore-

species flocks (Gibb 1954; Morse 1970, 1978; Austin and Smith 1972). The constancy in size of bushtit flocks throughout the nonbreeding season, however, and the high degree of relatedness of their members are unusual among the Paridae, and Ervin (1977) suggests that these characteristics strengthen flock cohesiveness and may be valuable in the exploitation of locally abundant but patchy resources. It has been demonstrated that flock foraging enables individuals to forage more efficiently, i.e. greater energy is consumed for the cost necessary to obtain it, and less energy is devoted to detection of predators (Murton 1971, Cody 1974, Powell 1974). This may mean that less energy is expended daily, and thus, in turn, less food is required for maintenance. The energetic savings obtained by the social nature of this species, in fact, reinforces their sociality. The diminished cost of being a member of a flock translates into the support of more individuals by the resources in a given area. Thus, there is positive feedback for maintenance of a flock that roosts and forages together to minimize their individual costs. White et al. (1975) described a similar response in Sociable Weavers (*Philetairus socius*) in their winter desert environment.

The necessity of such a social strategy to a bird as small as the bushtit is obvious when one realizes that a single individual must consume about 80% of its body weight daily in energy-rich insects just to maintain itself at 20°C and probably close to or greater than 100% of its body weight at lower temperatures. The burden on food acquisition may make existence at low temperatures untenable for single individuals as small as bushtits.

Communal roosting may represent one of the first lines of defense against cold in many species. Bushtits, however, do not appear to utilize other energy conservation strategies to the same extent as their parid relatives. They do not roost in holes or old nests, as do chickadees, titmice, and Verdins (Bent 1946, Goldstein 1974), although they do roost communally in dense branches as shelter from radiative and convective heat loss (Bent 1946). Their body temperature falls only slightly upon exposure to cold or following marked weight loss. Thus, they do not appear to utilize energy savings gained by hypothermia or torpor as do chickadees and titmice (Haftorn 1972, Chaplin 1976). They apparently do not have any denser than normal plumage to retard heat loss; conductive

heat loss (slope of single bird metabolism-temperature regression, Fig. 1) was almost exactly that predicted for a 5.5-g bird, $0.37 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot \text{C}^{\circ-1}$, by the Lasiewski et al. (1967) conductance-weight regression. Verdins, Black-capped Chickadees, and some Old World titmouse species all have a conductive heat loss that is lower than predicted for their body mass and denser plumage than other birds of similar size, 10.7–11.5% of body mass (Hissa and Palokangas 1970, Goldstein 1974, Chaplin unpubl. data). These species are continually exposed to severe cold during the winter, however, whereas bushtits rarely encounter freezing temperatures, especially in the southern part of their range, where this study was conducted. Nevertheless, the extent to which huddling behavior can ameliorate the local microenvironment is impressive and obviously is integral to survival during sudden inclement weather.

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