THE EFFECT OF THERMAL MICROCLIMATE ON FORAGING SITE SELECTION BY WINTERING MOUNTAIN CHICKADEES[1]

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Abstract. The relationship between the thermal microclimate and foraging site selection by Mountain Chickadees (*Parus gambeli*) was investigated during February and March 1992 in south central Wyoming. Air temperature, wind speed, and solar radiation were measured at 465 actual foraging sites and 525 available sites using battery powered dataloggers and sensors mounted on extendable poles. Mountain Chickadees selected sites that had higher air temperatures and lower wind speeds than available foraging sites. Solar radiation at actual foraging sites did not differ from available foraging sites. Standard operative temperatures at actual foraging sites were closer to idealized warm sites than were available foraging sites. The thermal environment, in addition to food availability, may contribute to foraging site choice by Mountain Chickadees in winter.

Key words: Parus gambeli; Mountain Chickadee; foraging site selection; winter microclimate; Parus; winter foraging; thermal microclimate.

INTRODUCTION

Factors such as predation, competition, and food availability can influence foraging site selection in small birds. The thermal environment may also contribute to choice of a foraging site (e.g., Grubb 1977). Most microclimate studies have focused on stationary points such as nests or roost sites (e.g., Walsberg 1981, Webb and Rogers 1988). No quantitative studies of the actual microclimates of free ranging, foraging birds have been conducted during the winter. Winter foraging site selection is potentially important to the energy budget of a small bird in harsh environments. Here I present a microclimate analysis of winter foraging sites of free-ranging Mountain Chickadees (*Parus gambeli*).

Several *Parus* species occupy cold habitats during the winter in spite of harsh environmental conditions. Numerous physiological and behavioral adaptations for energy conservation have been reported in this genus. Fat deposition and mobilization are enhanced during winter (Chaplin 1974). Nocturnal hypothermia may involve depressions in body temperature of up to 10°C, resulting in energy savings of as much as 33% (Budd 1972; Haftorn 1972; Chaplin 1974, 1976; Mayer et al. 1982, Reinertsen and Haftorn 1983). Careful microclimatic selection of winter roost sites by small birds reduces energy flux to the

environment through warmer air temperatures (Kendeigh 1961, Korhonen 1981), reduced forced convective heat loss (Kelty and Lustick 1977, Mayer et al. 1982, Walsberg 1986, Webb and Rogers 1988), and ameliorated radiative heat loss (Mayer et al. 1982, Walsberg 1986). Microhabitat selection in response to thermal conditions during foraging has been documented in Black-capped Chickadees (*Parus atricapillus*), Carolina Chickadees (*P. carolinensis*), and Tufted Titmice (*P. bicolor*). During cold or windy weather, these birds moved horizontally less often (Kessel 1976, Grubb 1978), tended to decrease foraging heights (Grubb 1975, 1977), spent more time in sheltered areas (Grubb 1977) and avoided windward substrates under cloudy conditions (Grubb 1977). These studies, however, did not include direct measurement of thermal parameters within the precise microhabitat selected by foraging birds.

The exploitation of a harsh winter habitat by small passerines may depend in part on their ability to effectively manage energy loss to the environment and to search for prey. Root (1988) found that the winter range of birds may be limited to areas where the energy required to compensate for a cold environment is less than about 2.5 times the standard metabolic rate. While peak metabolic rates can be maintained for short periods, long-term energetic capabilities of small birds could easily be exceeded were it not for selection of favorable microclimates to reduce energy expenditures. For example, Mayer et al.

(1982) concluded that Carolina Chickadees could not survive at the northern limit of their winter range without the selection of favorable microclimates and use of nocturnal hypothermia, because energy requirements would exceed their metabolic capabilities. Therefore, behavioral energy conservation should be readily apparent in small parids wintering in harsh climates.

The Mountain Chickadee (*Parus gambeli*) is a small, (10–12 g) year-round resident of high elevation, coniferous forests in western North America (Bent 1946). Its typical winter habitat is frequently characterized by low air temperatures, high wind speeds, and abundant solar radiation. Physiological and behavioral energy conservation strategies in Mountain Chickadees are not as well known as in Black-capped or Carolina Chickadees (Smith 1991). Since Mountain Chickadees have low thermal inertia and spend the winter in harsh environments, they should carefully choose foraging microclimates. Thus, I hypothesized that Mountain Chickadees should select winter foraging sites that have higher air temperature (T_a), lower wind speeds, and greater solar radiation than is generally available in the forest. To test these hypotheses, I examined the microclimates of foraging sites selected by free-ranging Mountain Chickadees during winter in south central Wyoming.

Implicit to the study of energy conservation strategies in foraging parids is the pervasive constraint of food availability. Careful selection of thermally favorable microclimates is adaptive only to the extent it does not severely restrict food availability. I did not measure winter food available to Mountain Chickadees. Rather, I examined energy conservation strategies recognizing that the birds must forage in areas of adequate food resources.

METHODS

STUDY AREA

I conducted the study on the Medicine Bow National Forest in the Sierra Madre Mountains of south central Wyoming (41°N, 107°W). The study area encompassed the Upper East Fork of the Encampment River (912 hectares) and Coon Creek (1,615 hectares) watersheds, at an elevation of 2,650 to 3,100 meters. Lodgepole pine (*Pinus contorta*) dominated the study area (58% by area), with Engelmann spruce (*Picea engelmannii*) and Subalpine fir (*Abies lasiocarpa*) pre-

dominating on north-facing slopes (38% by area). Meadows and rock outcrops covered the remaining 4% (Raphael 1986). Approximately 30% of the Coon Creek watershed was clearcut in small (0.2–6 h) patches during 1990–1992.

The area receives approximately 100 cm of precipitation annually, of which 70% is snow (Raphael 1986). Snow depth averaged 1–1.3 m during the sampling period of February and March 1992. Average February and March air temperatures were −10.2°C and −6.3°C, respectively (U.S. Forest Service weather station data). The study area provided a cold environment to test the processes of foraging site selection by chickadees.

MICROCLIMATE SAMPLING

Microclimate data were collected with electronic dataloggers (Model CR10, Campbell Scientific, Inc., Logan, Utah). Measurements at all dataloggers were taken once a second and averaged over one-minute intervals from sunrise to sunset. Temperatures were measured with 24-gauge copper constantan thermocouples. Wind speeds were measured using Thornthwaite sensitive cup anemometers (Model 901, C. W. Thornthwaite Associates, Elmer, NJ) and custom-made heated bead thermistor anemometers (Bergen 1971). Shortwave solar radiation was measured with Licor pyranometers (Model LS200SA, Licor Inc., Lincoln, NE).

Foraging Mountain Chickadees were located by snowshoeing along 3 km transects from sunrise to sunset for 13 days between 4 February and 14 March 1992. Six transects were located 400 m apart in each watershed, with permanent sampling points established every 200 m (180 points total). All 12 transects were traversed at least twice during the study. The transects were established by the U.S. Forest Service as a part of the Coon Creek Wildlife Research Project.

Microclimate sensors were mounted on extendable fiberglass poles capable of reaching 7 m above the snow and connected to dataloggers mounted on pack frames. The arrangement is hereafter termed a mobile unit. The group of sensors included a shaded thermocouple, a heated bead thermistor anemometer, and a pyranometer. I measured temperature, wind speed, and radiation 7 m and 2 m above each permanent sampling point on the transects at substrates commonly used by foraging Mountain Chickadees (Table 1). The probe was placed between

0–25 cm from the tip of the nearest branch or, if no branches existed at the sampling height, within 25 cm of a tree trunk directly above the permanent sampling point.

The transect point data were assumed to represent the microclimates of available foraging sites across the study area and are hereafter termed available foraging sites. The available foraging site sampling heights ($\bar{x}$ = 4.5 m, SD = 2.5) were chosen to approximate the sampling distribution of the actual foraging site heights ($\bar{x}$ = 5.39 m, SD = 2.06, range = 0 to 7 m). Sampling distributions of actual and available foraging sites were similar to each other, relative to substrate type and tree species (Table 1).

As foraging flocks of chickadees were encountered on the transects, the microclimates of their exact foraging locations were measured by placing the probe as near as possible to the birds. I was frequently (n = 44) able to place the probe within 1 m of actively foraging chickadees, but most commonly (n = 421) I would place the probe at the precise foraging site within 1–2 seconds after the bird left. The tame and tolerant nature of Mountain Chickadees, particularly while intensely foraging during the winter, permitted this close approach. For example, on seven occasions birds foraged within 15 cm of the probe and twice within 40 cm of my face. Observer presence could have had an influence on bird behavior. However, after many hours of observing foraging chickadees during the winter, the general patterns of microsite selection and rate of movement by the birds did not seem to differ between long and short distance observation. Consequently, I believe the methods used here generate data that are minimally affected by observer presence.

Data were collected at each foraging site beginning and ending with the start of a minute on the datalogger clock. Bird height, tree species, substrate type (i.e., live needles, dead branches, trunk, or snow), habitat type, time, and type of observation (i.e., actual or available foraging site) were recorded on cassette tape. All datalogger clocks and observer watches were synchronized daily.

Each morning I placed two stationary dataloggers with sensors (hereafter termed base stations) within 1 km of the transects to be sampled that day. The base stations continuously measured and averaged (at 1 minute intervals) T_a (shaded thermocouples), wind speed (cup ane-

TABLE 1. Tree species and substrate sampling frequencies from actual (n = 427) and available foraging sites (n = 525). ABLA = Subalpine fir (*Abies lasiocarpa*), PICO = Lodgepole pine (*Pinus contorta*), PIEN = Engelmann spruce (*Picea engelmannii*). Percentage of sample in parentheses.

	Actual foraging sites	Available foraging sites
Tree species		
ABLA	155 (36.3%)	182 (34.6%)
PICO	203 (47.5%)	254 (48.4%)
PIEN	59 (13.8%)	71 (13.5%)
SNAG	6 (1.4%)	18 (3.5%)
SNOW	4 (1.0%)	0 (0%)
Substrate type		
Dead branches (DB)	89 (20.8%)	169 (32.1%)
Live needles (LN)	332 (77.7%)	338 (64.4%)
Trunk (TR)	2 (0.5%)	18 (3.5%)
Snow (SN)	4 (1.0%)	0 (0%)
Tree + substrate		
ABLA + DB	39 (9.1%)	35 (6.7%)
ABLA + LN	116 (27.2%)	147 (28.0%)
ABLA + TR	0 (0%)	0 (0%)
PICO + DB	43 (10.1%)	94 (17.9%)
PICO + LN	159 (37.2%)	144 (27.4%)
PICO + TR	1 (0.2%)	16 (3.0%)
PIEN + DB	2 (0.4%)	22 (4.2%)
PIEN + LN	57 (13.3%)	47 (9.0%)
PIEN + TR	0 (0%)	2 (0.4%)
SNAG + DB	5 (1.1%)	18 (3.4%)
SNAG + TR	1 (0.2%)	0 (0%)
SNOW	4 (0.9%)	0 (0%)

mometers), and solar radiation (pyranometers) at 2 m above the snow. One station was placed in an open area (open base station), usually in a clearcut or meadow with only widely interspersed vegetation extending above the snow. While open areas were not a heavily used habitat type, Mountain Chickadees were observed on numerous occasions foraging within clearcuts and meadows during the course of the study. The other station was arbitrarily placed within 400 m of the open station in the densest canopy cover available (forest base station). Each day, the base stations were placed on an aspect similar to that of the transects sampled by the mobile units. The base stations were placed to measure microclimates representative of the most open and the most sheltered microhabitats available to the chickadees in the sampling area. The open base stations were assumed to represent the warmest, windiest, and sunniest locations available to the

birds. The forest base stations were assumed to represent the coolest, calmest, and shadiest locations available to the birds.

DATA ANALYSES

The actual and available foraging sites were not compared directly, rather the two groups were compared relative to the base stations. Due to the high temporal variation in T_a, wind speed, and solar radiation throughout the day, direct comparisons of actual foraging sites and available foraging sites would not be valid because both could not be sampled within the same minute. Data sets were compiled to include data from the actual or available foraging sites and base stations only for those minutes that foraging site data was collected. For example, a single set of points for T_a from a foraging site would include one average temperature from each of the following: the open base station, the mobile unit, and the forest base station, all from the same minute.

Standard operative temperatures (T_{es}) (Bakken 1980) were calculated for each one minute sample from actual and available foraging sites and their complementary base stations. T_{es} describes the effective temperature of a microhabitat by integrating the effects of T_a, wind speed, and incident solar radiation into a single variable. T_{es} was calculated from standard variables from the equation developed by Bakken (1990) for passerine birds (see Appendix 1 for equations). T_{es} was used to compare the thermal environment of foraging sites and base stations as a chickadee would experience it. Values for the parameters not directly measured were obtained from the literature and are summarized in Appendix 1.

Since all data sets deviated from a normal distribution (D'Agostino's normality test, $P < 0.05$), I used Kruskal-Wallis (K-W) non-parametric analysis of variance tests and Dunn's non-parametric multiple comparisons to test for differences in means. I tested two groups (actual foraging sites and available foraging sites) with three levels each (mobile unit, open base, and forest base) for differences in mean T_a, wind speed, solar radiation, T_e, and T_{es}.

RESULTS

Four hundred sixty-five minutes of microclimate data were collected at actual foraging locations of 66 Mountain Chickadee flocks, including 270 individual birds. Five hundred twenty-five min-

utes of microclimate data were collected at available foraging sites. Each minute represents a unique foraging site. The independence of actual foraging site samples was insured in three ways. First, when possible, foraging sites selected by the same bird were not sampled sequentially (Bell et al. 1990, Hejl et al. 1990), the next sample was taken from a foraging site selected by a different individual bird in a different tree at least 10 m away. Second, if the same bird was sequentially sampled it was noted on tape and the data from more than one minute were pooled to produce one sampling point. Third, to minimize repeated sampling of the same individuals, flocks were sampled only for a few minutes ($\bar{x} = 7.1$ minutes, range = 1 to 16 minutes, varying with terrain and size of flock) then observers returned to the transect. Encounters with chickadees that could be sampled were infrequent (< 1 flock/km of transect), therefore, the probability of encountering the same birds in the same day was low. Despite reasonable care to maintain the independence of the sample points, individual birds were not marked and a small amount of repeated sampling could have inadvertently occurred.

Mountain Chickadees selected foraging sites with T_a similar to the open base stations, but warmer than the forest base stations. Mean T_a from actual foraging sites and open base stations did not differ significantly (Dunn's $P > 0.05$), but both differed significantly from mean T_a at the forest base stations (K-W, $P < 0.0001$; Dunn's, $P < 0.05$; Table 2). The available foraging sites were cooler than the open base stations, but warmer than the forest stations (K-W, $P < 0.0001$; Dunn's, $P < 0.05$; Table 2). I conclude that Mountain Chickadees select foraging sites with higher T_a than is available because T_a at actual sites was statistically equal to the open base and T_a at available sites was colder than the open base.

Mountain Chickadees selected foraging sites with wind speeds similar to the forest base stations and lower than the open base stations. Means from actual foraging sites and forest base stations did not differ significantly (Dunn's, $P > 0.05$), but both differed from the open base station (K-W, $P < 0.0001$, Dunn's, $P < 0.05$, Table 2). Wind speeds at the available foraging sites were lower than the open stations but higher than the forest base stations (K-W, $P < 0.0001$; Dunn's, $P < 0.05$; Table 2). I conclude that Mountain Chickadees select foraging sites with

TABLE 2. Summary means of air temperature (T_a), wind speed, solar radiation, and standard operative temperature (T_{es}) of base stations and foraging sites. Values in parentheses are 95% confidence interval upper and lower limits. '*' denotes statistically equal means.

	T_a (°C)	Wind speed (m s^{-1})	Solar radiation (W m^{-2})	T_{es} (°C)
Actual foraging sites				
Open base	−0.89*	1.53	383	−13.09*
	(−0.47, −1.32)	(1.62, 1.44)	(407, 359)	(−12.4, −13.8)
Actual sites	−1.43*	0.75*	275	−10.15
	(−0.99, −1.88)	(0.83, 0.66)	(284, 267)	(−9.6, −10.7)
Forest base	−3.97	0.58*	181	−13.57*
	(−3.60, −4.36)	(0.62, 0.55)	(192, 169)	(−13.0, −14.1)
Available foraging sites				
Open base	−1.08	1.64	390	−12.96*
	(−0.67, −1.50)	(1.73, 1.55)	(420, 361)	(−12.1, −13.8)
Available sites	−1.78	0.83	263	−10.36
	(−1.39, −2.15)	(0.90, 0.76)	(273, 252)	(−9.8, −10.9)
Forest base	−3.63	0.56	183	−12.49*
	(−3.28, −3.97)	(0.60, 0.53)	(197, 170)	(−11.9, −13.1)

lower wind speeds than available sites because wind speed at actual sites was statistically equal to the forest base and wind speed at available sites were higher than the forest base.

Solar radiation means from the actual foraging sites, open base stations, and forest base stations all differed significantly from each other, as did solar radiation means from the available foraging sites, open base stations, and forest base stations (K-W, $P < 0.0001$; Dunn's, $P < 0.05$; Table 2). Solar radiation levels of both actual and available foraging sites were lower than the open stations, but higher than the forest stations. I could not detect foraging site selection based on solar radiation because the actual and available sites were both intermediate to their open and forest bases.

T_{es} means were significantly higher at both actual and available foraging sites than at their complementary base stations (K-W, $P < 0.0001$; Dunn's, $P < 0.05$; Table 2). T_{es} means indicated that the actual and available foraging sites were considerably better thermal environments than either the open or forest base stations (Table 2).

Since each type of base station characterized an unfavorable extreme of at least one microclimate variable (e.g., forest base stations had low T_a and open base stations had high wind speeds), an idealized warm base T_{es} (T_a and radiation from the open bases and wind speeds from the forest bases) was calculated for each sampling point. The mean difference between T_{es} at actual sites and T_{es} at their complimentary, idealized warm bases was significantly lower than the mean dif-ference between T_{es} at available sites and T_{es} at their complimentary, idealized warm bases (Mann-Whitney, $P < 0.00001$, Table 3). Mountain Chickadees selected foraging sites with T_{es} closer to the idealized warm bases than the available sites were to their idealized warm bases.

DISCUSSION

Many factors have been found to influence foraging site selection in small birds, e.g., predation risk (Lima 1985, Ekman 1986), competition (Alatalo 1981), food availability (Bell and Ford 1990, Hutto 1990, With and Morrison 1990), risk sensitivity (Barkan 1990), and dominance (Desroches 1989). My study provides evidence that the microclimate of foraging sites is another factor in the selection process.

TABLE 3. Summary means of standard operative temperature (T_{es}) of actual and available foraging sites and idealized warm bases. Values in parentheses are 95% confidence interval upper and lower limits. '*' denotes statistically different means ($P < 0.00001$)

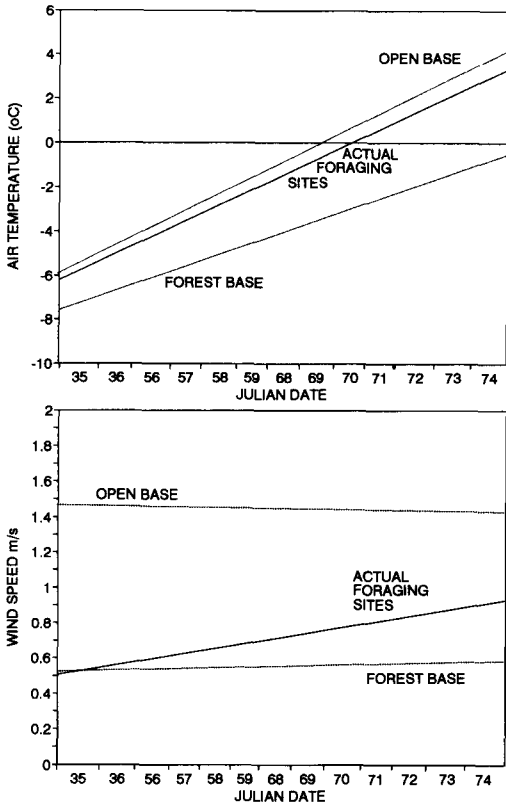|	Actual foraging sites T_{es} (°C)	Available foraging sites T_{es} (°C)
Warm base	−8.03	−7.23
	(−7.3, −8.8)	(−6.4, −8.1)
Foraging site	−10.15	−10.36
	(−9.6, −10.7)	(−9.8, −10.9)
Difference (warm − foraging)	−2.12*	−3.13*
	(−1.9, −2.3)	(−2.8, −3.4)

FIGURE 1.   Progressive change between 4 February and 14 March 1992 in air temperatures and wind speeds at foraging sites selected by Mountain Chickadees compared with nearby open and forest base stations. For visual clarity, only linear regression lines are presented.

Chickadees should benefit energetically from foraging site selection based on microclimate variables. The metabolic rate of Mountain Chickadees can be estimated by:

$$M - E = \frac{\rho c_p (T_b - T_e)}{r_{Hb} + r_e} \qquad (1)$$

where M is metabolic rate, E is the evaporative heat loss, ρc_p is the volumetric heat capacity of air, T_b is chickadee body temperature, r_{Hb} is body resistance to heat transfer, and r_e is equivalent resistance (see Appendix 1) (Campbell 1977). Assuming the E, r_{Hb}, and T_b are equal at all sites in the study area, a chickadee could reduce its metabolic rate approximately 5–7% by foraging within a T_a range of -0.89 to $-1.43°C$ (open base and actual foraging site means) rather than at $-3.97°C$ (forest base mean, Table 2). Wood and Lustick (1989) found that metabolic rates in

Tufted Titmice significantly increased with decreasing air temperature. Hence, the warmer foraging sites selected by Mountain Chickadees would have direct energy conservation benefits.

Mountain Chickadees also selected foraging sites with lower wind speeds than available sites. Studies have shown that the metabolic rates of several bird species increase linearly with the square root of wind speed (Gessaman 1972, Robinson et al. 1976, Kelty and Lustick 1977, Chappell 1980). Using equation 1 and assuming that other factors are equal at all sites, chickadees could reduce metabolic rates by 2–4% by foraging in a wind speed range from 0.59–0.76 m sec^{-1} (forest base and actual foraging site means, Table 2) over the open base mean of 1.53 m sec^{-1} at $-0.89°C$ (open base T_a mean).

The lack of clear selection for higher solar radiation at actual foraging sites refutes my original hypothesis and is in contrast to the field and laboratory studies on other parids. Grubb (1977) found that increased solar radiation allowed Carolina Chickadees and titmice to forage in windier habitats. He also found that solar radiation had no effect on foraging height or movement rates (Grubb 1975, 1978). Solar radiation has been shown to mitigate the effects of wind and low temperatures in birds (Lustick et al. 1979, Wood and Lustick 1989). The lack of selection by Mountain Chickadees for this variable at foraging sites may be due to the abundant and intense solar radiation at the study site. The sampling days were typically clear and direct solar radiation was intense at high elevation. The snow pack is highly reflective, but I only measured incoming radiation. Reflected radiation may have been an important source of solar radiation to the birds. Radiation may have been so readily accessible that the birds received sufficient levels at most foraging sites and therefore selected sites based on wind and T_a only. Alternatively, my sampling design may have been inadequate to distinguish selection of foraging sites based on solar radiation. The open base stations may have provided an unrealistically high upper limit for solar radiation comparisons. Solar radiation at the actual foraging sites might always be lower than the radiation levels measured in the open, regardless of any preference exhibited by chickadees for sites with higher solar radiation.

Three lines of evidence suggest that Mountain Chickadees are responding to several thermal variables at once rather than a single variable

independent of others. First, Mountain Chicka-dees chose sites that were both warmer and calm-er. Chickadees could reduce metabolic rates from 10–12% (calculated using equation 1) by select-ing foraging sites that combined both higher tem-peratures and lower wind speeds (-0.89 to $-1.43°C$ and 0.56 to 0.76 m sec^{-1}, open base and actual foraging site means versus $-3.97°C$ and 1.53 m sec^{-1}, forest base means). Second, Mountain Chickadees selected foraging sites with increasingly higher wind speeds as T_a increased through the sampling season (Fig. 1). The birds were more tolerant of higher winds at higher tem-peratures, suggesting that Mountain Chickadees are sensitive to the combination of T_a and wind speed. Third, the T_{es} analysis indicates that the birds were sensitive to the overall thermal mi-croclimate by selecting foraging sites with T_{es} closer to idealized warm bases than were the available sites.

Food availability is certainly an important component in foraging site selection. Birds readi-ly modify their foraging behavior in response to food availability (Paszkowski 1982, Pienkowski 1983, Terrill 1990). It is possible that microhab-itats that are thermally favorable to chickadees are also thermally favorable to invertebrates and contain higher densities of prey. The thermal benefit of foraging site selection could be indirect (i.e., site selection based on prey abundance) rather than direct selection for thermal benefits. I suspect that direct selection for thermal benefits operated to some extent at my study area, given that food items were essentially immobile during winter and that wind speed and direction, T_a, and solar radiation all varied greatly through time and space. Alternatively, the thermal environ-ment may have influenced both chickadees and their prey to simultaneously contribute to for-aging site selection. An interesting test of this hypothesis would be to determine the principal prey items of Mountain Chickadees, measure the prey availability relative to the thermal micro-climate (a potentially difficult task, e.g., Smith and Rotenberry 1990, Wolda 1990), manipulate both food densities and the thermal microcli-mate in the presence of the birds, and monitor their response.

Thermal microclimate variables are a factor in foraging site selection by Mountain Chicka-dees and direct energetic benefits should occur as a consequence of selecting warmer, calmer sites. By choosing foraging sites that reduce en-ergy loss, Mountain Chickadees are not only re-ducing energy flux from individual birds, but as a species may be able to utilize habitats and re-sources that would be potentially unavailable without such an energy conservation strategy. Foraging site selection based on thermal param-eters may be one of several energy conservation behaviors (e.g., nest or roost site selection) that cumulatively may permit the Mountain Chick-adee to survive, despite harsh thermal condi-tions, at the upper altitudinal and latitudinal fringes of its range.

ACKNOWLEDGMENTS

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APPENDIX 1

Calculation of standard operative temperature (T_{es}) for Mountain Chickadees. All equations and value estimates from Campbell (1977) unless otherwise cited.

$$T_{es} = T_b - (1 + 0.26\sqrt{\mu})(T_b - T_e) \qquad \text{(Bakken 1990)}$$

   T_b = body temperature (39°C)
   μ = wind speed (msec^{-1})
   T_e = operative temperature (°C)

$$T_e = T_a + \frac{r_e(R_{abs} - \epsilon_c\sigma T_s^4)}{\rho c_p}$$

T_a = air temperature (°C)
r_e = equivalent resistance to heat transfer (secm^{-1})

$$r_e = \frac{r_{Ha}r_r}{r_{Ha} + r_r}$$

r_{Ha} = resistance to convective heat transfer (secm^{-1})

$$r_{Ha} = 307 \sqrt{\frac{d}{\mu}} 0.7$$

   d = characteristic dimension (0.035 m, Robinson et al. 1976)
   r_r = resistance to radiative heat transfer (secm^{-1})

$$r_r = \frac{\rho c_p}{4\epsilon_c\sigma T_s^3}$$

ρc_p = volumetric heat capacity of air (1,200 Jm^{-3}K^{-1})
R_{abs} = radiation absorbed by a chickadee (Wm^{-2})

$$R_{abs} = a_s\left(\frac{A_{po}}{A}S_i\right) + a_L(\epsilon_s\sigma T_a^4)$$

   a_s = absorptivity to shortwave radiation (0.66)
A_{po}/A = ratio of projected area to total chickadee surface area (0.3)
   S_i = incident short wave radiation (Wm^{-2})
   a_L = absorptivity to long wave radiation (0.94)
$\epsilon_s\sigma T_a^4$ = thermal radiation emitted by the surroundings (Wm^{-2})
   ϵ_s = emissivity of the surroundings (0.98)
   σ = Stefan-Boltzmann constant (5.67·10^{-8} Wm^{-2}K^{-4})
   T_a = air temperature in K (T_a + 273°)
$\epsilon_c\sigma T_s^4$ = thermal radiation emitted by a chickadee (Wm^{-2})
   ϵ_c = emissivity of a chickadee (0.98)
   T_s = surface temperature of a chickadee in K (8.56 + 0.785 T_a, Hill et al. 1980)