The Condor 109:446–451 © The Cooper Ornithological Society 2007

HEAT PRODUCTION FROM FORAGING ACTIVITY CONTRIBUTES TO THERMOREGULATION IN BLACK-CAPPED CHICKADEES

SHELDON J. COOPER¹ AND SARAH SONSTHAGEN Department of Biology, University of Wisconsin Stevens Point, Stevens Point, WI 54481

Abstract. We measured metabolic heat production $(\dot{H}_{\rm m})$ of perching and foraging Black-capped Chickadees (Poecile atricapillus) to determine if the heat produced during foraging activity, or exercise thermogenesis, could replace thermoregulatory heat production requirements. $\dot{H}_{\rm m}$ and activity of chickadees in winter were measured at ambient temperatures (T_a) ranging from -11.5° to 15.5°C. Mean activity amplitude recorded with an activity detector was significantly higher in foraging birds than perching birds. $\dot{H}_{\rm m}$ did not vary significantly between perching and foraging birds, indicating that heat produced during foraging does substitute for heat produced by shivering for thermoregulation. Evaporative water loss and dry thermal conductance did not vary significantly between perching and foraging chickadees. These results suggest that heat produced from locomotor muscles during foraging activity substitutes for thermoregulatory requirements in glean-and-hang foraging species, such as chickadees, as well as in ground-foraging birds.

Key words: activity metabolism, Black-capped Chickadee, foraging, heat production, oxygen consumption, Poecile atricapillus.

El Calor Producido por la Actividad de Forrajeo Contribuye a la Regulación de la Temperatura en *Poecile atricapillus*

Resumen. Medimos la producción de calor metabólico $(\dot{H}_{\rm m})$ de individuos de la especie *Poecile* atricapillus que se encontraban perchados y forrajeando para determinar si el calor producido durante la actividad de forrajeo (termogénesis mediante ejercicio) podría reemplazar los requerimientos de producción de calor necesarios para la regulación de la temperatura. La $H_{\rm m}$ y la actividad de las aves en el invierno fueron medidos a temperatura ambiente (T_a) , entre -11.5° y 15.5°C. La amplitud media de la actividad registrada con un detector de actividad fue significativamente mayor en las aves que se encontraban forrajeando que en las que se encontraban perchadas. La $H_{\rm m}$ no varió significativamente entre aves que estaban forrajeando y aves que estaban perchadas, lo que indica que el calor producido durante el forrajeo sustituye al calor producido tiritando para regular la temperatura. La pérdida de agua por evaporación y la conductancia térmica seca no variaron significativamente entre aves que estaban forrajeando y aves que estaban perchadas. Estos resultados sugieren que el calor producido por los músculos locomotores durante la actividad de forrajeo sustituye los requerimientos de regulación de la temperatura en aves que forrajean colgándose y tomado presas del sustrato como lo hace P. atricapillus, así como en aves que forrajean en el suelo.

Overwintering of small passerines in cold temperate regions requires prolonged high rates of energy expenditure for thermoregulation. Thermoregulatory demands for wintering birds typically range from 20% to 40% of daily energy needs (Weathers et al. 1984, Weathers and Sullivan 1989) and may be nearly

Manuscript received 21 March 2006; accepted 29 November 2006.

¹ Present address: Department of Biology and Microbiology, University of Wisconsin Oshkosh, Oshkosh, WI 54901. E-mail: cooper@uwosh.edu

60% of the daily energy budget (Weathers and Sullivan 1993). To meet these high thermoregulatory demands, small birds must forage throughout much of the day. The time spent foraging during the day in wintering passerines may range from slightly more than 50% in chickadees and titmice (Cooper 2000) to 90% in Verdins (Auriparus flaviceps; Austin 1978). Heat produced from locomotor muscles during foraging activity, or activity thermogenesis, represents a possible source of energy for thermoregulation for birds in cold temperatures. The replacement of thermoregulatory heat production from shivering with activity thermogenesis is called substitution. In other words, the heat generated while foraging may replace heat that would otherwise be generated by shivering. If substitution occurs, the net energy cost of foraging is reduced (Webster and Weathers 1990). Estimating energy costs of foraging activity is important for modeling energy expenditure of birds and for testing theories of optimal foraging (Bruinzeel and Piersma 1998, Webster and Weathers 1990).

Substitution has been reported for a number of ground-foraging birds. Typically, heat production has been measured as oxygen consumption while at rest and during terrestrial locomotion, usually while a bird is walking or running on a treadmill (Bruinzeel and Piersma 1998). In addition, combining doubly labeled water measurements with laboratory measurements of metabolism and field time-budgets has shown that foraging activity substitutes for thermoregulation in both Verdins (Webster and Weathers 1990) and Yellow-eyed Juncos (*Junco phaeonotus*; Weathers and Sullivan 1993).

For small tree-foraging species such as chickadees, that store very little body fat and thus have fewer energy reserves compared to ground-foraging birds (Rogers 1987, Cooper and Swanson 1994), substitution of thermoregulatory costs from activity thermogenesis may be critically important in maintaining energy balance, especially during the nocturnal fast. Laboratory metabolic rates for daytime resting and daytime foraging birds did not differ significantly in Mountain Chickadees (Poecile gambeli) or Juniper Titmice (Baeolophus ridgwayi; Cooper 2000). These data, along with data on Verdins (Webster and Weathers 1990), demonstrate that heat produced during foraging activity may substitute for thermoregulation in tree-foraging species as well as ground-foraging birds. However, the data in Cooper (2000) were collected from birds in metabolic chambers constructed from paint cans and may not have allowed the chickadees and titmice to forage using their normal glean-and-hang maneuvers (Robinson and Holmes 1982). Thus, metabolic rates of birds foraging in paint can chambers may have been less than actual foraging costs for birds in the wild.

To test if substitution occurs in a typical treeforaging passerine we measured and compared metabolic rates of Black-capped Chickadees (*Poecile atricapillus*) while perching compared to foraging during the normal active phase of the daily cycle.

METHODS

Black-capped Chickadees were captured with mist nets before 10:30 CST at Schmeeckle Reserve, Stevens Point, Wisconsin (44°32'N, 89°33'W) from 17 November 1999 to 28 February 2000. Body mass was measured to the nearest 0.1 g upon capture with a portable electronic balance (Model Scout S-600, Ohaus, Pine Brook, New Jersey). Wing chord, tail length, and tarsus were also measured and visible fat depots in abdominal and furcular regions were scored using a scale of 0-5 (Helms and Drury 1960). Following morphometric measurements, birds were transported to the laboratory where they were housed individually in $0.3 \times 0.3 \times 0.3$ m cages at room temperature (20-25°C). While caged, birds were provided with water, grit, and food (Tenebrio larvae and wild bird seed) ad libitum. All birds maintained mass while in captivity. Daytime metabolic tests were performed on birds after allowing them to feed for a minimum of 2 hr. All birds were tested on the day of capture to avoid effects of captivity on metabolism (Warkentin and West 1990). Metabolism was measured only once for each bird. After testing, birds were banded with U.S. Fish and Wildlife Service aluminum bands and released at the site of capture.

MEASUREMENT OF FORAGING ACTIVITY

We measured metabolic heat production of birds during the active phase of the daily cycle between 09:30 and 15:30. Measurements were made on individual birds using two separate 33.0 \times 20.3 \times 20.3 cm metabolic chambers made of plexiglass. Both metabolic chambers were equipped with a small feeder attached to one wall and a perch attached to the opposite wall. The perch was a board that had several artificial crevices in which birds could store seeds. Below the perch and feeder was 1 cm wire mesh placed above a 1 cm layer of paraffin oil used for the collection of fecal material. Metabolic chambers sat on top of a motion activity detector (MAD-1, Sable Systems, Las Vegas, Nevada). The output of the MAD-1 is close to zero volts but fluctuates to either side of zero volts if the animal in the metabolic chamber is active. The output from the MAD-1 was recorded on a computer using Datacan 5.0 data collection and analysis software (Sable Systems). Mean activity amplitudes were then determined for foraging and perching birds. Birds were randomly assigned to one of two groups for metabolism measurements. Group one (foraging) birds foraged on sunflower seeds from the feeder inside the metabolic chambers. Lighting was provided by fluorescent lamps that provided illumination similar to natural early morning or late afternoon light but did not provide significant thermal heating ($<3 \text{ W m}^{-2}$). Group two (perching) birds rested in the metabolic chambers without food or lighting. Originally it was intended that the perching group would have lighting. However, even without food, chickadees exhibited significant hopping and gleaning activity. Thus, they could not be considered to be perching. Examples of activity records for perching and foraging birds are shown

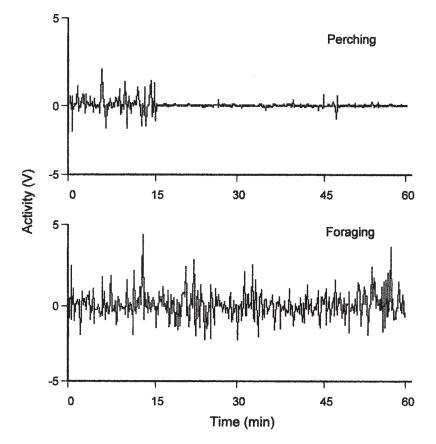


FIGURE 1. Activity records for a perching and a foraging Black-capped Chickadee. The records show a typical 60-min period inside a metabolic chamber. The beginning of the perching record shows the activity associated with entry into the metabolic chamber.

in Figure 1. The two separate metabolic chambers were placed inside a temperature-controlled incubator (Model 352602, Hotpack, Philadelphia, Pennsylvania) and one or two birds were tested at the same time using a multiplexer switching device (RM-4, Sable Systems). Air temperature (T_a) inside the chamber was monitored continuously throughout each test with a 30-gauge copper-constantan thermocouple connected to a Sable Systems thermocouple thermometer preamplifier (Model TC-102, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards). The output from the thermometer preamplifier was recorded on a computer using Datacan 5.0 data collection and analysis software.

MEASUREMENT OF METABOLIC HEAT PRODUCTION

Metabolic rates were determined by simultaneous measurements of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) by open-circuit respirometry. In addition, the dew point of each chamber was measured to determine evaporative water loss. Metabolic measurements were made at air

temperatures (T_a) between -11.5° and 15.5° C. This range of T_a was chosen to ensure that all metabolic rates were measured below the lower critical temperature for this population of Wisconsin chickadees (SJC, unpubl. data), for two reasons. Firstly, substitution does not occur within the thermoneutral zone where there are no thermoregulatory costs (Bruinzeel and Piersma 1998). Secondly, oxygen consumption of Mountain Chickadees in the thermoneutral zone was significantly higher for foraging than perching birds, indicating that activity thermogenesis significantly increases overall metabolic rate in the thermoneutral zone (reanalysis of data in Cooper [2000], $t_9 = 2.6$, P = 0.02).

Each metabolic measurement lasted 90 min, with the first 60 min used for equilibration. Birds were weighed to the nearest 0.1 g before and after each metabolic test. At the end of each trial, birds were removed from the chamber and body temperature (T_b) was recorded ($\pm 0.1^{\circ}$ C) by inserting a 30-gauge copper-constant thermocouple into the cloaca to a depth of approximately 10–12 mm. If T_b could not be obtained within 60 sec, the measurement was discarded. Inlet air was dried with indicating

Drierite® (anhydrous CaSO₄, W.A. Hammond Co., Xenia, Ohio) and scrubbed of CO2 with Ascarite® (Arthur H. Thomas Co., Swedesboro, New Jersey) before being pushed through the metabolic chamber with a diaphragm pump. Inlet flow rates were maintained at 1500–1525 mL min⁻¹ by a mass-flow controller (Model 840, Sierra Instruments, Monterey, California) calibrated to $\pm 1\%$ with a soap bubble meter. These flow rates yielded changes in oxygen and carbon dioxide content between influx and efflux gas of 0.3% and 0.7%, respectively, and maintained oxygen content of efflux gas above 20.2%. Excurrent air from the metabolism chambers was directed into a manifold to bleed the excess volume of air so that a subsample could be pulled through the respirometry system at a flow rate of 100 mL min⁻¹. The subsample of air first passed through a Sable Systems dew point humidity meter (model RH-100), then through a drying tube containing magnesium perchlorate. The air stream was next directed into a Sable Systems carbon dioxide analyzer (model CA-1A). Lastly, the air stream was directed through a tube of Ascarite® and Drierite® and a Sable Systems oxygen analyzer (model FC-1). Low permeability Bev-A-Line tubing was used throughout the system. The carbon dioxide analyzer was calibrated using both nitrogen and a calibration gas of 1% CO₂. Measurements of the excurrent gas were recorded every 1 sec on a computer using Datacan 5.0 data collection and analysis software and imported into LabAnalyst (Warthog Systems, Riverside, California) for analysis. To compensate for the washout characteristics of the respirometry system, oxygen consumption and carbon dioxide production values were calculated as instantaneous rates (Bartholomew et al. 1981). We used the individual respiratory quotients (RQ) to estimate total heat production for each metabolic trial using thermal equivalents from Brody (1945).

STATISTICAL ANALYSES

Data are presented as means \pm SD. For each individual trial, mean activity, $\dot{H}_{\rm m}$, and $\dot{H}_{\rm e}$ (evaporative heat loss) were calculated from the same 10min period taken from the last 30 min of the trial. Data were analyzed for normality (Shapiro-Wilks test) and for homogeneity (Levene's test) prior to parametric analyses. We compared means using independent two-tailed t-tests. Regression lines were fitted by the method of least squares. Slopes and intercepts of regression lines were compared using analysis of covariance (ANCOVA; Zar 1996). Statistical significance was accepted at P < 0.05. All statistics were computed with SPSS 13 (SPSS 2004). All values are presented on a whole-organism basis to avoid the possible confounding effects of ratios (Packard and Boardman 1999).

RESULTS

Mean body mass at capture was 10.9 ± 0.7 g (n = 41). Mean furcular visible fat score was 0.3 ± 0.5 and mean abdominal visible fat score was 0.3 ± 0.4 (n = 41). Mean body mass during metabolic tests was 11.2 ± 0.9 g (n = 14) for foraging chickadees, which did not differ significantly from the perching chickadee

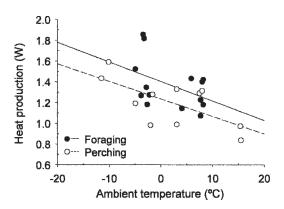


FIGURE 2. Metabolic heat production of foraging and perching Black-capped Chickadees increased with decreasing ambient temperature. Metabolic heat production was not significantly different between foraging and perching chickadees as revealed by ANCOVA.

body mass of 11.1 ± 0.5 g (n = 11, $t_{23} = 0.3$, P = 0.73). Chickadees in both experimental groups gained mass in captivity before testing.

Activity levels did not vary significantly with temperature for foraging chickadees ($F_{1,13} = 0.1$, P = 0.84) or for perching chickadees ($F_{1,10} = 1.0$, P = 0.35). The mean activity level during metabolic tests was 1.54 ± 1.00 V (n = 14) for foraging chickadees and 0.57 ± 0.51 V (n = 11) for perching chickadees. The mean activity level of foraging chickadees was significantly higher than that of perching chickadees ($t_{23} = 2.7$, P = 0.01).

Metabolic heat production of foraging and perching birds increased with decreasing T_a (Fig. 2). The analyses of metabolism yielded the following relationships between metabolic heat production (\dot{H}_{m}) and T_a. Foraging chickadees (n = 14, $r^2 = 0.35$, P = 0.02):

$$\dot{H}_{\rm m}({\rm W}) = 1.476 - 0.025 {\rm T}_{\rm a}.$$
 (1)

Perching chickadees ($n = 11, r^2 = 0.46, P = 0.02$):

$$\dot{H}_{\rm m}(W) = 1.236 - 0.018 T_{\rm a}.$$
 (2)

The regression equations for foraging and perching chickadees did not differ significantly in slope ($F_{1,21} = 0.03$, P = 0.87) or intercept ($F_{1,22} = 4.4$, P = 0.10).

Mean body temperature at the end of metabolic tests was 39.1 ± 1.3 (n = 10) for foraging chickadees, which did not differ significantly from the mean perching chickadee T_b of 39.6 ± 1.3 (n = 10, $t_{18} = -0.9$, P = 0.38). For perching chickadees, the rate of evaporative heat loss did not vary with T_a ($F_{1,8} = 3.1$, P = 0.12). However, evaporative heat loss (H_e) of foraging chickadees increased with decreasing T_a ($F_{1,13} = 26.2$, P < 0.001), with the following relationship (n = 14, $r^2 = 0.69$, P < 0.001):

$$\dot{H}_{\rm e}({\rm W}) = 0.220 - 0.008 {\rm T}_{\rm a}.$$
 (3)

Mean rate of evaporative water loss was 5.05 \pm

1.35 mg min⁻¹ (n = 14) in foraging birds and did not differ significantly from the rate in perching birds (5.04 ± 2.20 mg min⁻¹, n = 9, t = 0.01, P = 0.99).

To examine possible differences in heat loss from the body between foraging and perching birds we calculated dry thermal conductance as $C_{dry} = (H_m - H_e)/(T_b - T_a)$. Dry thermal conductance did not vary with T_a in perching birds ($F_{1,7} = 3.8$, P = 0.10) or foraging chickadees ($F_{1,9} = 5.0$, P = 0.06). Mean dry thermal conductance was 0.031 ± 0.002 W °C⁻¹ (n =10) for foraging birds, which was not significantly different from that of perching birds (0.027 ± 0.003 W °C⁻¹, n = 18, t = 1.3, P = 0.22).

DISCUSSION

Black-capped Chickadees in this study, similar to Black-capped Chickadees from South Dakota (Cooper and Swanson 1994), had very low visible body fat scores. Low visible body fat scores are typical of treeforaging birds such as chickadees. This is associated with more predictable food supplies for tree-foraging compared to ground-foraging birds (Rogers 1987, Rogers and Smith 1993).

Birds in the foraging treatment group had significantly higher activity levels than those in the perching group. Since activity was recorded as the voltage of an activity detector it is not possible to tell if the activity levels associated with foraging in the metabolic chamber are similar to those of birds foraging in their natural outdoor environment. However, chickadees foraging in metabolic chambers did store sunflower seeds in the perch block, thus exhibiting similar food storage behavior as chickadees foraging in the wild.

The heat production of foraging and perching chickadees did not differ significantly. Thus, the heat produced during foraging activity, or activity thermogenesis, substitutes for thermoregulatory requirements and indicates that Black-capped Chickadee foraging behavior incurs no significant additional energetic cost across a fairly wide range of temperatures. These data agree with findings for several species of ground-foraging birds using terrestrial locomotion (Bruinzeel and Piersma 1998). In addition, substitution in Black-capped Chickadees agrees with data from Mountain Chickadees, Juniper Titmice (Cooper 2000), and Verdins (Webster and Weathers 1990). This study is the first to quantify heat production associated with glean-and-hang foraging activity of birds in the laboratory.

Dry thermal conductance did not vary significantly between perching and foraging chickadees. This demonstrates that insulation is similar for perching and foraging chickadees, despite potential differences in posture between perching and foraging birds and possible plumage disruption in foraging birds that could decrease insulation.

Our data suggest that below the lower critical temperature, an active chickadee using glean-andhang foraging expends a similar amount of energy as a chickadee that is perching. Substitution of activity thermogenesis for thermoregulatory heat production may allow birds to devote more energy to elective activities such as social interactions and resource defense (Webster and Weathers 1990, Zerba et al. 1999).

Two anonymous reviewers and David S. Dobkin provided many useful suggestions on an earlier version of this paper. We are grateful to Ron Zimmerman for allowing us to mist-net birds at Schmeeckle Reserve. This study was funded by a University of Wisconsin Stevens Point Personnel Development Committee grant to SJC. Birds were collected under federal (MB003340-0) and state (SCP-WCR-58-C-01) collecting permits, and banded under Master Permit #22934. All experiments were performed in accordance with the Institutional Animal Care and Use Committee of the University of Wisconsin Stevens Point.

LITERATURE CITED

- AUSTIN, G. T. 1978. Daily time budget of the postnesting Verdin. Auk 95:247–251.
- BARTHOLOMEW, G. A., D. VLECK, AND C. M. VLECK. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturnid moths. Journal of Experimental Biology 90:17–32.
- BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York.
- BRUINZEEL, L. W., AND T. PIERSMA. 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. Ibis 140:323–328.
- COOPER, S. J. 2000. Seasonal energetics of Mountain Chickadees and Juniper Titmice. Condor 102: 635–644.
- COOPER, S. J., AND D. L. SWANSON. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. Condor 96:638–646.
- HELMS, C. W., AND W. H. DRURY JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird Banding 31:1–40.
- PACKARD, G. C., AND T. J. BOARDMAN. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? Comparative Biochemistry and Physiology 122A:37–44.
- ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among several tactics, diet, and habitat structure. Ecology 63:1918–1931.
- ROGERS, C. M. 1987. Predation risk and fasting capacity: do winter birds maintain optimal body mass? Ecology 68:1051–1061.
- ROGERS, C. M., AND J. N. M. SMITH. 1993. Lifehistory theory in the nonbreeding period: tradeoffs in avian fat reserves. Ecology 74:419–426.
- SPSS. 2004. SPSS for Windows, release 13.0. SPSS Inc., Chicago.
- WARKENTIN, I. G., AND N. H. WEST. 1990. Impact of long-term captivity on basal metabolism in birds. Comparative Biochemistry and Physiology 96A:579–581.
- WEATHERS, W. W., W. A. BUTTEMER, A. M. HAYWORTH, AND K. A. NAGY. 1984. An

evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459–472.

- WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs 59:223–246.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1993. Seasonal patterns of time and energy allocation by birds. Physiological Zoology 66:511–536.
- WEBSTER, M. D., AND W. W. WEATHERS. 1990. Heat produced as a by-product of foraging

activity contributes to thermoregulation by Verdins *Auriparus flaviceps*. Physiological Zoology 63:777–794.

- ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Upper Saddle River, NJ.
 ZERBA, E., A. N. DANA, AND M. A. LUCIA. 1999.
- ZERBA, E., A. N. DANA, AND M. A. LUCIA. 1999. The influence of wind and locomotor activity on surface temperature and energy expenditure of the eastern House Finch (*Carpodacus mexicanus*) during cold stress. Physiological and Biochemical Zoology 72:265–276.