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EFFECT OF TEMPERATURE AND WIND ON METABOLISM OF NORTHERN BOBWHITE IN WINTER

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) are widely distributed across more than half of the United States, and extending into Canada and Mexico. Within this distribution they tolerate a wide range of climatic conditions and thermal stress. Annual variation in weather can produce dramatic short-term population fluctuations, particularly in the northern portion of the distribution. To better understand effects of thermal stress on energy requirements of bobwhite, we measured roosting metabolic response to cold stress and wind speed using open respirometry in a closed-circuit wind tunnel. Oxygen consumption was measured for 8 winter-acclimated captive bobwhites at each of 8 temperatures (-15° , -10° , -5° , 0° , 5° , 10° , 20° , and 30° C) at free convection and at 3 wind speeds (0, 1, and 2 m/sec) at -15° and 0° C. Over the range of body mass we measured (201.5 ± 1.3 g, $n = 64$), metabolic rate varied with body mass ($P < 0.001$) but did not differ between sexes ($P = 0.187$). Mean standard metabolic rate ($\dot{V}O_2$) was 3.4 ± 0.11 mL O_2 /minute/bird (0.0171 ± 0.0004 mL O_2 /min/g) or 1.14 ± 0.04 W/bird. Below a lower critical temperature of 24.1° C, metabolic rate was linearly related to operative temperature (T_e) ($\dot{V}O_2 = 7.187 - 0.1568[T_e]$; $r^2 = 0.86$, $P < 0.001$). Metabolic rate (M-E) was linearly related to wind speed (WS) at -15° C ($\dot{V}O_2 = 9.741 + 0.4609[WS]$; $r^2 = 0.99$, $P = 0.001$) and 0° C ($\dot{V}O_2 = 6.713 + 0.4609[WS]$; $r^2 = 0.99$, $P = 0.001$). We discuss implications of these energy expenditures in the context of current research and management.

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Key words: *Colinus virginianus*, metabolism, northern bobwhite, operative temperature, roosting, thermoregulation

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) are widely distributed from Florida to Canada and west to South Dakota and Mexico. Within this distribution they tolerate a wide range of climatic conditions and thermal stress, ranging from near-lethal heat loads at southern latitudes (Guthery et al. 2001) to acute cold stress at northern latitudes (Swanson and Weinacht 1997). Within the geographic distribution determined by long-term climatic and habitat conditions, annual weather variation can produce dramatic short-term population fluctuations, particularly in the northern portion of the distribution (Roseberry and Klimstra 1984). Survival during winter has been identified as the

most important vital rate in central and northern parts of the species' distribution (Petersen et al. 2000, Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012). During winter, bobwhites at northern latitudes experience low ambient temperatures that may constrain space use (Tanner et al. 2017) and produce higher thermoregulatory costs during a period of declining food availability that is compounded by prolonged snow and ice cover that limit access to energy in food. Although direct mortality of bobwhites associated with winter weather is a minor component of total annual mortality (Roseberry and Klimstra 1984:60, Burger et al. 1995), the combination of low temperatures, deep or prolonged snow cover, and high winds can cause direct mortality (Errington 1939; Stanford 1972; Roseberry 1964; Roseberry and Klimstra 1972, 1984; Burger et al. 1995; Chavarria et al. 2012; Janke and Gates 2012; Janke et al. 2017) and deleterious

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indirect effects on populations. For example, reduced physiological fitness could occur, including increased susceptibility to toxins (Maguire and Williams 1987); and negative energy balance could reduce body condition, potentially delaying reproduction or predisposing quail to starvation or predation.

Bobwhite respond to thermal stress through selection of habitat with a favorable microclimate (Roseberry 1964, Hiller and Guthery 2005, Tanner et al. 2017), adjusting duration of foraging activity (Guthery 2002), huddling (Case 1973), increasing metabolic heat production (Case 1973, Case and Robel 1974, Spiers et al. 1983, Swanson and Weinacht 1997), metabolizing lipid stores (Koerth and Guthery 1987, Guthery 2002), and as a last resort, catabolizing muscle mass. Unlike some bird species, bobwhite exhibit little seasonal adjustment in basal metabolic rate or insulation and core temperature is independent across a wide range of ambient temperature (Swanson and Weinacht 1997). Physiologically, bobwhite respond to acute cold stress primarily through adjustment in metabolic heat production and devote a large percentage (60–70%) of their winter energy expenditures to thermoregulation (Swanson and Weinacht 1997, Guthery 2002).

Thermoregulation in bobwhite has been the focus of a small number of studies examining both cold and heat stress. Case (1973) estimated energy intake, excretory energy, and existence energy of bobwhite under a 10 light : 14 dark photoperiod at a range of temperatures from 5° to 35° C and described behavioral (huddling) and energetic responses of bobwhite to cold stress. Case and Robel (1974) reported empirical relationships between existence energy and temperature for nonlaying females and males at temperatures from 5° to 35° C. Spiers et al. (1983) used indirect respirometry to measure evaporative heat loss, O₂ consumption, CO₂ production, and body temperature of bobwhite at 10–35° C, in 5° increments. Swanson and Weinacht (1997) used indirect respirometry to measure basal metabolic rate (BMR), metabolic response to temperature (–10° to 30° C), and maximal capacity for thermogenesis during diurnal and nocturnal periods in both summer and winter. However, all of these studies were conducted under free convective conditions. Whereas the effects of temperature on metabolic rates of birds is well-understood, the effects of forced convection on metabolic heat loss have been measured for relatively few species, but include neonatal mallards (*Anas platyrhynchos*; Bakken et al. 1999), verdin (*Auriparus flaviceps*; Wolf and Walsberg 1996), white-crowned sparrow (*Zonotrichia leucophrys*; Wolf et al. 2000), Gambel's quail (*Callipepla gambelii*; Goldstein 1983), ruffed grouse (*Bonasa umbellus*; Thompson and Fritzell 1988), and greater sage grouse (*Centrocercus urophasianus*; Sherfy and Pekins 1995), among others. Simultaneous effects of wind and temperature on bobwhite thermoregulation have not been measured.

Bobwhites can mitigate effects of thermal stress through selection of microclimates that produce energetically more favorable standard operative temperatures (T_{es}; Guthery et al. 2005, Hiller and Guthery 2005, Tanner et al. 2017). Microhabitats alter heat balance of

individuals through effects of vegetation structure and substrate on radiant, conductive, and convective heat gain or loss. More specifically, during periods of cold stress, reflective and structural properties of roosting vegetation may increase T_{es} and reduce energy requirements by reducing radiant heat flow, conductive heat loss to soil surface, wind speed, and heat loss to forced convection. Empirical estimates of functional relationships between energy costs and temperature across a range of convective conditions would inform our understanding of the adaptive significance of microhabitat selection. Toward this end, we report on the effects of forced convection and temperature on the roosting metabolic heat production of winter-acclimated northern bobwhite.

METHODS

We acquired 8 bobwhites (4 M and 4 F) from a central Missouri commercial quail farm in December 1991. All bobwhites were 8–10 months old and 173–222 g (\bar{x} = 201.5, SE = 1.3 g) during the course of the experiment. We housed bobwhites colonially at ambient temperature in an open-air, covered pen at the Charles C. Green Wildlife Area 14.4 km south of Columbia, Missouri, USA. Birds were held on concrete floor with pine shavings litter. We provided bobwhites ad libitum water and commercial (Purina®; Purina Mills, LLC, Gray Summit, MO, USA) game bird feed. We conducted metabolic trials between 6 January and 9 March 1992. All birds were winter-acclimated at the time of trials. Mean monthly temperatures for Columbia, Missouri, during December 1991, January 1992, and February 1992 were 2.8°, 1.7°, and 4.4° C, respectively. Bobwhites were held at ambient winter photo periods without artificial light, and we conducted all trials during the dark portion of the diel cycle between 1900 and 0600 hours.

We estimated metabolic heat production using open circuit respirometry (Withers 1977) in a closed-circuit wind tunnel (Bakken et al. 1989). We measured oxygen concentration using an Applied Electrochemistry S-3A/1 oxygen analyzer with an R-1 flow control (Applied Electrochemistry, Inc., Sunnydale, CA, USA). Measurements of oxygen consumption at free convection used a 7.3-L (14.6 × 27.9 × 17.8 cm) rectangular chamber fabricated from galvanized sheet metal. Measurements under forced convection were in a 93.5-L dual-return, recirculating wind tunnel modeled after Bakken et al. (1989) and fabricated from galvanized sheet metal. The surfaces within the free-convection chamber and wind tunnel were coated with a nonhygroscopic, flat black paint. Within the wind tunnel, 2 stainless-steel wire-mesh screens confined birds within a 4.3-L chamber. We generated wind with a 25.4-cm-diameter × 20.3-cm blower wheel powered by a one-quarter horsepower electric motor regulated by a proportional controller. We regulated wind speed within the test chamber by varying voltage to the motor and measured wind speed at bird-level with a hot-wire anemometer. Stainless steel mesh screens (n = 2) in each of the 2 return chambers reduced turbulence and enhanced laminar flow character-

istics in the test chamber. We did not measure uniformity of airflow within the test chamber; however, based on similar design, it was likely comparable to the $\pm 5\%$ reported by Bakken et al. (1989). We regulated temperature in the free convection chamber and wind tunnel by nesting the chambers within a 651-L chest freezer. The freezer was modified to accommodate the blower motor shaft penetrating the end wall with the fan motor and controller outside the freezer. During experimental trials, mean deviation of air temperature in the chamber relative to desired set temperature was -0.1°C (SD = 0.9). Wall temperature differed from air temperature by $<0.5^\circ\text{C}$; consequently, T_a approximated T_e .

We measured metabolic heat production (VO_2 measured in mL O_2 per minute) for each of the 8 birds at each of 8 temperatures (-15° , -10° , -5° , 0° , 5° , 10° , 20° , 30°C) under free convection. Additionally, we measured metabolic heat production for each of the 8 birds at each of 6 combinations of 3 wind speeds (0, 1, 2 m/sec) and 2 temperatures (-15° and 0°C). We measured metabolic heat production under free convection during nocturnal roosting between 6 January and 9 March 1992. Metabolic measurements under forced convection were taken between 6 January and 4 March 1992. We generated a random order for individual bird, wind, and temperature combinations and conducted 1–3 trials/night. Individual birds experienced only 1 wind–temperature combination per night. We conducted nocturnal trials between 1900 and 0600 hours. At noon the day of the trial, we removed selected individuals from colony pens and confined them in a small cage to restrict access to food a minimum of 7 hours before the trial so that birds were in a postabsorptive state during the trials. Immediately prior to trials, we restrained birds in a nylon stocking and weighed them to 0.1 g on a precision balance. We placed birds unrestrained within the chamber on a wire mesh grate. We captured fecal droppings in a tray of mineral oil beneath the wire grate. Visual observations through a door in the top of the chamber confirmed that birds were resting during trials. We allowed birds to adjust to experimental temperature and convective conditions for 60 minutes prior to measurement of oxygen consumption. This equilibration period was adequate to allow VO_2 to achieve steady-state conditions.

Dry, CO_2 -free room air was drawn through the chamber at 1,000–2,500 mL/minute and regulated with a Cole-Parmer (Vernon Hills, IL, USA) precision rotameter. A sample of dry, CO_2 -free outflow chamber air was drawn through the S-3A Oxygen analyzer at 100 mL/minute and $p\text{O}_2$ continuously analyzed. We recorded fractional concentration of O_2 at 5-minute intervals and averaged over a 40-minute trial that followed the 60-minute acclimation–equilibration period. We calculated oxygen consumption using Withers (1977) equation 4a for dry, CO_2 -free air entering the chamber and the oxygen analyzer (e.g., H_2O and CO_2 absorbents upstream of flowmeter and O_2 sensor). For calculations of metabolic heat production from VO_2 , we assumed a respiratory quotient of 0.8 (Spiers et al. 1983) and 4.8 calories generated for each milliliter oxygen consumed (Rasmussen and Brander 1973). We express thermoregulatory

responses of bobwhite in conventional units of oxygen consumption and watts ($\text{VO}_2/\text{min}/\text{bird}$, $\text{VO}_2/\text{min}/\text{g}$, W/bird , W/m^2). We estimated surface area from body mass using the equation for galliforms from Leighton et al. (1966) as cited in equation 1 of Spiers et al. (1983). We calculated total thermal conductance ($^\circ\text{C}$ measured in $\text{W}/\text{m}^2/^\circ\text{C}$) according to Calder and King (1974) as illustrated in equation 3 in Spiers et al. (1983). We calculated dry thermal conductance (C_d measured in $\text{W}/\text{m}^2/^\circ\text{C}$) following Spiers et al. (1983) equation 4.

We tested effects of sex and body mass on VO_2 and C_d under free convection across the range of T_e using a repeated-measures, mixed-model analysis of covariance with VO_2 as response, sex and T_e as categorical fixed effects, and body mass as a continuous covariate in PROC MIXED, SAS 9.4 (SAS 2002). To account for the repeated nature of the measurements of VO_2 on the 8 individual birds at each of the 8 temperatures, we included BIRD ID as a random effect using SUBJECT = BIRD ID and REPEATED = T_e options. In our mixed-model analysis we considered 4 alternative covariance structures (variance components, first-order autoregressive, compound symmetry, and heterogeneous compound symmetry) and selected heterogeneous compound symmetry based on lowest Akaike Information Criterion and Chi-square model-fit statistics.

Based on work by Case and Robel (1974), Spiers et al. (1983), and Swanson and Weinacht (1997), we anticipated that the lower critical temperature (T_{lc}) was somewhere below, and the upper critical temperature (T_{uc}) somewhere above, 30°C . Assuming that this value was within the thermoneutral zone (TNZ), we estimated standard metabolic rate (SMR) from measurements of VO_2 at 30°C under free convection. We modeled VO_2 below the TNZ as a function of temperature with simple linear regression using PROC REG in SAS (SAS 2002). We estimated T_{lc} for winter-acclimated bobwhite under free convection as the intersection between the regression line of VO_2 on temperature and a horizontal line through the mean VO_2 at 30°C . We modeled effects of wind on VO_2 at -15° and 0°C with linear regression using PROC REG in SAS 9.4 (SAS 2002). We tested for differences in slope and intercept for the 2 temperatures using a dummy regression model with VO_2 as response; wind speed as a continuous variable (0, 1, 2 m/sec); T_e (0° and -15°C) as a dummy variable coded 0 and 1, respectively; and the interaction WIND \times T_e . The interaction between wind speed and T_e indicator variable was not significant ($t_1 = 1.05$, $P = 0.40$), indicating that the slopes of the regression lines for 0° and -15°C did not differ. We modeled common slopes but different intercepts using a reduced model with VO_2 as response, wind speed as a continuous variable, and T_e as a dummy variable (i.e., leaving out the interaction of WIND \times T_e). Estimates of metabolic response are reported in the results as $\bar{x} \pm$ standard error (SE).

We conducted bird husbandry, handling, and experimental trials in accordance with guidelines in the American Ornithologists Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists Union 1988) and consistent with those of the

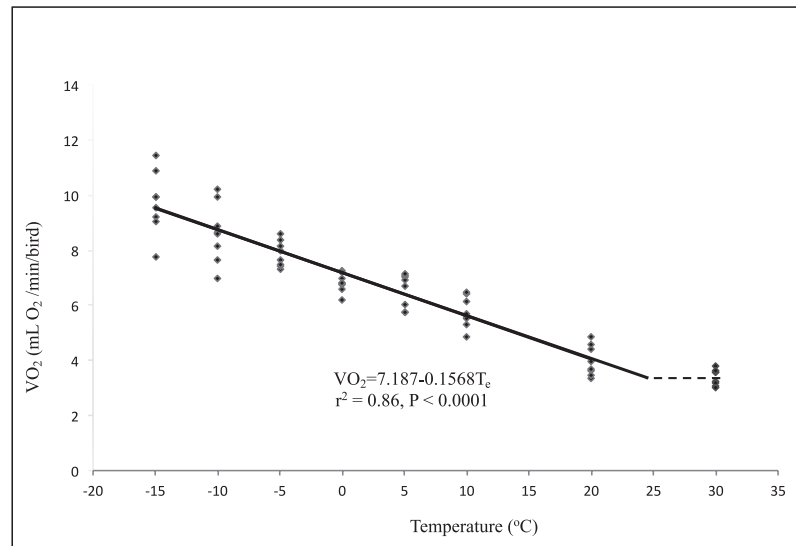


Fig. 1. Effect of operative temperature (T_e) on metabolic heat production (VO_2) of northern bobwhite below the lower critical temperature ($n = 64$), from tests conducted on captive birds in Columbia, Missouri, USA, during 6 January-9 March, 1992.

University of Missouri Institutional Animal Care and Use Committee.

RESULTS

Standard metabolic rate of bobwhite, measured at $T_e = 30^\circ\text{C}$, was 3.4 ± 0.11 mL O_2 /minute/bird or 1.14 ± 0.04 W/bird for a bird of mean weight 198.7 g (Table 1). Mass-specific SMR was 0.0171 ± 0.0004 mL O_2 /minute/g. Surface-area-specific SMR was 41.9 ± 1.1 W/m². Over the range of body mass of birds used in this study ($\bar{x} = 201.5 \pm 1.3$ g, $n = 64$), metabolic rate was influenced by body mass ($F_{1,48} = 25.85$, $P < 0.001$) but did not differ between males ($\bar{x} = 6.68 \pm 0.104$ mL O_2 /min/bird) and females ($\bar{x} = 6.54 \pm 0.104$ mL O_2 /min/bird). VO_2 increased by 0.024 mL O_2 /minute/bird for each 1-g increase in body mass. Outside the thermoneutral zone, BMR was negatively related to operative temperature (VO_2 (mL/min/bird) = $7.187 - 0.1568 \times T_e$, $r^2 = 0.86$, $P < 0.001$; or VO_2 (mL/g/hr) = $2.139 - 0.0470 \times T_e$, $r^2 = 0.86$, $P < 0.001$; Fig. 1). The mean lower critical temperature for bobwhite was estimated as 24.1°C . Metabolic rate (M-E)

was linearly related to wind speed (WS) at -15°C ($VO_2 = 9.741 + 0.4609 \times WS$, $r^2 = 0.98$, $P = 0.001$) and at 0°C ($VO_2 = 6.713 + 0.4609 \times WS$, $r^2 = 0.98$, $P = 0.001$; Fig. 2). Dry thermal conductance (C_d) differed across operative temperatures (Fig. 3; $F_{7,48} = 30.39$, $P < 0.001$). Dry thermal conductance at 30°C was greater than at all other operative temperatures but C_d did not differ among operative temperatures below the lower critical temperature ($P > 0.05$).

DISCUSSION

Our findings represent 1 of just 3 experimental studies that directly measure the metabolic heat production of bobwhite within and below the thermoneutral zone and the only estimate of effect of wind speed on roosting metabolism. Our estimates of standard metabolic rate are within the range of values previously reported but we were able to more specifically estimate the lower critical temperature and the linear relationship between metabolic heat production and temperature below the lower critical temperature. The observed standard metabolic rate of 3.4

Table 1. Mean (SE) body mass, metabolic heat production measured as VO_2 (mL O_2 /min/bird), VO_2/g (mL O_2 /min/g), W (watts per bird), W/m² (watts/m²); thermal conductance, C (W/m²/°C); and dry thermal conductance C_d (W/m²/°C) for winter-acclimated, nocturnal roosting northern bobwhite across operative temperatures (T_e) from -15°C to 30°C under free convection. Data derived from tests conducted on captive birds in Columbia, Missouri, USA, during 6 January-9 March, 1992.

T_e	n	Mass (g)	VO_2	VO_2/g	W	W/m ²	C	C_d
-15	8	200.4 (4.9)	9.74 (0.40)	0.0487 (0.0019)	3.27 (0.13)	119.4 (4.7)	2.13 (0.08)	2.11 (0.08)
-10	8	203.8 (3.4)	8.67 (0.38)	0.0426 (0.0021)	2.90 (0.13)	104.9 (5.0)	2.05 (0.10)	2.03 (0.10)
-5	8	200.0 (4.1)	7.89 (0.17)	0.0395 (0.0010)	2.64 (0.06)	96.9 (2.3)	2.10 (0.05)	2.06 (0.05)
0	8	201.5 (3.2)	6.86 (0.12)	0.0340 (0.0003)	2.23 (0.04)	83.6 (0.8)	2.03 (0.02)	1.98 (0.02)
5	8	204.9 (4.4)	6.56 (0.22)	0.0320 (0.0009)	2.20 (0.07)	79.0 (2.2)	2.18 (0.06)	2.11 (0.06)
10	8	201.4 (3.7)	5.78 (0.20)	0.0287 (0.0009)	1.94 (0.07)	70.5 (2.2)	2.26 (0.07)	2.15 (0.07)
20	8	201.4 (3.7)	4.02 (0.20)	0.0200 (0.0010)	1.35 (0.07)	49.1 (2.5)	2.32 (0.12)	2.09 (0.11)
30	8	198.7 (3.9)	3.40 (0.11)	0.0171 (0.0004)	1.14 (0.04)	41.9 (1.1)	3.74 (0.10)	2.99 (0.08)

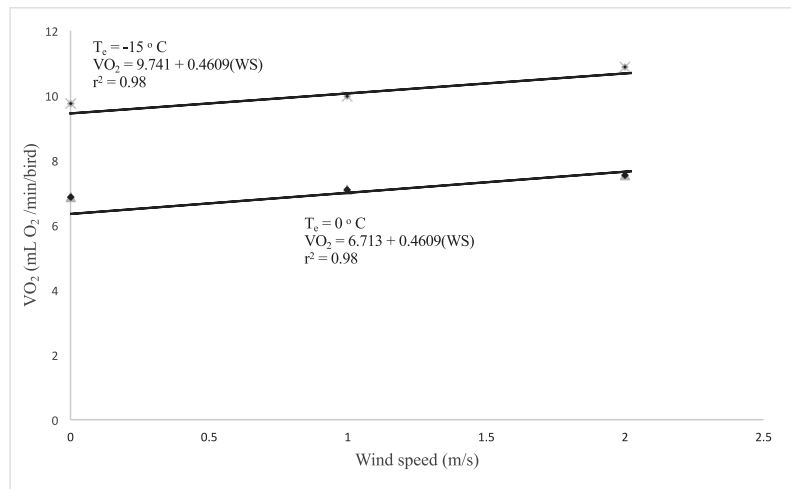


Fig. 2. Effect of forced convection on mean metabolic heat production of northern bobwhite at operative temperature (T_a) of -15°C ($n = 3$), $P < 0.001$) and 0°C ($n = 3$, $P < 0.001$), from tests conducted on captive birds in Columbia, Missouri, USA, during 9 January-4 March, 1992. Error bars are ± 1 standard error (SE).

mL O₂/minute/bird converted to kilocalories and extrapolated to a 24-hour period (23.50 kcal/bird/day) was 16% less than the 28.06 kcal/bird/day predicted from allometric equations for a 198.7-g bird (Zar 1969) and 8% less than existence metabolism (25.56 kcal/bird/day) reported by Case and Robel (1974) for bobwhite at 30°C and 10-hour photoperiod. Similarly, Guthery (2002:13) used equations derived from Case and Robel (1974) to estimate daily energy requirements of bobwhite, adjusted for active and inactive periods, during winter under a 10-hour day length at 25°C . The daily energy requirement of 117.1 kJ/day estimated by Guthery (2002) was approximately 16% greater than the 98.37 kJ/day/bird predicted from our measurement of VO₂ at 30°C . Insofar as SMR in our study was measured only during the inactive period and both the Case and Robel (1974) study and Guthery (2002)

included both active and inactive periods, a slightly lower value is not unexpected. Only 2 studies—Spiers et al. (1983) and Swanson and Weinacht (1997)—have measured metabolic heat production of bobwhites using indirect calorimetry. Spiers et al. (1983) reported metabolic heat production of bobwhite at 30°C as 47.76 W/m^2 or 12% greater than the 41.9 W/m^2 that we observed. However, the mass-specific SMR ($1.03 \pm 0.03\text{ mL O}_2/\text{g/hr}$) that we observed was only 3% less than that ($1.06\text{ mL O}_2/\text{g/hr}$) reported by Spiers et al. (1983). The mean SMR of $3.4 \pm 0.11\text{ mL O}_2/\text{minute/bird}$ observed during our study was approximately 9.6% less than the $3.76\text{ mL O}_2/\text{minute/bird}$ BMR reported by Swanson and Weinacht (1997) for winter-acclimated bobwhites. Winter-acclimated birds used in Swanson and Weinacht (1997) had approximately 10% greater mean body mass

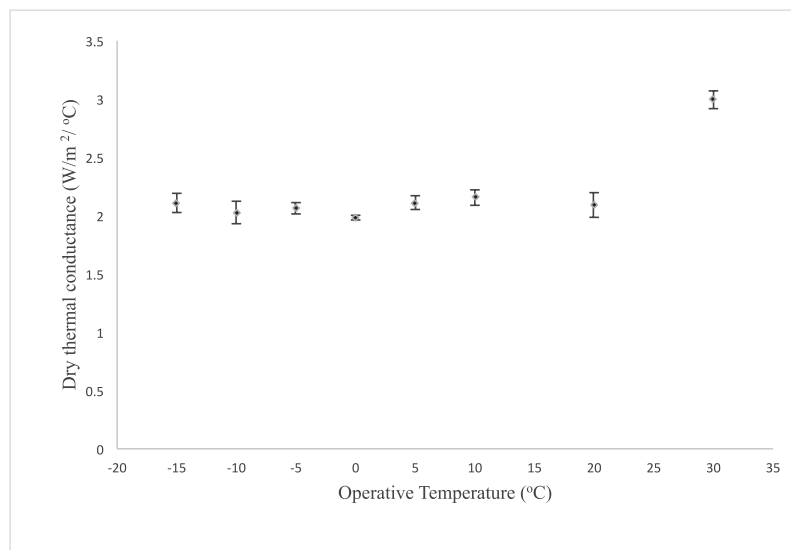


Fig. 3. Dry thermal conductance of northern bobwhite ($n = 8$) at operative temperatures (T_a) of -15 – 30°C , from tests conducted on captive birds in a Columbia, Missouri, USA, during ###-###. Error bars are ± 1 standard error (SE).

(228 ± 36 g) and the mass-specific BMR observed in our study ($1.03 + 0.03$ mL $O_2/g/hr$) was similar to that reported in their study ($1.01 + 0.11$ mL $O_2/g/hr$).

Hiller and Guthery (2005) estimated that bobwhites exhibited heat-seeking behavior at $T_e < 26.7^\circ$ C. Case (1973) speculated that the lower critical temperature for bobwhite was between 10° and 20° C. Spiers et al. (1983) did not specifically determine T_{lc} but speculated it might be between 30° and 35° C. Our estimate of T_{lc} (24.1° C) was intermediate between the values reported by Swanson and Weinacht (1997) for winter- (22.4° C) and summer- (25.5° C) acclimated bobwhite and similar to the 26.7° C determined by Hiller and Guthery (2005). Below the thermoneutral zone, metabolic response of bobwhite increased linearly with decreasing T_e . The slope of the relationship between mass-specific metabolic rate and T_e (-0.0470 mL $O_2/g/hr$) was nearly identical to that reported for winter nocturnal bobwhite (-0.05 mL $O_2/g/hr$) in Swanson and Wienacht (1997) and similar to that (-0.0717 mL $O_2/g/hr$) reported in Spiers et al. (1983).

Dry thermal conductance within the thermoneutral zone (2.99 ± 0.08 W/m $^2/^\circ$ C or 0.07 ± 0.002 mL $O_2/g/hr$) was approximately 50% greater than that observed below the T_{lc} (2.03 – 2.32 W/m $^2/^\circ$ C or 0.048 – 0.051 mL $O_2/g/hr/^\circ$ C). Dry thermal conductance below the thermoneutral zone was relatively invariant, indicating that below the T_{lc} bobwhites had adopted all available behavioral and postural means of energy conservation. Our observed C_d below the T_{lc} was less than the 3.18 – 3.35 W/m $^2/^\circ$ C reported by Spiers et al. (1983) but similar to the winter nocturnal rate (0.058 ± 0.007 mL $O_2/g/hr/^\circ$ C) reported by Swanson and Weinacht (1997).

Metabolic rate of bobwhites increased linearly with wind speed at both -15° C and 0° C and the slopes of the relationship between VO_2 and wind speed did not differ between operative temperatures. Although avian metabolic rate has commonly been reported to vary with the square root of wind speed (e.g., Thompson and Fritzell 1988), Goldstein (1983) reported that metabolic rate of Gambel's quail increased linearly with wind speed. Goldstein (1983) reported that the slope of the relationship between metabolic rate and wind speed varied across T_a with greater slope at lower temperatures. Thompson and Fritzell (1988) also reported that, for ruffed grouse, slopes differed between T_e . However, they observed the steepest slope at the higher temperature, opposite the pattern reported by Goldstein (1983). As Goldstein (1983) acknowledged, at temperatures below the thermoneutral zone, the difference between T_b and T_a (ΔT) creates the gradient that drives the rate of heat loss; and loss is greater at lower T_a , assuming constant T_b . Therefore, heat loss will increase to a greater degree across wind speeds at a lower temperature than higher (Goldstein 1983). Consequently, the slope of the relationship between metabolic heat production and wind speed should increase with ΔT (i.e., lower T_a). The failure to detect T_e -specific slopes in our study may have been, in part, a function of low power associated with the relatively small number of wind speeds examined ($n = 3/T_e$ vs. $n = 5/T_e$ in Goldstein 1983).

Across much of the bobwhite distribution, winter night-time temperatures commonly fall below -15° C and impose substantive thermoregulatory costs on bobwhites. At a temperature of -15° C with no wind, our predicted metabolic rate was 2.9 times greater than SMR. A wind speed of 2 m/second increased metabolic rate by an additional 9.5%. At temperatures below the TNZ, birds may respond to thermal stress by regulating metabolic heat production (Case 1973, Case and Robel 1974, Spiers et al. 1983, Swanson and Weinacht 1997), huddling (Case 1973), and selection of favorable microclimate (Roseberry 1964, Hiller and Guthery 2005, Tanner et al. 2017). Guthery et al. (2005) used thermal radiotransmitters to demonstrate that at ambient temperatures $< 16.2^\circ$ C, roosting bobwhites experience standard operative temperatures greater than ambient air temperatures, meaning that roost sites and roosting behavior collectively improve the thermal environment for bobwhite, leading to energy conservation. The magnitude of this effective thermal increment was 8.6° C at an ambient air temperature of 0° C and increased with decreasing temperature (Guthery et al. 2005). Vegetation structure at roost sites that reduces wind speed will diminish heat loss from forced convection and microhabitat features that decrease convective, radiant, and conductive heat loss may improve energy balance. Tanner et al. (2017) concluded that lack of favorable microhabitats during severe winter weather can substantially limit distribution of individual bobwhite coveys. They found a significant reduction in usable space below -15° C and predicted that, during the lowest temperatures studied in northern Oklahoma, favorable microhabitats occurred on only 18.6% of the landscape. If microhabitat structure alters the radiative or convective environment, it will almost certainly affect T_{es} . As illustrated in our study, microhabitat structure that simply reduces wind speed at bird-level from 2 m/second to free convective conditions will result in nearly 10% reduction in thermoregulatory costs. Tanner et al. (2017) emphasized the fitness-reducing effect of winter conditions and cautioned that habitat measurements averaged across years or seasons will incorrectly identify critical habitat elements, and confound understanding of bobwhite energy conservation and predator avoidance. Our empirical estimates of functional relationships between energy costs and temperature across a range of convective conditions provide a basis for understanding the adaptive significance of bobwhite microhabitat selection.

MANAGEMENT IMPLICATIONS

Our finding of increased energy expenditures by bobwhites in response to low temperature and increasing wind speed reinforces the need by bobwhite managers to consider factors that provide a positive energy balance (i.e., more energy intake; for example, via high-energy seeds) and less energy loss (e.g., via habitat, less distance traveled within habitats, less harassment by hunters and dogs).

With few exceptions bobwhite populations are declining, more so on the northern fringe from Wisconsin

to New Jersey, with bobwhites extirpated in Pennsylvania (McKenzie et al. 2015:46). Bobwhite management is closely scrutinized, with citizens simultaneously expecting very large populations for hunting, populations that are viable, and population restoration in areas of extirpation. In areas subject to severe winter, managers should thoughtfully consider energy balance of individual bobwhite.

As noted in this proceedings, there is considerable demand and need for translocation of bobwhites and among the uncertainties of this practice is the appropriateness for energy balance of moving smaller southern bobwhites to northern latitudes. Our finding of increased thermoregulatory energy expenditure adds emphasis to existing knowledge for bobwhites in this regard and reinforces the importance of considering ecological principles (i.e., Allen's and Bergmann's Rules). The bobwhites' relatively small size and high surface-area-to-volume ratio translates to size-specific energy capacity. Beyond generalizations, however, researchers should provide managers with bobwhite energy budgets for translocation destinations and data regarding the capacity of different-sized bobwhites to thrive energetically in those locations.

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