

The Wilson Journal of Ornithology 127(3):510–514, 2015

Resting Metabolic Rates of Adult Northern Shrikes (*Lanius excubitor*) Wintering in Northern Wisconsin

James D. Paruk,^{1,4,5} Sheldon J. Cooper,² Anna O. Mangan,¹
Ryan S. Brady,³ and Logan Tucker¹

ABSTRACT.—Resting metabolic rate (RMR) represents a significant component of an animal's energy budget and is correlated with ecological, physiological and life-history parameters. We measured resting metabolic rates of 14 adult Northern Shrikes

(*Lanius excubitor*) wintering in northern Wisconsin (Ashland and Bayfield Counties) over a 2-year period (Jan–Apr 2008 and 2009). The average (\pm SE) RMR was 3.09 ± 0.45 ml O₂/g/hr (range 2.46–3.83) and represent the first reported RMR values for adults of this species from the Nearctic. Our RMR values were 50% higher than RMRs gathered from summer adult Northern Shrikes in the Palearctic. These data suggest Northern Shrikes exhibit seasonal variation in their RMR as a potential means of winter acclimatization. Received 16 April 2014. Accepted 17 January 2015.

¹Northland College, 1411 Ellis Ave., Ashland, WI 54806, USA.

²University of Wisconsin-Oshkosh, 800 Algoma Blvd, Oshkosh, WI 54901, USA.

³Wisconsin Department of Natural Resources, 2501 Golf Course Rd, Ashland, WI 54806, USA.

⁴Biodiversity Research Institute, 276 Canco Road, Portland, ME 04106, USA.

⁵Corresponding author; e-mail: jim.paruk@briloon.org

Key words: avian physiology, basal metabolic rate, *Lanius excubitor*, Northern Shrike, winter acclimatization.

The rates at which birds use energy may have profound effects on fitness, thereby influencing evolution, ecology, behavior and physiology (McKechnie and Swanson 2010). Overwintering of small birds (<100 g) in cold temperate regions requires prolonged expenditure of energy in regulating thermogenesis (Cooper and Swanson 1994). Also, foraging time is decreased in winter due to shorter days and can be further restricted by heavy snow or ice cover. To cope with these harsh environmental conditions, wintering passerines undergo seasonal acclimatization which helps them maintain thermoregulatory homeostasis. Seasonal acclimatization in birds is largely a metabolic process (Swanson 1991) and metabolic adjustments should play a prominent role in explaining both seasonal and interspecific variation in cold tolerance. Winter acclimatized passerines are better at tolerating cold than summer ones (Cooper and Swanson 1994, O'Connor 1995, Swanson 2010) and it is suspected that birds overwintering in cold climates have a high capacity for cold tolerance through metabolic adjustments (Swanson 2001, Cooper 2002).

The Northern Shrike (*Lanius excubitor*) is a small passerine (60–75 g) that breeds in taiga and taiga-tundra ecotones across Canada and Alaska, but many individuals migrate and spend the winter in the northern USA. These individuals remain for 4.5–5.5 months, before returning to their breeding areas (Cade and Atkinson 2002; JDP, pers. obs.). Shrikes are sit-and-wait predators that perch near or at the tops of trees, exposed to the rigors of the environment, where they scan for small mammals, birds, and insects (Atkinson 1993, Atkinson and Cade 1993). In winter, they feed on microtine rodents, and occasionally, birds (Cade 1967, Cade and Atkinson 2002). Basal metabolic rate been determined for a few summer individuals from the Palearctic (Kendeigh et al. 1977), and for nestlings (Cade 1967), but no metabolic data for adults of this species has been gathered in the Nearctic. Metabolic data on Northern Shrikes would be useful to assist in understanding any physiological adjustments they make to survive harsh winter environmental conditions. In addition, it would assist conservationists in making better predictions on how this species' range may change during periods of rapid climate change (Bradshaw and Holzapfel 2006). The role of winter temperature and the interplay between temperature and metabolism in affecting bird distributions is unclear (Root 1988) and

currently under further investigation (Canterbury 2002, Swanson and Garland 2008). Thus our objective was to provide measures of metabolic data for adult Northern Shrikes inhabiting the Nearctic.

METHODS

We captured Northern Shrikes in Ashland and Bayfield counties (46° 34' N, 90° 58' W) located in northern Wisconsin from 1 February–6 April 2008 and 22 January–13 April 2009.

Because the winter ranges of the two potential subspecies (*invictus* and *borealis*) overlap in our study area, we cannot be certain of the subspecies we studied. The Northern Shrike is distributed widely across the Holarctic, and their taxonomy is unresolved both in North America and across the Palearctic (Patten and Unitt 2002). Depending on the authority, there are 18–20 recognized subspecies divided into two to four groups (Cade and Atkinson 2002). In North America they are listed as one variable subspecies, *L. e. borealis* but some authorities recognize two subspecies, *borealis* and *invictus* (Cade and Atkinson 2002).

Decadal (2000–2009) winter monthly (Jan, Feb, Mar and Apr) average temperatures, wind speed, and snowfall for the area were as follows: temperature (–11, –8.3, –2.8, 4.2°C), wind speed (13.5, 8.5, 10.5, 14.5 kph) and snowfall (40.1, 31.5, 30.7, 15.2 cm) (www.NOAA.gov). Birds were caught during the afternoon hours (1400–1700 hrs) using a round Potter trap baited with live mice (*Peromyscus* sp.; Craig 1997). In the field, age and fat deposits were determined by a combination of molt and plumage features (Pyle 1997, Brady et al. 2009) and using the well-established Kaiser method (Pyle 1997), respectively. Sex was determined genetically by using DNA from a breast feather (see Brady et al. 2009). After field measurements, shrikes were transported to the laboratory (<25 min) and body mass was determined to the nearest 0.1 g using a portable electronic balance (Scout II, Ohaus Corp., Parsippany, NJ, USA). Shrikes were then housed in avian cages at room temperature (20–25°C) without food or water.

Ecophysiologicals use basal metabolic rate (BMR) for comparisons of energetics among species, or across seasons, measured as ml O₂ consumed/g/hr (Hudson et al. 2013). Theoretically, BMR is the minimum metabolic rate required for maintenance in endotherms and is measured under a suite of conditions (e.g., within an animal's

thermoneutral zone, under post-absorptive digestive conditions, see McNab 1997). There is some concern that BMR can never be achieved in the laboratory, so the term resting metabolic rate (RMR) is often used, even when BMR conditions are met (Swanson 2010). We report our values as RMR instead of BMR, but because the terms are closely linked and BMR predominates the literature, we use BRM in the discussion when comparing our results.

Laboratory Metabolism Measurements.—Resting metabolic tests were performed at night (2200–0400) (rest-phase), ≥ 4 hrs post capture in order to minimize captivity effects on metabolic rate (Warkentin and West 1990). Birds were fasted for at least four hours prior to rest-phase measurements. We determined the metabolic rate of Northern Shrikes by measuring their oxygen consumption (VO_2) at stable air temperatures of 30°C. Birds were placed in 1.5-L glass metabolic chambers, which were equipped with a wire platform affixed over a container of mineral oil. Each chamber was located inside an insulated cabinet in which the temperature was controlled using a Pelteir device. The temperature was controlled within 1.0°C and monitored using a thermocouple thermometer (TC-1000, Sable Systems International, North Las Vegas, NV, USA). Each bird was placed in the chamber for 90 min, the first 30 min was used for equilibration, followed by 60 min test in which the minimum 10-min period was used for oxygen consumption. An open-circuit respirometry system was utilized to measure metabolic rates and VO_2 was recorded with an oxygen analyzer (FoxBox Respirometry System, Sable Systems International, North Las Vegas, NV, USA). Flow rates of dry, CO_2 -free air of 600–620 ml/min were maintained upstream of the metabolic chambers for all tests using a precision rotameter (model FL-3802, OMEGA Engineering Inc., Stamford, CT, USA). The rotameter was calibrated $\pm 1\%$ accuracy using a soap bubble meter. These flow rates provided changes in oxygen content between influx and efflux gas of 0.4–0.8% and maintained oxygen content of efflux gas above 20.1%. The oxygen analyzer was referenced against incurrent gas before and after each measurement period in order to correct for any drift in the baseline. Oxygen consumption was calculated as steady state VO_2 and corrected for standard temperature and pressure (Depocas and Hart 1957, Hill 1972: equation 2). Prior to metabolic measurements,

TABLE 1. Resting metabolic rates of 14 adult Northern Shrikes caught in northern Wisconsin (Ashland, Bayfield counties), in winter and early spring of 2008 and 2009.

Sex	Mass	O ₂ ml/min	Fat ^a	Date
Male	60.5	3.318	0	29 Feb
Male	62.6	3.088	0	27 Feb
Unknown	62.7	3.829	0	5 Feb
Female	64.4	3.032	2	10 Apr
Male	64.5	2.483	0	22 Jan
Male	64.5	2.463	1	30 Mar
Unknown	67.5	3.122	1	6 Apr
Male	68.5	2.853	1	1 Apr
Male	69.7	3.277	3	13 Apr
Male	70.2	3.010	2	8 Apr
Male	71.0	3.307	0	18 Mar
Female	72.1	2.774	4	7 Apr
Unknown	73.5	3.719	2	28 Mar
Male	74.7	3.012	0	1 Feb

^a Kaiser scoring index, 0–8 (Pyle 1997).

chambers were checked for leaks by momentarily monitoring efflux gas flow rates with a rotameter. Leaks would have been evident as a marked decrease flow rate from the upstream rotameter; no leaks were detected in our chambers. After metabolic tests, birds were banded with an aluminum USFWS band and a unique series of color bands (for other studies). Shrikes were released at the site of capture the following day (≤ 17 hrs after being caught).

RESULTS

We caught 14 adult Northern Shrikes, seven in 2008 and 2009, respectively. Eleven of the 14 individuals were sexed genetically, three were not. Of these, nine were males and two were females. The average mass was 67.6 ± 1.5 g (range 60.5–74.7 g) and the average RMR was 3.09 ± 0.45 ml O₂/g/hr consumed (range 2.46–3.83) (Table 1). There was no correlation between body size and RMR ($r = 0.05$). Winter birds (Jan–21 Mar) showed no measurable (or observable) body fat whereas spring birds (>21 Mar) displayed various levels of fat deposits likely associated with premigratory condition (Table 1).

DISCUSSION

Our mean RMR value of 3.09 ml O₂/g/hr for adult wintering Northern Shrikes in the Nearctic is greater than that reported from breeding *L. excubitor excubitor* in the Palearctic, 0.81 ml O₂/g/hr (Kendeigh et al. 1977) and 2.01 ml O₂/g/hr

(Bennett and Harvey 1987), but neither of these studies report sample size or methods. Cade (1967) reported a BMR of 2.0 ml CO₂/g/hr from 10 Northern Shrike nestlings (12 days post-hatching) and concluded that this value was likely very close to adult birds (based on Lasiewski and Dawson 1967). Using Cade's measured value of 2.0 ml CO₂/g/hr in 12-day old chicks and a respiratory quotient of 0.8 (Gessaman and Nagy 1988) this converts to 2.5 ml O₂/g/hr. Thus, our value of 3.03 ml O₂/g/hr is a 21% increase in winter relative to summer in Northern Shrikes. Basal metabolic rate is thought to be closely tied to phylogeny (Freckleton et al. 2002, Swanson 2010) and the closest relative of *L. excubitor* in the Nearctic is the Loggerhead Shrike (*L. ludovicianus*). Fortunately, the BMR from summer individuals for this species has been determined and is reported to be 1.79 ml O₂/g/h (Weathers et al. 1984). In addition, if BMR/RMR is close between these two congeners, RMR for winter birds in this study is more than 50% higher than summer Loggerhead Shrikes.

Laboratory acclimation experiments have shown that temperature can influence BMR, with it increasing during cold acclimation, and decreasing during warm acclimation (Swanson 2010). Winter acclimatization is primarily a metabolic response in birds and results in an increased ability to sustain high levels of shivering thermogenesis over prolonged periods, although it is unknown if increases in BRM contributes to increases in cold tolerance (Swanson 2010). Raising BMR is one way many small passerines survive and acclimatize to winter conditions in temperate zones. For example, many but not all birds show an increased BMR seasonally in apparent response to the low temperatures encountered during the winter (Dawson et al. 1985, Cooper 2002, Liknes et al. 2002, McKechnie 2008). Seasonal variation in BMR from both captive and wild birds ranges from 5–120% (Swanson 2010), with the maximum degree of seasonal variation in BMR for wild birds being 64% (documented for House Sparrows, *Passer domesticus*; Arens and Cooper 2005). Due to their small size, and ecological habits (e.g., predatory, perched in exposed places), we suspect Northern Shrikes exhibit seasonal variation in BRM as well, with higher rates in winter compared to summer.

A central goal of ecological and evolutionary physiology is to understand how animals partition energy resources and to identify sources of selection potentially responsible for variation in

maintenance requirements, such as BMR (Elgar and Harvey 1987, Ricklefs et al. 1996, Lovegrove 2000). The Northern Shrike is a small (<80 g) predatory species that spends the winter perched in exposed places, and faces many thermal and ecological challenges. For example, thermal conductance is inversely related to body size in birds, thus any given level of cold exposure should represent a greater cold challenge to small birds than to large ones (Aschoff 1981, Swanson 2001). More research focusing on obtaining BRM from breeding Northern Shrikes is needed before we can fully interpret and understand our metabolic data from wintering individuals. Lastly, studies examining seasonal morphological and behavioral adjustments wintering shrikes undertake would be welcomed.

ACKNOWLEDGMENTS

We thank B. Braden and S. Krerowicz for assisting in the capture of the shrikes, T. Kern for DNA sexing and H. B. Rinker, V. Spagnuolo and two anonymous reviewers for providing constructive comments on earlier versions of the manuscript. This project was partially funded by the Parsonage Fund at Northland College. Birds were banded under state and Federal Banding Permit number (22636). All procedures in the study were approved by the University of Wisconsin-Oshkosh IACUC and were consistent with guidelines provided by the American Ornithologists' Union.

LITERATURE CITED

- ARENS, J. R. AND S. J. COOPER. 2005. Metabolic and ventilatory acclimatization to cold stress in House Sparrows (*Passer domesticus*). *Physiological and Biochemical Zoology* 78:579–589.
- ASCHOFF, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comparative Biochemistry and Physiology, Part A* 69:611–619.
- ATKINSON, E. C. 1993. Winter territories and nights roosts of Northern Shrikes in Idaho. *Condor* 95:515–527.
- ATKINSON, E. C. AND T. J. CADE. 1993. Winter foraging and diet composition of Northern Shrikes in Idaho. *Condor* 95:528–535.
- BENNETT, P. M. AND P. H. HARVEY. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *Journal of Zoology* 213:327–363.
- BRADSHAW, W. E. AND C. M. HOLZAPFEL. 2006. Evolutionary response to rapid climate change. *Science* 312:1477–1478.
- BRADY, R. S, J. D. PARUK, AND A. J. KERN. 2009. Sexing adult Northern Shrikes using DNA, morphometrics, and plumage. *Journal of Field Ornithology* 80:198–205.
- CADE, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. *Living Bird* 6:43–86.

- CADE, T. J. AND E. C. ATKINSON. 2002. Northern Shrike (*Lanius excubitor*). The birds of North America. Number 671.
- CANTERBURY, G. 2002. Metabolic adaptation and climatic constraints on winter bird distribution. *Ecology* 83:946–957.
- COOPER, S. J. 2002. Seasonal metabolic acclimatization in Mountain Chickadees and Juniper Titmice. *Physiological and Biochemical Zoology* 75:386–395.
- COOPER, S. J. AND D. L. SWANSON. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. *Condor* 96:638–646.
- CRAIG, S. H. 1997. What goes around—gets caught!! An improved trap for shrikes. *North American Bird Bander* 22:124–125.
- DAWSON, W. R., W. A. BUTTEMER, AND C. CAREY. 1985. A reexamination of the metabolic response of House Finches to temperature. *Condor* 87:424–427.
- DEPOCAS, F. AND J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *Journal of Applied Physiology* 10:388–392.
- ELGAR, M. A. AND P. H. HARVEY. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Functional Ecology* 1:25–36.
- FRECKLETON, R. P., P. H. HARVEY, AND M. PAGEL. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160:712–726.
- GESSAMAN, J. A. AND K. A. NAGY. 1988. Energy metabolism: errors in gas-exchange conversion factors. *Physiological Zoology* 61:507–513.
- HILL, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *Journal of Applied Physiology* 33:261–263.
- HUDSON, L. N., N. J. B. ISAAC, AND D. C. REUMAN. 2013. The relationship between body mass and field metabolic rate among individual birds and mammals. *Journal of Animal Ecology* 82:1009–1020.
- KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pages 127–204 in *Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact and control* (J. Pinowski and S. C. Kendeigh, Editors). Cambridge University Press, Cambridge, UK.
- LASIEWSKI, R. C. AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.
- LIKES, E. T., S. M. SCOTT, AND D. L. SWANSON. 2002. Seasonal acclimatization in the American Goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor* 104:548–557.
- LOVEGROVE, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *American Naturalist* 156:201–219.
- MCKECHNIE, A. E. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. *Journal of Comparative Physiology B* 178:235–247.
- MCKECHNIE, A. E. AND D. L. SWANSON. 2010. Sources and significance of variation in basal, summit and maximal metabolic rates in birds. *Current Zoology* 56:741–758.
- MCNAB, B. K. 1997. On the utility of uniformity in the definition of basal rate of metabolism. *Physiological Zoology* 70:718–720.
- O'CONNOR, T. P. 1995. Metabolic characteristics and body composition in House Finches: effects of seasonal acclimatization. *Journal of Comparative Physiology B* 165:298–305.
- PATTEN, M. A. AND P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119:26–35.
- PYLE, P. 1997. Identification guide to North American birds. Part I. Columbidae to Ploceidae. Slate Creek Press, Point Reyes Station, Bolinas, California, USA.
- RICKLEFS, R. E., M. KONARZEWSKI, AND S. DAAN. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *American Naturalist* 147:1047–1071.
- ROOT, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- SWANSON, D. L. 1991. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. *Condor* 93:538–545.
- SWANSON, D. L. 2001. Are summit metabolism and thermogenic endurance correlated in winter-acclimatized passerine birds? *Journal of Comparative Physiology B* 171:475–481.
- SWANSON, D. L. 2010. Seasonal metabolic variation in birds: functional and mechanistic correlates. *Current Ornithology* 17:75–129.
- SWANSON, D. L. AND T. GARLAND JR. 2008. The evolution of high summit metabolism and cold tolerance in birds and its impact on present-day distributions. *Evolution* 63:184–194.
- WARKENTIN, I. G. AND N. H. WEST. 1990. Impact of long-term capacity on basal metabolism in birds. *Comparative Biochemistry and Physiology, Part A* 96:579–581.
- 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.