Am. Midl. Nat. 162:327–334

Seasonal Field Metabolic Rates of American Martens in Wisconsin

JONATHAN H. GILBERT[1]
Great Lakes Indian Fish and Wildlife Commission, P. O. Box 9 Odanah, Wisconsin 54861

PATRICK A. ZOLLNER[2]
North-Central Forest Experiment Station, USDA Forest Service, Rhinelander, Wisconsin 54501

ADAM K. GREEN[3]
Department of Wildlife Ecology, University of Wisconsin - Madison, Madison 53706

JOHN L. WRIGHT[4]
North-Central Forest Experiment Station, USDA Forest Service, Rhinelander, Wisconsin 54501

AND

WILLIAM H. KARASOV
Department of Wildlife Ecology, University of Wisconsin - Madison, Madison 53706

ABSTRACT.—We report on FMR of free-living American martens (*Martes americana*) in autumn and winter in northern Wisconsin. Mean body mass was significantly higher in males (1099 ± 43 [S.E.] g) than females (737 ± 28 g), with no significant difference by season. Daily mass change rates of martens did not differ from zero, and mass change rate and percent of body fat did not differ by gender or season. These data are consistent with our expectation that non-reproductive martens balance their energy budget on a near daily basis, even in winter, and rely little on body energy reserves. Energy expenditure, and hence food requirements, declined 24% from fall (1006 ± 96 kJ/d) to winter (725 ± 96 kJ/d), despite colder temperatures and deep snow. Both males and females were active nearly 50% less in winter (4.8 ± 1.0 h/d) than in autumn (9.1 ± 0.7). It appears that, in addition to lowering core body temperature and seeking thermal cover, martens decreased activity levels from fall to winter to reduce energy expenditures and food requirements.

INTRODUCTION

Field metabolic rate (FMR) measured with doubly labeled water (DLW) is the respiration energy expenditure of a free-living animal (Nagy *et al.*, 1999b; Speakman, 2000a). It can be used to estimate the resource demands of populations or in other kinds of studies that use energy as a currency in foraging, behavioral and life history analyses.

Body size of a species is the single most important predictor of FMR (Nagy, 2005), and a number of recent reviews have sought to identify additional predictors such as phylogeny,

[1] Corresponding author: Jonathan Gilbert, Telephone: (715) 685-2121; email - jgilbert@glifwc.org
[2] Present address: Department of Forestry and Natural Resources, Purdue University, 195 Marstellar Street, West Lafayette, Indiana 47907; email: pzollner@purdue.edu
[3] Present address: Santa Barbara Community College, Department of Biology, Santa Barbara, California 93101; email: green@sbcc.edu
[4] Wisconsin Department of Natural Resources, Tomahawk, Wisconsin 54487; email: John.Wright@Wisconsin.gov

diet and ambient temperature (Anderson and Jetz, 2005; Humphries *et al.*, 2005; Nagy *et al.*, 1999b; Speakman, 2000a). In temperate environments, the impact of ambient temperature, or its correlate ''season,'' on FMR is unclear and seems almost paradoxical. Nagy *et al.* (1999a) concluded that season had no effect on FMR, a result that challenges the expectation that a mammal would increase energy expenditure in winter when thermoregulatory costs presumably increase. Among the 10 studies of mammals reviewed by Covell *et al.* (1996) in which seasonal FMRs were reported, five studies reported lower FMR in winter than in summer. On the other hand, in an interspecific analysis Anderson and Jetz (2005) found that FMR was inversely related to ambient temperature during the FMR measurement period, which is a reasonable expectation considering that resting energy expenditure rate increases with decreasing temperatures in endotherms regulating body temperature. But, there are relatively few studies which allow comparisons of FMR between warm and cold seasons and, as pointed out by (Humphries *et al.*, 2005), there is a notable paucity of studies (<3% of 112 studies) obtained under conditions where average temperature was below 0 C.

Here, we report on FMR of free-living American martens (*Martes americana*) in autumn and winter in northern Wisconsin. Our study is important because it adds to the very small number of studies of mammals during very cold conditions, or that allow seasonal comparison. Our study also advances knowledge because it is one of a small number of studies on FMR of Carnivora. Martens' FMR during non-reproductive periods provides an excellent basis for estimating prey requirement, given information on prey energy content and fecal and urinary energy losses, because martens store relatively little body fat and must balance on a nearly daily basis their energy budget (Buskirk and Harlow, 1989), which is composed mainly of respiration.

Martens exhibit several attributes that could permit them to avoid high thermoregulatory and activity expenditures during the coldest season, and we predicted that in winter they would reduce their activity level and FMR, compared with autumn. These attributes include reduction in activity time from warm seasons to cold seasons (Thompson and Colgan, 1994; Zielinski *et al.*, 1983), seeking out under-ground or subnivean cover (Buskirk *et al.*, 1989; Gilbert *et al.*, 1997) which is generally warmer than ambient air temperature and can be warmed by the heat loss from resting animals, and lowering their body temperature when at rest in winter (Buskirk *et al.*, 1988).

The objective of this project was to measure the FMR of free-living martens in two seasons (autumn-Oct.–Nov. and winter-Jan.–Feb.) that place different thermal and locomotion stresses upon these animals. Jan.–Feb. was selected because they provided the coldest temperatures and deepest snows, which increase the cost of locomotion (Karasov, 1992). The autumn (Oct.) was selected to improve trapping efficiency over summer trapping (Gilbert, unpublished data). Interpretation of seasonal FMR would be difficult if associated activity patterns were not described (Covell *et al.*, 1996). Thus, the second objective of this study was to quantify activity patterns between the seasons and compare them to seasonal variation in FMR. We predicted that martens in winter would reduce their activity level and FMR, compared with autumn.

MATERIALS AND METHODS

STUDY AREA

Research was conducted on the Great Divide District of the Chequamegon-Nicolet National Forest, Ashland County, Wisconsin (46°09′N 90°56′W). The area has gently rolling drumlins and a mosaic of forest cover types including upland and lowland hardwood and

coniferous forests (Dumyahn *et al.*, 2008). Open water and non-forested upland and lowland areas (less than 10% stocking of trees) are also found within the study area. Average precipitation is 76.2 cm, and average annual snow is 127–152 cm. Average temperatures measured nearby in Hayward, WI during the periods of our DLW measurements were lower in winter (-10.3 ± 3.1 [S.D.] C) than in autumn (3.6 ± 1.4 (S.D.)).

Capture and handling of martens.—We captured American martens during two sessions; 15 Oct.–16 Nov. 2001 and 14 Jan.–22 Feb. 2002. Martens were captured in wire box traps ($23 \times 23 \times 66$ cm or $25 \times 30 \times 81$ cm, Tomahawk Trap Co., Tomahawk, WI) set as cubby sets baited with meat and commercial lure and checked daily. Captured martens were immobilized using an intramuscular injection of ketamine hydrochloride mixed 10:1 with xylazine (0.1 mg/kg body wt.). All captured animals were collared with radio-telemetry packages equipped with microprocessor activity sensors (Telonics, Mesa, AZ). Physical measurements were taken and the first lower premolar was extracted for aging using counts of cementum annuli Matsons Laboratory Milltown, MT). All animals were captured and handled in a manner consistent with the American Society of Mammalogists guidelines (ASM, 1998) and with approval of the animal care and use committee of the University of Wisconsin Madison.

Measurement of FMR.—FMR was determined during a 3–7 d period by the two-point DLW methodology (Schoeller *et al.*, 1986). Upon capture, a baseline blood sample (2 ml) was collected in a dry EDTA vacutainer and a premixed dose of DLW was injected intraperitoneally. The dose contained 0.27-g/kg (estimated TBW) 94% $H_2{}^{18}O$ (Rotem Industries Ltd., Israel), 0.13-g/kg (estimated TBW) 99% ^2H_2O (Cambridge Isotope Laboratories, Andover, MA, USA) and was diluted with 3% NaCl to physiological osmolarity (total dose 1.5 g/(kg estimated total body water, TBW)). The doses were calculated to ensure an in vivo enrichment of about 200 and 1200 δ ‰ for 18- oxygen and deuterium, respectively [(δ ‰ delta per mil) = $(R_{sample}/R_{standard} - 1) * 1000$ with R being the ratio of heavy to light isotope]. A second blood sample was drawn 3 h post-dose, when it was assumed isotopic equilibration in the body water had occurred. The marten was released at site of capture, and recaptured 2–7 d later when a third blood sample was taken. Blood was centrifuged (4 C, 15 min at 3500-rpm) for serum separation. Serum was stored at −20 C in cryogenically stable tubes until analysis by isotope ratio mass spectrometry. Water from serum samples was extracted by centrifugation (4 C, 45 min at 10,000-rpm) on regenerated cellulose filters (YM-50, Centricon, Bedford, MA, USA). Deuterium isotopic enrichments in hydrogen gas were measured after chromium reduction using a dual-inlet isotope ratio mass spectrometer (Delta Plus Mass Spectrometer, Finnigan MAT, San Jose, CA, USA), as previously described (Schoeller *et al.*, 2000). The ^{18}O isotopic analysis was performed by the CO_2 equilibration method on a Delta –S isotope ratio mass spectrometer (Finnigan MAT San Jose, CA, USA) using a continuous flow inlet system developed in the laboratory (Schoeller and Luke, 1997). CO_2 production was calculated according to the equation provided by Schoeller *et al.* (1986) corrected for isotopic change by the factors 1.041 and 1.007, respectively (Racette *et al.*, 1994). Total energy expenditure was calculated by the (Weir, 1949) equation using a food quotient of 0.8 estimated from the animal's diet. Lean body mass was estimated based on the isotopic dilution space, and fat mass was estimated as total body mass minus lean mass (Schoeller *et al.*, 1986).

Measurement of activity.—Activity levels of collared martens were monitored during the FMR measurement period. Activity sensors in each collar tallied the number of switch closures (seconds during which the collar moved) that occurred during 16 min moving time

windows. This 16 min moving window of activity was updated every 2 min for the life of the collar. Information on the number of switch closures occurring during the previous 16 min was transmitted to the data logger using a variable pulse period (1080–1320 msec) VHF signal where a 1320 msec pulse period represented no active switch closures (no collar movement during the 16 min time period) and a 1080 msec pulse period represented 960 switch closures (collar movement during every second of the 16 min interval).

An activity monitoring station was established at the top of a hill roughly in the center of the study area. An omni-directional antenna was erected and connected to a TR5 data logger (Telonics, Mesa AZ) set to search for each radio frequency every 16 min. For each frequency the data logger recorded five readings during a 1 min session and then moved on to the next frequency. The resulting data set of activity included between 0 and 5 activity readings for each animal for a 16 min block of time. This set was reduced to one reading per 16 min block by taking the modal activity reading collected during that block.

Activity readings were reclassified as high activity (percent activity $>$ 55%), moderate activity (percent activity between 15% and 55%) or low activity (percent activity $\leq$ 15%). The three activity categories were determined based upon pilot field work observing martens wearing collars and upon observations of captive ferrets (*Mustela putorius furo*) wearing collars while being monitored with a receiver and video recorder (Wright *et al.*, in prep). Ferrets that were awake, in place and grooming or changing positions had low activity readings. The ferret had to be walking or running before activity levels increased to medium or high levels. We based the classification of activity into low, medium and high on observations of tame ferrets and the occasional observation of free-ranging martens in various states of activity. Activity patterns of individual martens during the doubly labeled water experiment were determined by calculating the proportion of telemetry readings in each of the three activity classes.

Statistical Analyses.—Body mass data were analyzed with a two-way analysis of variance (ANOVA) with season and gender as factors and their interaction also included in the model. Repeated measures ANOVA was used to analyze masses of martens captured multiple times to document within season changes in body mass. Log_{10}FMR was analyzed by analysis of covariance (ANCOVA) with log_{10}body mass as the covariate and season as the factor. The distribution of activity counts in the high, moderate and low classes were compared between males and females and between the two seasons using chi-square tests for independence. In all tests alpha was set at 0.05.

RESULTS

In autumn, 8 martens (3F, 5M) were injected with DLW, but only 4 (2F, 2M) were captured within sufficient time to allow estimation of FMR before isotope levels declined to background level. In winter, 9 martens (4F, 5M) were injected, but only 6 (2F, 4M) were captured within sufficient time to allow estimates. Mean body mass was higher in males (1099 $\pm$ 43 g, n = 10 males) than females (737 $\pm$ 28 g, n = 6) ($F_{1,12}$ = 32.7, P $>$ 0.0001)), with no difference by season ($F_{1,12}$ = 0.05, P = 0.83) and no gender*season interaction ($F_{1,12}$ = 0.42, P = 0.53). Daily mass change rates of martens (0.25 $\pm$ 0.27%/d, n = 9 individuals), based on repeated captures within each season, did not differ significantly from zero (t_8 = 0.93; P = 0.38) and did not differ by gender or season (or interaction), although our power to detect differences (especially for gender) was poor due to low sample size. Body fat (% of body mass) did not differ between autumn (15.4 $\pm$ 4.5%, n = 4) and winter (12.3 $\pm$ 2.0%, n = 7) ($F_{1,8}$ = 0.26, P = 0.62), or by gender ($F_{1,8}$ = 0.44, P = 0.53) or by their interaction ($F_{1,7}$ = 0.0004, P = 0.98).

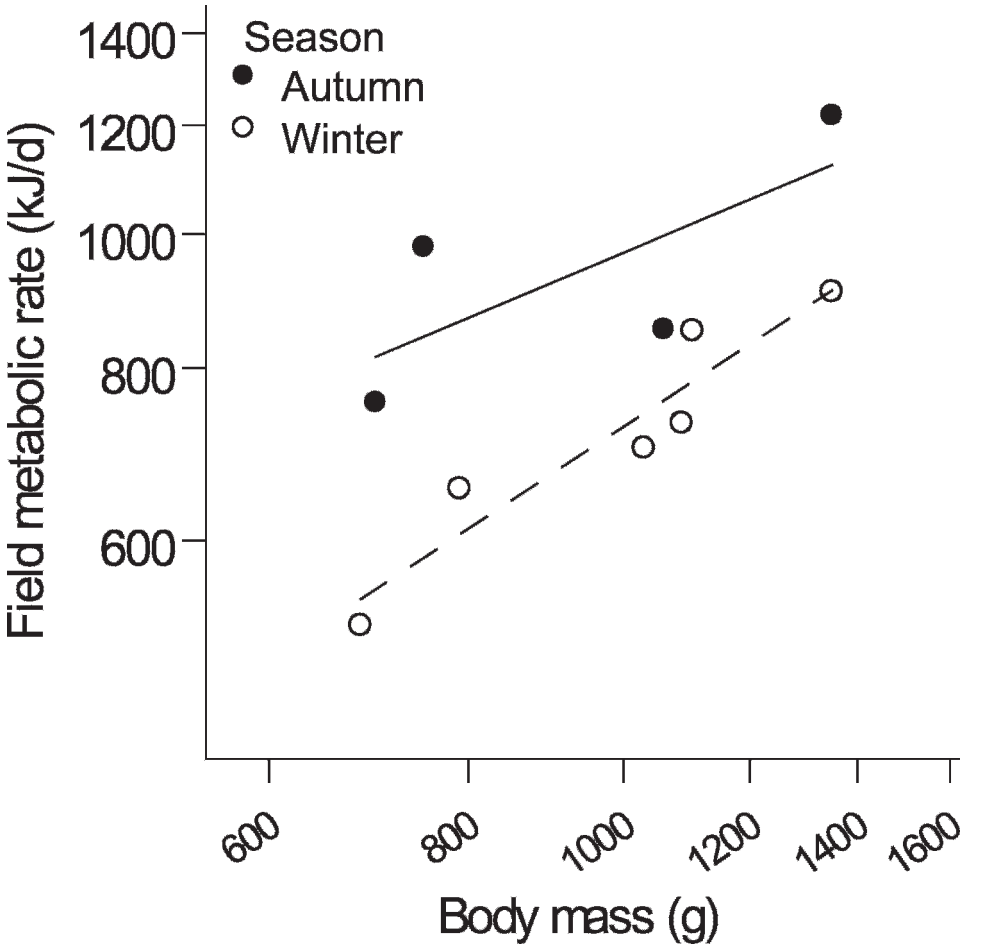

FIG. 1.—Relationship between body mass and field metabolic rate (FMR) in two seasons. Martens used less energy in winter than in fall and energy use increased with body mass. All animals greater than 1000 g body mass are male and all animals less than 1000 g are female. The data presented on both axis are in $\log_{10}$ scales

Three martens (1 male in autumn, 1 male and female each in winter) had more than one estimate of FMR in a single season. For these three animals coefficients of variation (100*S.D./mean) on repeated measures of FMR were 11.6 ± 8.8% (range 0.4–19.8%).

Log_{10}FMR was correlated with $\log_{10}$body mass ($F_{1,7} = 17.7$, P = 0.004) and was higher in autumn (1006 kJ/d, SE = 96) than in winter (709 kJ/d, SE = 48) ($F_{1,7} = 16.6$, P = 0.005), with no interaction between mass and season (*i.e.*, in slope; $F_{1,6} = 0.8$, P = 0.4; pooled slope = 0.63) (Fig. 1). There was no effect of gender on $\log_{10}$FMR when that was included in the model ($F_{1,6} = 2.8$, P = 0.14).

Activity levels during the FMR experiments indicated that there were no differences in the distribution of counts of activity classes (high, moderate and low) between males and females within season during either the autumn ($X^2 = 4.1$ df = 2, P = 0.128) or winter (X^2

= 4.3 df = 2, P = 0.114). Male and female activity levels were combined for seasonal analysis. During the autumn session, martens were highly active 31% (SD = 8) of the time, moderately active 7.6% (SD = 4.2) and inactive (low activity classification) 61.6% (SD = 7.2) of the time. During the winter session martens were highly active 12.1% (SD = 8.8), moderately active 8.8% (SD = 3.2) and inactive 79.2% (SD = 9.3) of the time. There were differences in seasonal activity distributions with martens spending more time in a highly active state and less time in an inactive state in autumn than in winter (X^2 = 114.5 df = 2, P < 0.0001). In summary, and expressed and analyzed in another way, martens were active (sum of high and medium activity classification) significantly less in winter (4.8 ± 1.0 h/d, n = 6) than in autumn (9.1 ± 0.7, n = 4) ($F_{1,7}$ = 11.6, P = 0.011), with no significant difference between the sexes) ($F_{1,7}$ = 1.2, P = 0.36).

DISCUSSION

The observation that the percent of martens' body mass consisting of fat did not differ between seasons or genders was consistent with our expectation that non-reproductive martens balance their energy budget on a near daily basis, even in winter, and rely little on body energy reserves.

As we predicted, energy expenditure by martens was significantly lower in winter than in autumn, despite colder temperatures during the winter measurement period. Although seemingly at odds with the converse expectation based simply on how resting metabolism increases in endotherms as temperature declines, our finding is consistent with those of other studies and partly explicable based on our measures of daily activity and also on documented thermoregulatory features of martens.

Previous studies that have documented FMR in non-hibernating species in winter have similarly found that energetic costs are lower than in warmer seasons (Covell *et al.*, 1996). For example, the FMR of a northern population of red squirrels (*Tamiasciurus hudsonicus*) was found to be unexpectedly low and to decrease with declining temperature (Humphries *et al.*, 2005). In part, FMR reduction in colder months seems to result from declines in animal activity, as we observed. Declines in marten activity during the winter should result in energy saving by both reducing the time spent in energy intensive activities, such as locomotion, and by increasing the time spent within an insulated environment. In winter months, martens in Wisconsin seek out underground or subnivean structures for shelter and rest sites (Gilbert *et al.*, 1997). These structures include old red squirrel middens, old white pine (*Pinus strobus*) stumps and tip-up mounds from fallen trees. Such structures provide ambient temperatures of a nearly constant −2.5 C to −1.0 C, substantially warmer than outside air temperatures (MacLean *et al.*, 1974).

At least one physiological feature of martens further enhances energy conservation. Buskirk *et al.* (1989) demonstrated that martens lower their core body temperature by 2.9 C on average while at rest. They estimated that martens can save between 4.0% and 6.4% of their total daily energy costs by reducing core body temperatures, assuming 12 h of rest each day. Our study reveals that martens rest on average 18 h per day in winter, so savings should be even larger.

The FMR, as well as the resting metabolic rate (RMR), of martens is relatively high compared with similar-sized eutherian mammals. Our measured mean FMR was 857 kJ/d, nearly 40% more than predicted for an average sized (body mass = 1000 g) marten (Speakman, 2000a). Buskirk *et al.* (1989) calculated a marten RMR of 227 kJ/day for an average sized (body mass = 1000 g) marten (0.51 mL O_2/g * hr) or 16% above that predicted by Speakman (2000a). But, the ratio of these values (FMR/RMR) falls within the

range of other such ratios reported for other small-bodied mammals (Humphries *et al.*, 2005; Speakman, 2000b).

Martens are active at all seasons and balance their energy budget on a near daily basis, therefore, they must provision themselves regularly. The reduction in energy use from autumn to winter means that martens need 29% less food to sustain themselves in winter as opposed to autumn. Lowering food requirements will result in reduced time spent hunting (thus, saving more energy) and may result in less exposure to predation (Gardner and Gustafson, 2004). Based on seasonal differences we detected in marten FMR and carnivore prey composition values in Nagy *et al.* (1999a) [16.8 kJ/g dry matter and 3 g fresh mass/g dry matter (*i.e.*, 67% water content)], we estimate that martens would require 179 g fresh matter (FM) per day in autumn and 126 g FM per day in winter. If martens are feeding primarily on red-backed voles (*Clethrionomys gapperi*) (25 g) and red squirrels (200 g), as reported by Strickland and Douglas (1987), then martens must obtain about seven voles in autumn and five in winter per day, or they must obtain 0.9 red squirrel in autumn and 0.6 red squirrels in winter per day to meet their energetic demands.

Acknowledgments.—This research was conducted under the auspices of a memorandum of understanding between the Great Lakes Indian Fish and Wildlife Commission and the North Central Research Station of the US Forest Service. D. Schoeller's lab ran the DLW analysis. The Chequamegon-Nicolet National Forest provided logistic support for field work including housing for field personal. Dr. G. Gerber provided veterinary assistance with animal care and handling. J. Dumyahn, R. Parisien, and D. Soullier spent long hours collecting data. E. Gustafson, A. Wydeven, and W. Zielinski gave us helpful comments on early drafts of this manuscript.

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SUBMITTED 8 APRIL 2008 ACCEPTED 4 DECEMBER 2008