

## RESEARCH ARTICLE

### The energy cost of voluntary running in the weasel *Mustela nivalis*

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#### SUMMARY

The small size and elongate shape of weasels (*Mustela nivalis*) probably evolved to facilitate movement within the burrow systems of prey species, but result in high energy costs of thermoregulation. In this study we measured metabolic rates of weasels during voluntary locomotion to determine whether energy costs of transport are also high in these unusually shaped mammals. In addition, we measured the lower and upper limits of aerobic metabolism [resting metabolic rate (RMR) and maximal oxygen consumption in forced exercise ( $\dot{V}_{O_{2,max}}$ )], and used the wide size range of adult weasels to investigate the intraspecific scaling of energy metabolism. Finally, we combined measurements of energy use during running with radiotracking and doubly labeled water data from free-living weasels to estimate the importance of locomotor costs in daily energy budgets. We found that weasels have higher than predicted costs of running, largely because of an elevated intercept of the speed *versus* metabolic rate relationship. Running costs were strongly affected by the approximately fourfold range of body size in adults. As reported in other studies, the RMR of weasels was considerably higher than predicted from body mass. Maximal oxygen consumption was also higher than predicted, but factorial aerobic scope ( $\dot{V}_{O_{2,max}}/\text{RMR}$ ) was within the normal range for mammals. Intraspecific mass scaling of RMR and  $\dot{V}_{O_{2,max}}$  did not differ from typical interspecific mammalian allometries. In wild weasels, locomotor costs comprised roughly 5% of daily energy expenditures; this low value was primarily a result of short travel times and distances.

Key words: mustelid, metabolism, cost of transport, locomotion.

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#### INTRODUCTION

The small weasels in the genus *Mustela* have one of the more unusual morphologies among terrestrial mammals, characterized by very elongate bodies, narrow heads, long necks and short legs. This body form is presumed to have evolved to facilitate movement within the burrows of rodents, which are the principal prey of weasels (King, 1983; King, 1989; Jedrzejewska and Jedrzejewski, 1998). This ability to maneuver within confined tunnels is probably a key factor in the ecological success of weasels, which have a very wide Holarctic distribution and occupy a diverse range of habitats including deserts, grasslands, tundra and forests. However, it also has costs. Coupled with fairly short pelage and an inability to store substantial subcutaneous fat deposits, the elongate shape of weasels is thought to be a causal factor in their exceptionally high basal metabolism and thermal conductance (Scholander et al., 1950; Iversen, 1972; Brown and Lasiewski, 1972; Moors, 1977; Casey and Casey, 1979; Szafrńska et al., 2007). Inclusion of these traits into biophysical models suggests that weasels are seldom active in themoneutral conditions in many parts of their extensive Holarctic range (Chappell, 1980), and recent doubly labeled water studies (Zub et al., 2009) show that the daily energy expenditures (DEE) of weasels are higher than allometric predictions for carnivores (Nagy et al., 1999).

In the context of ecology and energetics, another possible repercussion of weasel body form is the metabolic cost of locomotion. Although their shape seems adapted to moving within burrows, weasels are often active elsewhere in their habitats and, at least in some circumstances, may travel over substantial distances (King,

1989; Jedrzejewski et al., 2000). The morphology of weasels is strikingly different from the compact body form and long, thin legs of 'classic' cursorial species such as canids, horses, deer and antelope (e.g. Alexander, 2003). Given that contrast in shape, a reasonable inference is that the short legs and elongate bodies of weasels could result in a high energetic cost of terrestrial movement. Results from several studies suggest that elongate mustelids do have higher than predicted transport costs, but all are from animals considerably larger than weasels and two of the tested species were semi-aquatic (Taylor et al., 1982; Williams, 1983; Williams et al., 2002).

More broadly, the importance of locomotor costs as a component of DEE in small mammals is controversial. Estimates of the 'ecological cost of transport' for daily movement distances derived from home range size suggested that the fraction of DEE used to power locomotor exercise is quite minor in most small mammals, but could comprise a substantial portion of the daily energy budget of carnivores with large home ranges (Garland, 1983). In contrast, studies of movement distances, running behavior and exercise metabolism of rodents in natural habitats (e.g. Kenagy and Hoyt, 1989), or of voluntary running of small mammals in captivity (e.g. Koteja et al., 1999; Chappell et al., 2004; Chappell and Dlugosz, 2009), suggest that movement costs could comprise 5–20% of DEE. The importance of locomotor expenditures in the DEE of weasels is of interest because they are both small and carnivorous (*Mustela nivalis* is the smallest member of the order Carnivora) and seem to show a seasonal trade-off between activity and thermoregulation, which is consistent with a relatively high cost of activity (Zub et al., 2009).

In this study we examined several aspects of running performance and energetics in weasels. We performed laboratory measurements of energy metabolism during voluntary locomotor exercise to obtain the energy cost of transport in semi-natural conditions. We also determined maximal oxygen consumption in forced exercise for comparison with voluntarily attained exercise intensity. We took advantage of the unusually large fourfold range in weasels' adult body mass (King, 1989; Zub et al., 2009) to examine intraspecific metabolic scaling and its effect on energy expenditures. Finally, we combined the laboratory measurements with radiotracking studies of movements and previously reported doubly labeled water measurements of DEE to estimate the importance of locomotor costs in weasel energy budgets in natural habitats.

## MATERIALS AND METHODS

We worked with a well-studied population of weasels (*Mustela nivalis* Linnaeus 1766) in the Białowieża Forest region in northeastern Poland, including the Białowieża Glade and Białowieża National Park (23.86°E, 52.70°N). Local habitats included old-growth hardwood forest, agricultural fields and meadows, and in riparian areas, sedge meadows, wet grassy meadows and reedbeds. Weasels were captured in wooden box-traps (Jedrzejewski et al., 1995) under the auspices of Polish nature conservancy authorities (permits DOPweg-4201-04-6/03/jr, DOPog-4201-04-43/05/aj, LKE 2003/04 and LKE 2004/06).

Previous work on this weasel population has included measurements of activity patterns (Jedrzejewski et al., 1995; Jedrzejewski et al., 2000), resting energy metabolism (Szafranska et al., 2007), habitat use (Jedrzejewski and Jedrzejewski, 1998; Zub et al., 2008) and field metabolic rates (Zub et al., 2009), and we followed the handling procedures detailed in those studies. In brief, captured weasels were transported to our laboratory at the Mammal Research Institute in the town of Białowieża, housed in cages that included a shelter with bedding, and provided with water *ad libitum* and one to two laboratory mice per day (depending on weasel body mass). Animals were released the day after all measurements were completed. All procedures complied with the Principles of Animal Care (publication no. 86-23, revised 1985) of the US National Institutes of Health and were approved by the Institutional Animal Care and Use Committee of the University of California, Riverside, and the Local Research Ethics Committee in Białystok (permits LKE 2003/04, LKE 2004/06, LKE 2005/08, LKE 8/2006 and LKE 42/2008).

### Radiotracking

Weasels used for radiotracking studies were fitted with a neck-collar radio transmitter under ketamine-xylazine anesthesia (Jedrzejewski et al., 2000). Collared animals were released at the site of capture and their position and activity were checked every 15–60 min throughout the period of daylight [weasels in the Białowieża region are rarely active at night (Jedrzejewski et al., 2000)]. Bearings were taken from a distance of at least 50 m to avoid disturbance by the observer. These studies were carried out in June through November in 1997–2006, and included 35 animals tracked. In analyses we used data collected over one to four consecutive days of radiotracking.

### Respirometry

We measured energy costs as rates of oxygen consumption ( $\dot{V}_{O_2}$ ) using open-circuit respirometry, with a conversion factor of 20.1 J ml<sup>-1</sup> O<sub>2</sub>. Outside air was pumped into the metabolic system under positive pressure. Incurrent air was dried with Drierite (Hammond, Xenia, OH, USA) and metered ( $\pm 1\%$ ) with ERG-1000

mass flow controllers (Warsaw, Poland) before entering the metabolic chambers. Excurrent air from the chambers was subsampled with an SS-3 pump (Sable Systems, Las Vegas, NV, USA), dried and flowed through a Sable Systems FC-1b oxygen analyzer. Instrument outputs were digitized with a Sable Systems UI2 and recorded with a Macintosh Powerbook running LabHelper software (www.warthog.ucr.edu).

Most of the metabolic tests were performed on weasels captured in September and October 2007, with a few animals tested in June and July 2008.

### Maximum oxygen consumption in exercise

We measured maximum rates of oxygen consumption ( $\dot{V}_{O_{2,max}}$ ) during forced exercise in an enclosed running wheel constructed of plexiglass. The wheel had a circumference of 0.69 m and an internal volume of 3.0 l. The running surface was lined with friction tape for traction. Air entered and exited through airtight axial bearings equipped with manifolds to disperse flow and increase mixing, which was also facilitated by wheel rotation and by movements of the animals. Flow rates were 2000 ml min<sup>-1</sup> STP. Subsampled excurrent air ( $\sim 150$  ml min<sup>-1</sup>) was scrubbed of CO<sub>2</sub> with soda lime and dried prior to oxygen analysis. Flow rate and O<sub>2</sub> content were recorded every 1 s.

Weasels were weighed to the nearest  $\pm 0.1$  g, sealed into the running wheel, and left undisturbed for several minutes to acclimate with the wheel locked against rotation. During this period we took a reference reading of unbreathed air and then monitored  $\dot{V}_{O_2}$  prior to the onset of forced exercise. Wheel rotation was initiated at low r.p.m. when weasels were facing in the appropriate direction. Several individuals ran spontaneously as soon as the wheel was unlocked, and these animals were allowed to run at their preferred speed initially. We increased rotation speed every 20–30 s while closely monitoring running behavior and  $\dot{V}_{O_2}$ , halting rotation when animals were unable to maintain position or  $\dot{V}_{O_2}$  did not increase with increasing speed. While running, weasels remained approximately on the bottom of the wheel until  $\dot{V}_{O_2}$  had peaked. The duration of exercise ranged from 5.5 to 8.1 min. Immediately after the cessation of rotation, weasels showed indications of exhaustion (panting, prone posture, lack of movement), but most resumed exploratory behavior or grooming within 1–2 min. We took a second reference reading after several minutes of recovery and removed the animal from the wheel. Tests were performed during the day (the normal activity period for weasels) at room temperature (16–24°C). We calculated  $\dot{V}_{O_2}$  as:

$$\dot{V}_{O_2} = F \times (F_{IO_2} - F_{EO_2}) / (1 - F_{EO_2}), \quad (1)$$

where  $F$  is flow rate (STP corrected) and  $F_{IO_2}$  and  $F_{EO_2}$  are incurrent (reference;  $= 0.2095$ ) and excurrent fractional oxygen concentrations, respectively. Because  $\dot{V}_{O_2}$  did not attain steady-state during exercise tests, we computed 'instantaneous'  $\dot{V}_{O_2}$  [ $i\dot{V}_{O_2}$  (Bartholomew et al., 1981)] to counteract mixing effects and resolve short-term metabolic changes. In these calculations the effective volume of the wheel (derived from washout curves) was 3.1 l. Exercise  $\dot{V}_{O_{2,max}}$  was computed as the highest 1 min running average of  $i\dot{V}_{O_2}$ . Calculation and analysis of  $\dot{V}_{O_2}$  were performed with LabAnalyst software (www.warthog.ucr.edu).

### RMR, maximal voluntary O<sub>2</sub> and energy cost of running

We used a larger enclosed running wheel respirometer to measure energy costs and behavior during voluntary running and resting. The chamber [fig. 1 in Chappell et al. (Chappell et al., 2004)] was constructed of plexiglass and contained a standard polycarbonate

mouse cage as well as a 1.12 m circumference stainless steel and plexiglass running wheel (Lafayette Instruments, Lafayette, IN, USA). Bedding and a drinking tube were available in the mouse cage, which was connected to the wheel through a short 7.7 cm diameter tunnel. Flow rate was 2500 ml min<sup>-1</sup> STP, and a small fan circulated air within the chamber to improve mixing. A tachometer transduced the speed and direction of wheel rotation. A computer-driven multiplexer (Sable Systems TR-1) obtained a reference reading of unbreathed air for 2.5 min every 45 or 60 min. Wheel motion, flow rate and O<sub>2</sub> concentration were recorded every 1.5 s. Weasels were left in the wheel chambers for 8–24 h and were given food (laboratory mice) when kept in wheels for more than 10 h. Tests were run at the ambient photoperiod (the laboratory was illuminated through windows) and temperature (17–24°C). As during  $\dot{V}_{O_{2,max}}$  tests, weasels running voluntarily remained near the bottom of the wheel, with little tendency to run 'uphill' or 'downhill'.

To avoid frequent scrubber changes or large scrubber volumes, we did not remove CO<sub>2</sub> from subsampled air prior to  $\dot{V}_{O_2}$  analysis, and used the Mode 2 conversion in LabAnalyst to calculate  $\dot{V}_{O_2}$  as:

$$\dot{V}_{O_2} = F \times (F_{I_{O_2}} - F_{E_{O_2}}) / [1 - F_{E_{O_2}} \times (1 - RQ)], \quad (2)$$

where RQ is the respiratory quotient. The RQ was assumed to be 0.85, which is reasonable for a meat diet. Potential errors if real RQ was different from 0.85 are small: at typical  $F_{E_{O_2}}$  (>0.205) the maximum error in  $\dot{V}_{O_2}$  is approximately 3% for real RQ between 0.7 and 1.0. Because the effective volume of the wheel chamber (17 l) was large relative to the flow rate, we removed electrical noise with nearest-neighbor smoothing and applied the 'instantaneous' transformation to resolve rapid changes in  $\dot{V}_{O_2}$  changes. We lag-adjusted  $\dot{V}_{O_2}$  to synchronize it with running data (this was necessary because changes in speed were instantly detected but detection of changes in  $\dot{V}_{O_2}$  was delayed due to the flux of air through the system).

We computed minimal resting metabolic rate (RMR<sub>min</sub>) as the lowest 10 min continuous mean of  $\dot{V}_{O_2}$  during periods when animals were inactive (as indicated by low and stable  $\dot{V}_{O_2}$ ). Maximal voluntary  $\dot{V}_{O_2}$  was calculated as the highest 1, 2 and 5 min continuous means of  $\dot{V}_{O_2}$  when animals were running in the wheel. We also determined the total distance run and time spent running, the maximum instantaneous speed (i.e. the highest speed in a 1.5 s interval), the highest 1, 2 and 5 min continuous means of speed, and the mean speed (total distance run/total time spent running).

To obtain the relationship between running speed and  $\dot{V}_{O_2}$  we used the LabAnalyst stepped-sampling procedure to compute 1 min sample means of speed and  $\dot{V}_{O_2}$ , with successive 1 min samples separated by 3 min to avoid autocorrelation problems (Chappell et al., 2004; Rezende et al., 2005; Rezende et al., 2006). Samples with mean speed <0.03 km h<sup>-1</sup> were discarded (data from speeds this low were inaccurate due to background electrical noise in the tachometer). We also discarded data from weasels that did not run faster than 0.9 km h<sup>-1</sup>. For the remaining animals, we regressed the 1 min means of speed and  $\dot{V}_{O_2}$  to obtain slopes and intercepts.

Regressions of speed and  $\dot{V}_{O_2}$  can be used to calculate costs of transport (COT; energy used to move a unit mass a given distance; i.e. kJ kg<sup>-1</sup> km<sup>-1</sup>). To convert O<sub>2</sub> consumption to energy, we assumed 20.1 J ml<sup>-1</sup> O<sub>2</sub>. Absolute COT at a given speed is computed as power/speed; this typically decreases as speed increases because the speed versus power regression has a non-zero (positive) intercept. A speed-independent measure of transport costs is the 'incremental' COT (iCOT), which is the slope of the speed versus power regression.

The stepped-sampling procedure is not readily applicable for short bouts of wheel activity, and most weasels did not run for extended

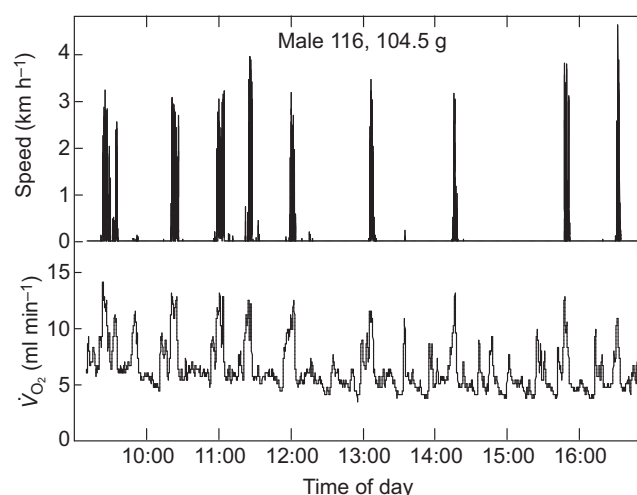


Fig. 1. Typical record of voluntary running activity and oxygen consumption ( $\dot{V}_{O_2}$ ) in a male weasel. As was the case for other tested weasels, running activity occurred in short bursts separated by extensive periods with little activity.

periods (Fig. 1). Accordingly, we used a second approach to estimate costs of transport in a larger number of individuals. When bouts of wheel-running occurred in the absence of other activity (as determined from  $\dot{V}_{O_2}$ ), we integrated each bout's running speed data (to obtain total distance traveled in km) and  $\dot{V}_{O_2}$  (to obtain total ml O<sub>2</sub> consumed). We also measured bout duration and the resting metabolic rate (RMR, ml O<sub>2</sub> min<sup>-1</sup>) immediately before or after the bout. Mean speed was computed as total distance/bout duration, and net O<sub>2</sub> consumption due to running was computed as: total O<sub>2</sub> consumption – (RMR × bout duration). Cost of transport (kJ km<sup>-1</sup>) at the mean speed was calculated as net O<sub>2</sub> consumption/total distance, using a conversion factor of 20.1 J ml<sup>-1</sup> O<sub>2</sub>.

### Statistics

Because there was a wide body mass range in our animals and metabolic rates are a power function of mass, we log<sub>10</sub>-transformed mass and metabolism prior to analyses. We used ANOVA, ANCOVA and simple and multiple least-squares regression models for most analyses. A linear mixed model with animal ID as a random variable was used in analyses with repeated measurements. Results are presented as means ± s.d. unless otherwise noted. Tests were performed with JMP 10 or SAS (SAS Institute, Cary, NC, USA).

### RESULTS

Twenty-four weasels (four female, 20 male; 37–130 g) were tested for voluntary running; of these, five were also tested for  $\dot{V}_{O_{2,max}}$ . Several individuals did not use the voluntary wheel or ran in such brief bouts that the data were not usable. Among the weasels that spent substantial time running, most exercise bouts lasted less than 10 min and were followed by periods of inactivity (no wheel rotation and low and relatively stable  $\dot{V}_{O_2}$ ). Although there was occasional activity within the cage (as indicated by peaks in  $\dot{V}_{O_2}$  not associated with wheel movement), all weasels spent most of their time resting (e.g. Fig. 1).

#### Minimum and maximum metabolism

Minimal RMR was strongly correlated with body mass ( $RMR_{min}$  in ml O<sub>2</sub> min<sup>-1</sup> =  $0.105M^{0.724}$ , where  $M$  is mass in g;  $N=21$ ,  $r^2=0.744$ ,  $P<0.0001$ ; Fig. 2; mean mass =  $86.0 \pm 24.4$  g, mean  $RMR_{min}$  =  $2.64 \pm 0.67$  ml O<sub>2</sub> min<sup>-1</sup>). Although sample size was small,  $\dot{V}_{O_{2,max}}$  in



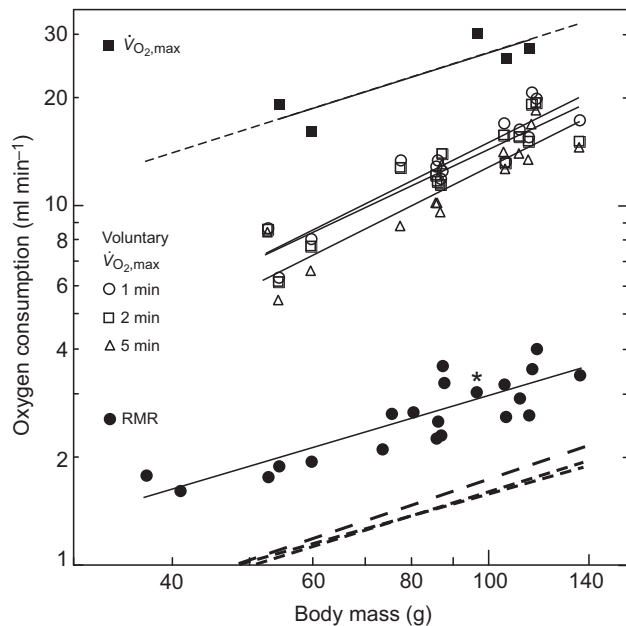


Fig. 2. Resting metabolic rate (RMR), maximum oxygen consumption during forced exercise ( $\dot{V}_{O_{2,max}}$ ) and maximum  $\dot{V}_{O_2}$  ( $\dot{V}_{O_{2,max}}$ ) averaged over 1, 2 and 5 min of voluntary exercise in weasels. For comparison to RMR, the asterisk (\*) is the mean RMR for 96 g male weasels from Białowieża in a different study (Szafranska et al., 2007). The heavy dashed lines are the basal metabolic rates predicted by allometries for Carnivora and small Palearctic mammals (White and Seymour, 2004) and by a phylogenetic generalized least-squares regression for mammals (White et al., 2009).

forced running was also correlated with body mass ( $\dot{V}_{O_{2,max}} = 1.05M^{0.701}$ ;  $N=5$ ,  $r^2=0.704$ ,  $P=0.047$ ; mean mass =  $89.1 \pm 29.5$  g, mean  $\dot{V}_{O_{2,max}} = 23.7 \pm 5.9$  ml  $O_2$  min $^{-1}$ ). Similarly, maximum voluntary  $\dot{V}_{O_2}$  averaged over 1, 2 and 5 min intervals was correlated with body mass ( $0.189M^{0.932}$ ,  $r^2=0.50$ ,  $P=0.003$ ;  $0.204M^{0.905}$ ,  $r^2=0.50$ ,  $P=0.003$ ;  $0.171M^{0.918}$ ,  $r^2=0.48$ ,  $P=0.006$ , respectively;  $N=14$ ). The mass exponents for  $\dot{V}_{O_{2,max}}$  and RMR $_{min}$  did not differ significantly ( $P>0.6$ ). Mass exponents for maximum voluntary  $\dot{V}_{O_2}$  were significantly higher than for RMR $_{min}$  ( $P<0.014$ ) but did not differ from that for  $\dot{V}_{O_{2,max}}$  ( $P>0.117$ ), possibly because of low sample size for the latter.

### Voluntary running behavior

We obtained acceptable voluntary running data for determining COT from 11 weasels (52.6–130 g, mean mass  $98.1 \pm 22.7$  g). Mean maximum speed for animals used for slope and intercept calculations was  $2.8 \pm 1.1$  km h $^{-1}$  (range 1.3–4.9 km h $^{-1}$ ). Measurements on these individuals lasted from 9.75 to 24 h. The mean distance run was  $1.75 \pm 1.12$  km and cumulative run time averaged  $68.2 \pm 25.5$  min, for a mean speed of  $1.48 \pm 0.59$  km h $^{-1}$ . Nearly all wheel running activity occurred during daylight, but nine of the 11 measurements included less than one complete diurnal activity cycle (i.e. less than 12 h of daylight, which was approximately the ambient photoperiod for the majority of measurements). For these individuals, times and distances were scaled to 12 h of daylight by multiplying by 12 h and dividing by measurement hours, yielding a mean distance run per day of  $1.94 \pm 1.15$  km and a mean cumulative run time of  $78.8 \pm 29.3$  min. The maximum instantaneous speed (the fastest 1.5 s of running) averaged  $5.1 \pm 1.1$  km h $^{-1}$  (range 3.7–7.8 km h $^{-1}$ ). There was no relationship between body mass and any measure of running speed or distance ( $P>0.60$ ).

### Relationship between speed and energy consumption

Nine of the 11 speed versus  $\dot{V}_{O_2}$  regressions were linear; two had significant quadratic terms (they tended to level out at high speeds). For these two individuals, addition of the quadratic term had little effect on predictive power ( $r^2$  increased from 0.933 to 0.967 for male 119, and from 0.901 to 0.914 for male 130). Accordingly, for simplicity we used linear regressions for all individuals (e.g. Fig. 3); all were highly significant, with a mean  $r^2$  of 0.71 (range 0.43–0.93).

The relationship between  $\dot{V}_{O_2}$  and speed differed considerably among the 11 weasels (ANCOVA,  $P<0.001$ ; Fig. 4). A substantial part of the variation in both slope and intercept was mass related. In least-squares regression, body mass explained 54% of the variation in intercept (intercept in ml  $O_2$  min $^{-1}$  =  $1.17 + 0.0543M$ ;  $t=3.26$ ,  $P=0.0098$ ) and 54% of the variation in slope (slope in ml  $O_2$  g $^{-1}$  km $^{-1}$  =  $-0.0249 + 0.0159M$ ;  $t=3.27$ ,  $P=0.0097$ ). Total  $\dot{V}_{O_2}$  (ml min $^{-1}$ ) for a weasel of a given mass (g) at a given running speed ( $v$ ; km h $^{-1}$ ) can be calculated by adding the intercept to the product of slope  $\times$  speed (Taylor et al., 1982):

$$\dot{V}_{O_2} = 1.17 + 0.0543M + v(0.0159M - 0.0249). \quad (3)$$

After a log $_{10}$  transformation of mass and  $\dot{V}_{O_2}$  to account for nonlinear scaling of mass and metabolism, mass explained 59% of the variation in intercept ( $t=3.59$ ,  $P=0.0058$ ) and 46% of the variation in slope ( $t=2.79$ ,  $P=0.0212$ ). The summed equation (intercept plus the product of slope  $\times$  speed) for total  $\dot{V}_{O_2}$  is:

$$\dot{V}_{O_2} = 0.1435M^{0.829} + v(0.0218M^{0.997}). \quad (4)$$

Converting to energy consumed ( $E_c$ ; kJ h $^{-1}$ ) using mass in kg and an energy equivalence of 20.1 J ml $^{-1}$   $O_2$ , we obtain:

$$E_c = 51.7M^{0.829} + v(26.3M^{0.997}). \quad (5)$$

If RMR $_{min}$  (the lowest 10 min continuous mean during the measurement period) is subtracted from  $\dot{V}_{O_2}$  to yield net running costs, the intercept increased significantly with increasing mass in a one-tailed test but not in a two-tailed test (intercept =  $18.1M^{0.907}$ ;  $P=0.075$ ). Here, the intercept is equivalent to the 'postural cost' [the zero-speed elevation of  $\dot{V}_{O_2}$  above resting metabolism (Taylor et al., 1970; Taylor et al., 1982)]. The combined equation for the net cost of running ( $E_{net}$ ) (including the mass effect on the intercept) is:

$$E_{net} = 18.1M^{0.907} + v(26.3M^{0.997}). \quad (6)$$

### Energy costs from integrated distance and $\dot{V}_{O_2}$

This analysis included 118 running bouts by 18 weasels, including the 11 individuals used to calculate the relationship between  $\dot{V}_{O_2}$  and speed. The mean bout duration was  $3.99 \pm 2.26$  min (range 0.725–10.8 min), the mean distance traveled per bout was  $115 \pm 119$  m (range 7–689 m) and the mean speed (=distance/duration) was  $1.54 \pm 0.88$  km h $^{-1}$  (range 0.25–4.01 km h $^{-1}$ ). Preliminary tests indicated that including individual ID as a random effect in a mixed model (to account for multiple measurements on individuals) did not improve model fit; accordingly, it was not included in subsequent analyses. A simple linear model including body mass (kg), mean speed (km h $^{-1}$ ) and distance (km) as predictors accounted for 90% of the variation in the amount of  $O_2$  or energy consumed in a running bout (Table 1, Fig. 4). All predictors were highly significant ( $P<0.0001$ ), as was the overall regression. The strongest predictor of running cost was distance traveled (Table 1). Regressions predicting the net cost of running ( $O_2$  or energy consumed less RMR) were also highly significant ( $r^2=0.761$ ; Table 1). After accounting for the effects of size and speed, there was no difference in integrated

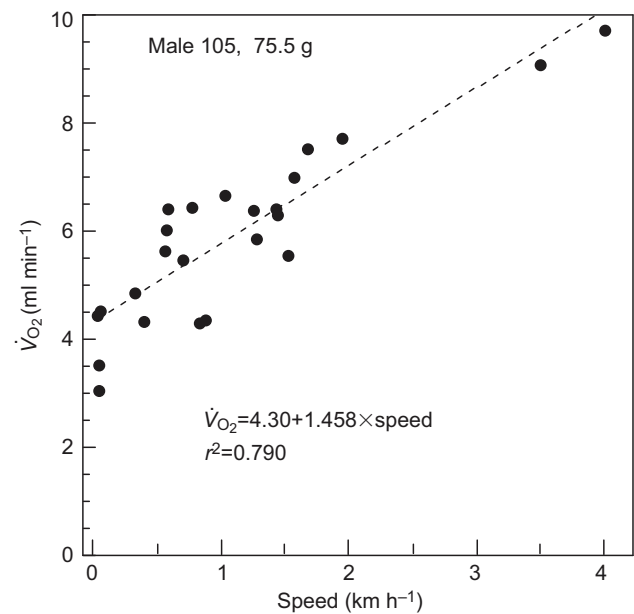


Fig. 3. Relationship between speed and energy use (measured as oxygen consumption,  $\dot{V}_{O_2}$ ) during voluntary running by a male weasel.

running costs between the 11 animals used to calculate relationships between power and speed and the other seven weasels (ANCOVA;  $P=0.45$ ).

As a comparison of the two models for calculating energy use during running, we regressed costs determined from distance, time and energy consumption (i.e. total kJ consumed, total km and mean  $\text{km h}^{-1}$  per bout of running; Table 1) against costs predicted from speed, duration, and slopes and intercepts as described in Eqn 5. Body mass was included in both models. For all 118 bouts of running, the predicted and measured values were similar and highly correlated ( $r^2=0.867$ ,  $P<0.0001$ ); a  $\log_{10}$  conversion slightly improved predictive power ( $r^2=0.896$ ). We also compared net costs (after subtracting RMR; Table 1, Eqn 6); again, results were highly correlated ( $r^2=0.775$ ,  $P<0.0001$ ).

Radiotracking

We obtained 832.4 h of tracking data from 35 weasels (mean body mass 99.2 g, range 61–133 g) in June through September in 1997–2006. Mean daily linear distance traveled by radiotracked animals was  $1.32\pm0.83$  km and mean daily activity time was  $4.25\pm1.81$  h. Their mean speed of movement, derived by dividing the linear distance traveled in the interval between successive position fixes by the duration of that interval, was  $0.32\pm0.15$   $\text{km h}^{-1}$ . Ambient temperature ( $T_a$ ) affects the activity and movement of

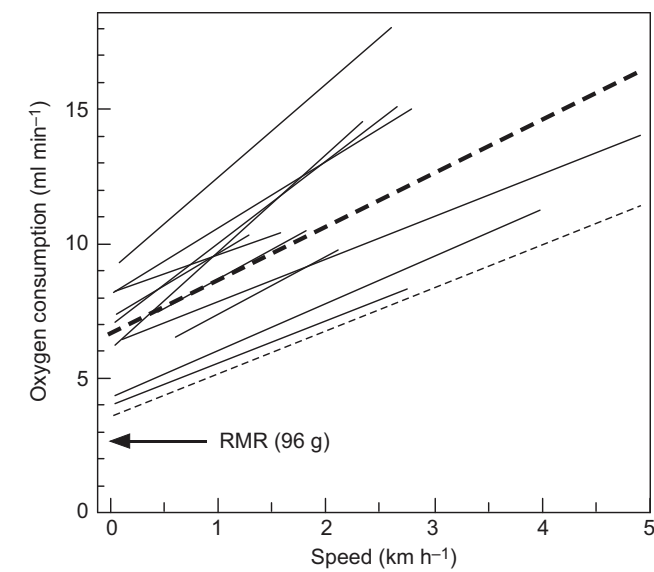


Fig. 4. Regressions of speed versus power output (oxygen consumption) for 11 weasels performing voluntary running. The regression lines extend between the lowest and highest 1 min means of running speed for each individual (see Results and Fig. 3). The mass range was 53 to 130 g. All regressions were highly significant ( $r^2=0.43$ – $0.93$ ). Approximately 54% of the variation in intercept and 54% of the variation in slope is explained by body mass differences ( $P<0.05$  for both). The heavy dashed line is the averaged value for a weasel of mean body mass (96 g) and the thin dashed line is the predicted relationship for terrestrial endotherms (Taylor et al., 1982). The arrow indicates resting metabolic rate for a 96 g weasel (from Fig. 2).

weasels during summer (K.Z., M.K. and P.A.S., unpublished data). Therefore, we also calculated travel distances for the subset of tracking data when  $T_a$  was between 18 and 24°C, similar to conditions during laboratory COT measurements. At these temperatures, the mean daily distance traveled by 11 individuals was  $1.45\pm0.59$  km ( $N=24$  observations), assuming linear travel between position fixes. Despite a lack of detailed knowledge of weasel locomotor behavior in the field, we can estimate energetic costs of transport. If wild weasels ran at the average speed observed for weasels in running wheels ( $1.54$   $\text{km h}^{-1}$ ), a 96 g animal would have a total daily travel cost of 13.6 kJ (Table 1), and a net daily travel cost (excluding RMR; Table 1) of 9.0 kJ. Both of these estimates include postural costs. If only iCOT is considered (excluding both RMR and postural costs), the energy expended for travel would average 6.4 kJ  $\text{day}^{-1}$ .

Using radiotracking, Zub et al. (Zub et al., 2009) found an average duration of all types of activity of approximately 4 h  $\text{day}^{-1}$ , but there was considerable individual variation and some male weasels were

Table 1. Metabolic costs of running predicted from integrated distance, time and body mass in discrete bouts of running in wheel respirometers

	Overall $r^2$	Intercept	Distance exponent	Mass exponent	Speed exponent
$O_2$ consumption (ml)	0.904	$3199\pm60.7$	$0.867\pm0.0379$	$0.816\pm0.061$	$-0.755\pm0.0625$
$t$			22.9	13.4	-12.8
Net $O_2$ consumption (ml)	0.761	$2482\pm71.1$	$0.867\pm0.0679$	$0.889\pm0.109$	$-0.725\pm0.112$
$t$			12.8	8.13	-6.47

Equations are in the form of:  $O_2$  consumption (in ml) = intercept  $\times \text{km}^{\text{distance exponent}} \times \text{kg}^{\text{mass exponent}} \times \text{km h}^{-1 \text{ speed exponent}}$ . Net  $O_2$  consumption =  $O_2$  consumption – resting metabolic rate (which was measured for every individual). To convert  $O_2$  consumption to kJ, multiply by 0.0201 kJ  $\text{ml}^{-1} O_2$ .  $P$ -values for all terms and for the overall regressions are  $<0.001$ ;  $N=118$  measurements from 18 individuals.

active for as much as  $10\text{ h day}^{-1}$ . Assuming that average running speed is constant and that the distance traveled is directly proportional to activity time, the most active males were traveling approximately  $4.4\text{ km day}^{-1}$ , which would cost a 96 g animal  $18.0\text{ kJ day}^{-1}$  above RMR, or  $12.8\text{ kJ day}^{-1}$  (iCOT only).

## DISCUSSION

### Metabolic limits and scaling

Several studies of small mustelids (Scholander et al., 1950; Iversen, 1972; Moors, 1977; Casey and Casey, 1979) have reported unusually high basal or resting metabolic rates. Our findings (Fig. 2) are consistent with those results: minimal resting metabolism in *Mustela nivalis* –  $2.86\text{ ml O}_2\text{ min}^{-1}$  for an individual of the mean mass of 96 g – is considerably higher than the ca.  $1.4\text{--}1.5\text{ ml O}_2\text{ min}^{-1}$  predicted by either ‘classical’ least-squares (e.g. White and Seymour, 2003; White and Seymour, 2005) or phylogenetically adjusted (e.g. White et al., 2009) allometries for mammalian basal metabolic rate (BMR). We caution that the RMR we report are not directly comparable to BMR because our animals may not have been post-absorptive, and because  $T_a$  values in our study were below the estimated lower critical temperature of weasels [ $\sim 25^\circ\text{C}$  (Casey and Casey, 1979)]. Nevertheless, our animals had access to (and used) insulative bedding and hence were probably in or close to thermoneutrality when resting.

There are few published data on maximal metabolic rate in mustelids. Weasels in our study had a forced-exercise  $\dot{V}_{\text{O}_{2,\text{max}}}$  approximately ninefold greater than RMR, and although our sample size for  $\dot{V}_{\text{O}_{2,\text{max}}}$  was small, the factorial aerobic scope ( $\dot{V}_{\text{O}_{2,\text{max}}}/\text{RMR}$ ) is the same as the scope of 9 reported for exercised North American mink [*Neovison (Mustela) vison* (Williams, 1983)]. An aerobic scope of 9 is also consistent with results from other small mammals (e.g. Hinds et al., 1993; Weibel et al., 2004; Weibel and Hoppeler, 2005). The  $\dot{V}_{\text{O}_{2,\text{max}}}$  of weasels is  $\sim 70\%$  higher than predicted for mammals [fig. 1 in Weibel et al. (Weibel et al., 2004)], and the ‘normal’ aerobic scope stems from a proportionally high RMR in conjunction with the high  $\dot{V}_{\text{O}_{2,\text{max}}}$ . A possible confounding factor is the fact that our weasels were tested on a wheel and hence were not running on a flat surface (as is typical for exercise  $\dot{V}_{\text{O}_{2,\text{max}}}$  studies). However, a comparative analysis including  $>70$  species revealed no difference between  $\dot{V}_{\text{O}_{2,\text{max}}}$  elicited on wheels *versus* that elicited on treadmills (E. L. Dlugosz, unpublished data).

A particularly interesting aspect of weasel biology is their extraordinary range of adult body mass [as much as fourfold (King, 1989; Zub et al., 2009)], which has obvious implications for energy requirements and ecology (Zub et al., 2011). A wide mass range is evident in our sample (Fig. 2) and permits estimation of intraspecific metabolic scaling. The scaling exponents for the upper and lower limits to aerobic metabolism (RMR and  $\dot{V}_{\text{O}_{2,\text{max}}}$ ) in weasels are consistent with numerous studies of interspecific metabolic allometry in mammals (recent reviews in White and Seymour, 2004; White and Seymour, 2005; White et al., 2009). Both parameters show intraspecific scaling approximately to  $M^{0.7-0.72}$  in weasels and do not differ from ‘typical’ scaling to  $M^{0.75}$  or  $M^{0.67}$ . Although the scaling of  $\dot{V}_{\text{O}_{2,\text{max}}}$  in weasels (to  $M^{0.701}$ ) is lower than the interspecific scaling to  $M^{0.872}$  reported for 34 eutherian species (Weibel and Hoppeler, 2005), the difference is not significant. Curiously, the maximal  $\dot{V}_{\text{O}_2}$  weasels attained in voluntary exercise scaled to a mass exponent (approximately  $M^{0.91}$ ; Fig. 2) that was considerably (but not significantly) higher than the mass exponent for  $\dot{V}_{\text{O}_{2,\text{max}}}$ , and significantly higher than the mass exponent for RMR. We are unsure of the reason for this. One possibility is a size-related difference in position on the wheel during running (e.g. larger individuals might

have a greater tendency than smaller animals to run ‘uphill’ and hence incur higher costs). We lack data to robustly test this idea, but observations of running weasels suggested that all individuals remained at or near the bottom of the wheels. Another possibility is size-related differences in gait or posture while running; again, we cannot formally test this hypothesis but our subjective impression is that there were no differences in gait or posture between small and large weasels.

### Running behavior

Compared with a number of rodent species tested for voluntary locomotion in wheel respirometers, weasels were notable for their limited propensity to run. Total distances run per day were short, averaging less than 2 km, and bouts of running were brief and usually separated by long periods of inactivity (Fig. 1). In contrast, many rodents, including deer mice (*Peromyscus maniculatus*), California mice (*P. californicus*), laboratory mice (*Mus domesticus*), golden-mantled ground squirrels (*Spermophilus lateralis*), least chipmunks (*Tamias minimus*) and several other species of wild rodents, often run  $5\text{--}12\text{ km day}^{-1}$  in the same wheel systems (sometimes more) and running bouts may last for many minutes to hours (Chappell et al., 2004; Rezende et al., 2006; Chappell and Dlugosz, 2009; Dlugosz et al., 2012). The short running distances for weasels are somewhat surprising: carnivores generally have larger home ranges than non-carnivores (e.g. Kelt and Van Vuren, 2001) and hence might be expected to exhibit greater voluntary movement distances. Without additional data, it is unclear whether the difference is due to nonadaptive lineage divergence between rodents and carnivores, or results from differential selection on species with carnivorous *versus* herbivorous or omnivorous diets. In the latter context, we speculate that the short voluntary running distances we observed in the laboratory might reflect selection on weasels to minimize activity, both to conserve energy and to minimize exposure to predators (Korpimäki and Norrdahl, 1989; Zub et al., 2009). In that context, a potentially important factor is the high hunting efficiency of weasels in the Białowieża area: weasels in this area are often able to capture prey sufficient for their daily energy requirements in 1 to 2 h of active hunting (Zub et al., 2011). Field studies show that weasels preferentially use areas with high prey abundance, which increases their hunting efficiency and allows activity time to be minimized (Zub et al., 2008).

Radiotracking data from free-living weasels were consistent with the short voluntary movement distances in wheels. At ambient temperatures similar to those in the metabolic wheel tests, wild weasels moved an average of  $1.45 \pm 0.83\text{ km per day}$ . That value is based on assumptions of linear movement between position fixes. Results from other species (Musiani et al., 1998; Rowcliffe et al., 2012), including another mustelid, the fisher [*Martes pennanti* (Powell, 1979)], indicate that radiotracking underestimates real movement distances by 30–90%. Assuming a correction factor of 50% (Powell, 1979), our free-living weasels traveled  $2.2\text{ km day}^{-1}$ , quite similar to the  $1.94\text{ km day}^{-1}$  of wheel-running we observed in captive weasels.

### Energy cost of running

Compared with allometric predictions of running costs derived from a broad range of terrestrial endotherms (Taylor et al., 1982), weasels in our wheel respirometers spent more energy than typical terrestrial runners when locomoting (Fig. 4). For example, when traveling at  $4\text{ km h}^{-1}$ , a 96 g weasel has a metabolic rate of  $14.6\text{ ml O}_2\text{ min}^{-1}$  (Eqn 4, Fig. 5), while the metabolic rate predicted by the Taylor et al. (Taylor et al., 1982) allometry is  $10.6\text{ ml O}_2\text{ min}^{-1}$ , a difference of 37%. The



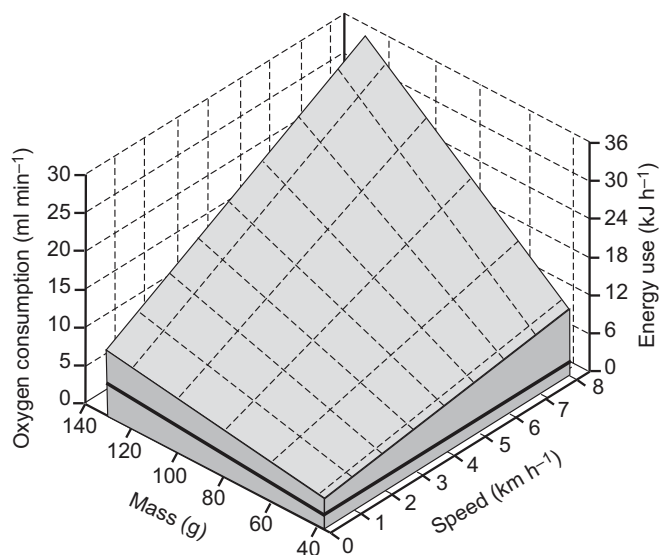


Fig. 5. Predicted rates of oxygen consumption and energy use for weasels of different body mass running at the range of speeds observed during voluntary running tests (0–8 km h<sup>-1</sup>). Tests were performed at room temperature (16–24°C). The mass range shown (37–130 g) encompasses the mass range of weasels used in this study. Predictions are based on slopes, intercepts and body masses of the 11 individuals shown in Fig. 4. Oxygen consumption was converted to energy use assuming 20.1 J ml<sup>-1</sup> O<sub>2</sub>. The heavy black lines show the predicted resting metabolic rate, which ranged from 1.44 ml O<sub>2</sub> min<sup>-1</sup> (1.73 kJ h<sup>-1</sup>) for a 37 g animal to 3.64 ml O<sub>2</sub> min<sup>-1</sup> (4.39 kJ h<sup>-1</sup>) for a 130 g animal.

difference in energy cost is largely due to a higher intercept of the speed *versus* power regression: for a 96 g weasel, the slope (i.e. iCOT) is only 35% higher than predicted (144 *versus* 107 ml O<sub>2</sub> km<sup>-1</sup>, respectively; Fig. 4), while the intercept is 80% higher than predicted [6.31 *versus* 3.51 ml O<sub>2</sub> min<sup>-1</sup>, respectively; Eqn 4 (Taylor et al., 1982)]. Across all 11 animals for which we have slope and intercept values, intercepts differed significantly from predictions ( $P < 0.001$ ) but slopes did not ( $P = 0.38$ ). It is perhaps coincidental, but the magnitude of the difference between predicted and observed intercepts in weasels is close to the ca. 90% difference between their predicted and observed minimal metabolic rates. The 'postural cost' [intercept–RMR (Taylor et al., 1970; Taylor et al., 1982)] is also high in weasels: 3.45 ml O<sub>2</sub> min<sup>-1</sup> for a 96 g animal, compared with approximately 2.0 ml O<sub>2</sub> min<sup>-1</sup> predicted from an intercept of 3.51 ml O<sub>2</sub> min<sup>-1</sup> (Taylor et al., 1982) and a BMR of approximately 1.45 ml O<sub>2</sub> min<sup>-1</sup> derived from recent mammalian allometries (White and Seymour, 2003; White et al., 2009).

Other elongate mustelids also have high transport and postural costs during terrestrial locomotion. Like weasels, fishers and ferrets had roughly similar slopes but higher intercepts than expected from mass allometry (Taylor et al., 1982; Powell, 1979). Williams (Williams, 1983) found a higher than predicted energy cost of running in semi-aquatic American mink (800–1000 g), and again this was largely due to a high intercept (approximately twice the predicted value). Running costs in the even more aquatic North American river otter (11 kg) were also greater than predicted (Williams et al., 2002). Moreover, the phylogenetically distant but similarly semi-aquatic Australian water rat [*Hydromys chrysogaster* (Fish and Baudinette, 1999)] has a higher than expected cost of terrestrial locomotion, leading Williams et al. (Williams et al., 2002) to suggest that compromises inherent in species that must both run and swim lead to increased running costs.

In that context it is interesting that weasels, which have no morphological specializations or behavioral propensities for swimming, also have high running costs. This suggests that their short-legged elongate shape is responsible for the high COT. However, it is possible that the high costs we observed in weasels were an artifact of thermoregulatory expenditures. In small mammals running at temperatures below the thermal neutral zone, locomotor costs are often partially or fully additive to thermoregulatory expenditures, not substitutive, as is frequently the case in large mammals and birds (e.g. Wunder, 1970; Hart, 1971; Brooks and Fahey, 1984; Chappell et al., 2004; Webster and Weathers, 1990). As the weasels in our wheel respirometers were probably running at temperatures somewhat below their thermal neutral zone, the metabolic expenditures in excess of predicted values might be due to regulatory thermogenesis, not to transport costs *per se*. A counterargument is that some small mammals in the Taylor et al. (Taylor et al., 1982) data set may also have been running at sub-thermoneutral temperatures [22–27°C (Taylor et al., 1970)].

Like nearly all other species thus far tested during voluntary locomotion, weasels rarely ran at speeds that are predicted to require substantial anaerobic power production [some lactate accumulation often occurs at exercise intensities below  $\dot{V}_{O_{2,max}}$  (e.g. Brooks and Mercier, 1994)]. The estimated maximal aerobic speed [ $=(\dot{V}_{O_{2,max}} - \text{intercept})/iCOT$ ] of a 96 g weasel is 9.4 km h<sup>-1</sup>. For the 11 animals used to generate COT data, the mean maximum speed averaged over 1 min was 3.3 km h<sup>-1</sup>, and the maximum 'instantaneous' speed (the highest speed in a 1.5 s sample interval) averaged 5.3 km h<sup>-1</sup>. The highest single instantaneous speed was 8.2 km h<sup>-1</sup> in a male weighing 104.7 g.

Gait changes as a function of speed (e.g. walking to running or bounding) have been reported for several small mammals, including elongate mustelids [mink (Williams, 1983); river otters, *Lontra canadensis* (Williams et al., 2002)] and a ground squirrel [*Spermophilus saturatus* (Kenagy and Hoyt, 1988)]. These transitions were associated with inflections in relationships between speed and metabolic rate. In much larger animals (horses), gait shifts may reduce costs of transport and peak musculoskeletal forces (e.g. Hoyt and Taylor, 1981; Wickler et al., 2003). In weasels, we observed walking (at low speed) and bounding (at high speed) both in the wild and in our wheel respirometers. However, COT data provided no clear evidence of changes in the speed *versus* power relationship at the speeds where gait transitions typically occurred (roughly 3–3.5 km h<sup>-1</sup>). Gait-related shifts in power requirements were also lacking in two other mustelids tested in forced running on treadmills: a ferret [*Mustela nigripes*, 540 g (Taylor et al., 1982)] and two fishers [*M. pennanti*, 3–5 kg (Powell, 1979)]. Similarly, no inflections in speed *versus* power regressions have been reported in rodents tested during voluntary running [deer mice, California mice, laboratory mice, golden-mantled ground squirrels, least chipmunks and Mongolian gerbils (Chappell et al., 2004; Chappell et al., 2007; Rezende et al., 2006; Chappell and Dlugosz, 2009; Dlugosz et al., 2012)].

#### Energy expenditures for locomotion by free-living weasels

The importance of locomotor costs in animal energy budgets is of considerable interest to behavioral, community and conservation ecologists as well as to physiologists. Typically, it is assumed that energy acquisition is ultimately limiting and therefore the energy used for locomotion must be traded off against other life history components such as maintenance, growth and reproduction. Animals can adjust the energy expended on locomotion, but that plasticity is constrained by the need to move about the habitat to find food

and perform other necessary behaviors. One approach for calculating the importance of locomotion expenditures is to use home range size to estimate daily movement distance (DMD) and measurements of COT to compute an 'ecological cost of transport' (ECOT) (Garland, 1983). If the ECOT is calculated as  $iCOT \times DMD$ , the predicted costs for small mammals are very small [roughly 1% or less of DEE (Garland, 1983)]. However, laboratory and a few field studies of voluntary locomotion in small mammals often show considerably larger costs, ranging from 5% to more than 30% of DEE (Kenagy and Hoyt, 1989; Kenagy et al., 1989; Koteja et al., 1999; Chappell et al., 2004; Rezende et al., 2006; Chappell and Dlugosz, 2009). The difference stems in part from considerably greater DMD than predicted simply from home range dimensions, and because many studies include postural costs as well as  $iCOT$  in the total energy expended for movement.

Doubly labeled water measurements of free-living weasels in Białowieża indicate DEE of approximately  $200 \text{ kJ day}^{-1}$  throughout the year, with an apparent trade-off between thermoregulatory and locomotor costs (Zub et al., 2009; Zub et al., 2011). Thus our estimates of average locomotor costs range from 3.2% of DEE (excluding postural costs and RMR) to 4.5% of DEE (including postural costs but excluding RMR). For the most active males, locomotor costs amounted to 6.4–9.0% of DEE. These transport costs are greater than the predicted ECOT of approximately 1% (Garland, 1983), but lower than values for wild and voluntarily running rodents (Kenagy and Hoyt, 1989; Kenagy et al., 1989; Koteja et al., 1999; Chappell et al., 2004; Rezende et al., 2006; Chappell and Dlugosz, 2009). Although their COT is higher than expected from body mass, weasels have considerably lower daily movement distances than have been reported for other small mammals. Accordingly, transport costs amount to a relatively minor fraction of weasel DEE. A potentially important caveat is that we do not know the distance weasels moved in burrows, or the energy costs of locomotion in burrows, which might be different from the cost of running in open areas.

The low daily expenditures by weasels for locomotion *per se* must be interpreted with caution when assessing the comprehensive energetic requirements of moving about the habitat. Our measurements of COT were taken in warm conditions, so costs of thermoregulation during movement were probably relatively minor. During winter in Białowieża, weasels outside of insulated nests experience environmental temperatures that require substantial regulatory thermogenesis (Casey and Casey, 1979; Jedrzejewski et al., 2000; Zub et al., 2009). Even in spring and autumn, temperatures in the early morning, when weasels begin activity, can be 5–10°C. We did not determine whether heat produced as a byproduct of locomotor exercise can be substituted for thermogenic heat requirements in weasels. However, in several small mammals, substitution is minimal or incomplete [e.g. thermogenic costs must be added to transport costs (Wunder, 1970; Hart, 1971; Wunder and Morrison, 1974; Chappell et al., 2004)], and it is reasonable to assume this is also the case for weasels. The high summed costs of activity and temperature regulation are probably important drivers for the quite low activity of weasels in winter, which is part of an apparent seasonal trade-off between activity and thermoregulation that results in surprisingly constant DEE throughout the year (Zub et al., 2009).

In conclusion, our study confirmed that the long-bodied and short-legged morphology of weasels is associated with high transport costs, as is the case in several larger elongate mustelids. The high transport costs are largely the result of high 'postural costs' and hence a high zero-speed intercept of the speed *versus* power

relationship. The incremental cost of transport (the slope of the speed *versus* power relationship) is similar to predicted values. Weasels also have very high maximal rates of oxygen consumption, but because these are matched with unusually high RMR, the factorial aerobic scope of weasels falls within the range of values typical for mammals. Similarly, the mass scaling exponents of weasels' lower and upper limits of aerobic metabolism are consistent with interspecific metabolic allometries of mammals. Although their energy costs during running are high, weasels have relatively short daily travel distances and times, presumably because of high hunting efficiency. As a result, metabolic costs of transport comprise a small fraction (~5%) of DEE.

## LIST OF SYMBOLS AND ABBREVIATIONS

BMR	basal metabolic rate
COT	energy cost of transport
DEE	daily energy expenditure
DMD	daily movement distance
$E_c$	energy consumed
ECOT	ecological cost of transport
$E_{net}$	net energy consumption
$iCOT$	incremental cost of transport
$i\dot{V}O_2$	'instantaneous' oxygen consumption
$M$	body mass
RMR	resting metabolic rate
$v$	speed
$\dot{V}O_2$	oxygen consumption
$\dot{V}O_{2,max}$	maximal oxygen consumption

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