

# Individual variation in thermogenic capacity affects above-ground activity of high-altitude Deer Mice

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## Summary

1. Understanding an animal's ecology requires knowledge of how individual variation in behaviour and physiology interact with each other and with the environment that an animal experiences.
2. Environmental variation affects behaviour, but whether individual variation in physiological performance also affects behaviour is poorly known.
3. We studied a high-altitude population of Deer Mice (*Peromyscus maniculatus*) inhabiting an environment cold enough that above-ground activity (behaviour) may be limited by the thermogenic capacity (maximal rate of oxygen consumption [ $VO_{2max}$ ] during cold exposure) of mice.
4. We measured thermogenic capacity and operative environmental temperature (an integrated measure of the thermal environment), and then used robust-design capture–mark–recapture (CMR) models to test whether the thermal environmental and individual variation in thermogenic capacity affected capture probabilities (a likely indicator of above-ground activity).
5. Models including environmental covariates and thermogenic capacity were strongly favoured over models that did not include them.
6. Our results demonstrate that individual variation in physiological performance may constrain behaviour in nature.
7. Besides contributing to our understanding of interactions in the multivariate phenotype, our results suggest that it may be possible to elucidate the mechanistic factors influencing capture probabilities. Such information could be valuable to ecologists, life historians and wildlife managers.

*Key-words:* Deer Mouse, maximal oxygen consumption, *Peromyscus*, thermogenic capacity

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## Introduction

The population dynamics of animals depend on many factors (e.g. behaviour, physiology and environmental circumstances) that influence the survival and reproductive success of individuals. Behaviour and physiology often vary among individuals, resulting in multiple strategies to maximize individual fitness within a population (Bennett 1987; Hayes & Jenkins 1997; Bolnick *et al.* 2003; Sih, Bell & Johnson 2004). Beyond the separate effects of behaviour and physiology on individual performance, an animal's physiological capacities can affect its behavioural options, and its behavioural choices (e.g. with respect to microenvironment selection) can

affect its physiological capacities (Walsberg 1985; Huey 1990). Hence, understanding an animal's ecology will require that we comprehend not only behaviour, physiology and environment, but also how they interact (Crespi 1990). This paper reports our attempt to discern how temporal environmental variation affects the above-ground behaviour of Deer Mice living in a well-studied high-altitude environment. Other studies have reported similar efforts to show how environmental variables affect population level behaviour (Seabloom, Schwab & Loeb 1994; Rezende *et al.* 2003; Kenagy *et al.* 2004). What makes the current report significant is that we also demonstrate that individual variation in physiological performance affects behaviour in nature.

Specifically, we test whether individual variation in maximal rate of oxygen consumption ( $VO_{2max}$ ) affects the propensity of Deer Mice to be active above-ground

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when it is cold. High-altitude (3800 m) Deer Mice inhabit cold environments where their ability to be active above ground may be constrained (Hayes & O'Connor 1999). Mice that are unable to produce sufficient heat may become hypothermic, and even die, if they are active above ground when it is too cold (Sealander 1951; cf. Merritt 1984; Bozinovic, Novoa & Veloso 1990). Alternatively, mice may starve if they elect to remain below ground when it is too cold for them to sustain their core body temperature above ground. At the high-altitude study site where this research was conducted, deer mice typically operate relatively close to their maximal thermogenic capacities (i.e. capacity to produce heat), as indicated by the small difference between the field metabolic rate of these mice and their  $\dot{V}O_{2\max}$  (Hayes 1989a,b). Genetic and physiological evidence from common environment experiments strongly suggest that deer mouse  $\alpha$ -globins have been selected to maintain high  $\dot{V}O_{2\max}$  at high altitude despite the reduced  $pO_2$  found at high altitude (i.e. at high altitudes the most common  $\alpha$ -globin haplotype has higher oxygen affinity than the haplotype prevalent at low altitudes; Snyder, Hayes & Chappell 1988). When tested at high altitude, mice with the high-altitude  $\alpha$ -globin haplotype had higher  $\dot{V}O_{2\max}$  which is presumed to be advantageous in this cold environment (Chappell & Snyder 1984). In addition, not only does directional selection for high  $\dot{V}O_{2\max}$  still act on high-altitude Deer Mice at least during some years, but biophysical analysis combined with data on thermogenic capacities suggests that the environment is likely cold enough to limit above-ground activity of mice (Hayes & O'Connor 1999). Hence, it seems likely that the thermogenic capacity of high-altitude Deer Mice may affect their propensity to be active above-ground.

To examine the extent that environmental conditions and individual thermogenic capacities influenced above-ground activity in Deer Mice, we estimated the probability of capture conditional on the animal being present in the population (hereafter conditional capture probabilities) from capture-mark-recapture (CMR) models. We integrated data on wind speed and environmental temperature to estimate severity of the thermal environment, and we measured individual variation in  $\dot{V}O_{2\max}$  (i.e. thermogenic capacity). These data were used to constrain estimates of conditional capture probabilities (our proxy for above-ground activity) in the context of a CMR model using Pollock's robust design (Pollock 1982; Kendall, Nichols & Hines 1997). The analyses allowed us to test *a priori* hypotheses that the propensity for above-ground activity was negatively affected by colder environmental conditions and that the propensity for above-ground activity was enhanced by increased thermogenic capacity of individuals. Besides contributing to our understanding of the interactions among behaviour, physiology and environment, the approach we take may be useful for elucidating the mechanistic (physiological) factors influencing recapture probabilities.

## Materials and methods

### STUDY ANIMALS

For this study, 31 Deer Mice (*Peromyscus maniculatus* Wagner) were trapped near the Barcroft Laboratory at the White Mountain Biological Station near Bishop, CA, at an altitude of ~3800 m. The trapping area was located in an alpine habitat, characterized by scattered rocky outcrops and open vegetation. A grid of 100 Sherman traps, supplied with cotton batting and baited with peanut butter and oats, were used to capture mice. Traps were spaced 10 m apart from one another. Deer Mice are active nocturnally, so we checked traps in the early morning around sunrise. Upon initial capture (between 2 and 9 September 1995), mice were taken to the laboratory, given a permanent ear tag under light Metofane anaesthesia, housed individually, and supplied with rodent chow (PMI Feeds Laboratory Diet, Turlock, CA). Because mice were held only briefly in the laboratory, and because it may take some time for wild mice to become accustomed to using a water bottle, we supplied mice with water indirectly by giving them fresh fruit (primarily watermelon). Mice were held in the laboratory until they had completed two metabolic trials (see below). After metabolic trials, mice were released into the field at the location where initially captured and were subsequently followed during the period of 11–25 October 1995 for a total of eight trap nights. During each trapping night, traps were checked for mice every hour from 19.00 to 07.00. If a mouse was captured, its presence was recorded and the mouse was immediately released. Our trapping included data from some of the coldest nights during which it is possible to trap at this high-altitude site, i.e. we trapped shortly before the first heavy snows of autumn, when air temperatures were low, wind speeds were high and there was no layer of insulating snow on the ground.

### MICROMETEOROLOGY

Micrometeorological data were collected concurrently during trapping periods at two weather stations located on the trapping grid. Each weather station consisted of four operative temperature ( $T_o$ ) models (i.e. unheated hollow copper Deer Mouse models covered with natural pelage), four 36-gauge thermocouples and one anemometer attached to a Campbell CR10 datalogger via an AM416 multiplexer (Campbell Scientific, Inc., Logan, UT). Air temperature ( $T_a$ ) was measured to the nearest 0.1 °C at ~2 cm above the ground surface using 36-gauge thermocouple wire. Wind speed ( $V$ ) was measured to the nearest 0.01 km h<sup>-1</sup> using a cup anemometers 1 m above ground. Operative temperatures (i.e. the temperature of an inanimate object of zero heat capacity with the same size, shape and radiative properties as the animal experiencing the same environmental conditions; Bakken 1992) were measured to the nearest 0.1 °C. Data were measured, averaged and recorded

once per half hour during the trapping periods. Hourly averages for air temperature, operative temperature and wind speed were recorded for subsequent analysis.

#### MEASUREMENT OF MAXIMAL OXYGEN CONSUMPTION

Maximal oxygen consumption was measured via cold exposure during open-circuit respirometry as described previously (Hayes & O'Connor 1999). Mice were initially captured from the field and brought into the laboratory for metabolic measurements during 2–9 September 1995. On the day immediately following the night of initial capture, we weighed animals (to the nearest 0.1 g) and measured their  $VO_{2\max}$ . For  $VO_{2\max}$  measurements, mice were placed inside a wind tunnel that generated a 4–5 m s<sup>-1</sup> wind. The wind tunnel was placed inside an environmental chamber with a high cooling capacity. Over the course of ~15 min, the temperature in the wind tunnel was reduced from about 0 °C to about -10 to -15 °C. Dry air was supplied to the wind tunnel at 1000 ml min<sup>-1</sup> with a Sierra Designs (Monterey, CA) thermal mass-flow controller. The oxygen concentration of air leaving the chamber was measured with an AMETEK S3/IIA (AEI Technologies, Pittsburgh, PA) oxygen analyser interfaced to a computer via Sable Systems DATACAN V (Sable Systems International, Henderson, NV). Because excurrent oxygen concentrations changed rapidly under the test conditions, oxygen consumption was calculated using the instantaneous method developed by Bartholomew, Vleck & Vleck (1981). The instantaneous method accounts for the dynamics of chamber (i.e. the wind tunnel) washout, so that an accurate measure of oxygen consumption is obtained even though mice were not in steady state. Under the test conditions, oxygen consumption was initially high as mice attempted to meet the thermogenic demands produced by cold air and wind. Eventually, the thermogenic demands were sufficient to overwhelm each mouse's ability to produce heat, so that its body temperature declined, and its thermogenic capacity was reduced. The test was ended when rapidly declining oxygen consumption indicated that an animal's thermogenic capacity had been exceeded. We defined  $VO_{2\max}$  as the highest 1 min of oxygen consumption. Extensive early studies with this species have demonstrated that the testing procedure reliably and repeatably elicits  $VO_{2\max}$  of Deer Mice (Chappell 1984; Hayes & Chappell 1990). On the second day after capture, each animal's mass and  $VO_{2\max}$  were measured again. Following the second  $VO_{2\max}$  determination, mice were released at their original capture locations. Almost all mice spent less than 48 h in the laboratory.

#### CAPTURE–MARK–RECAPTURE DESIGN AND ANALYSIS

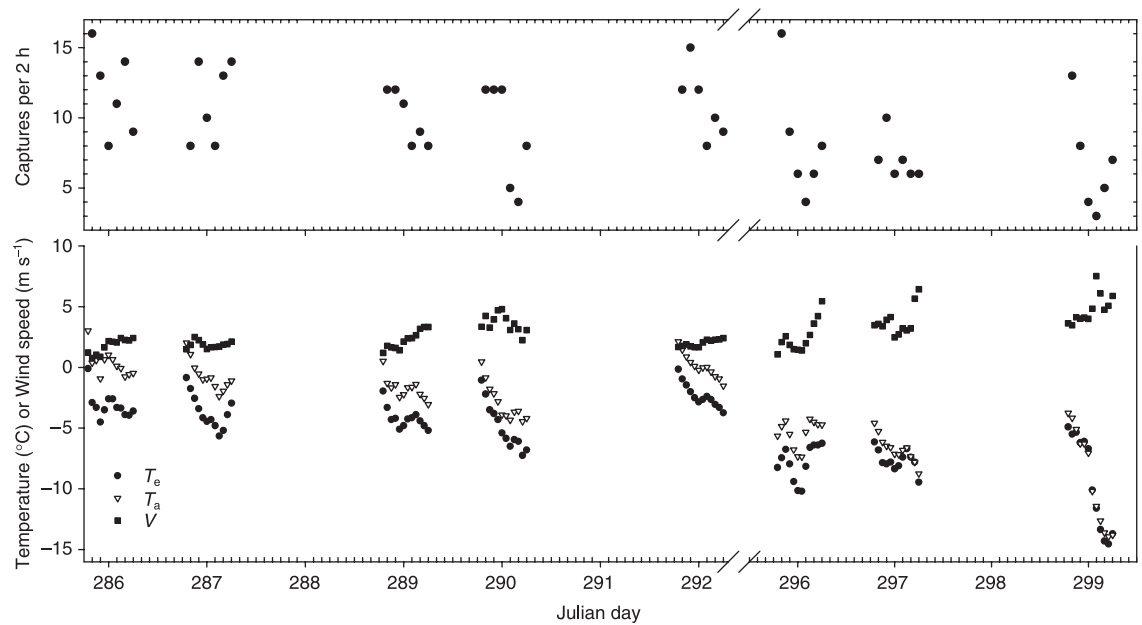
We used Pollock's robust mark–recapture design (Pollock 1982; Kendall *et al.* 1997) to estimate the conditional

probability of capture. Our trapping design consisted of hourly sampling over 8 days. The primary sampling period was over a day; the secondary period pooled hourly samples into 2-h time periods. No two primary sampling periods were separated by more than 3 days. Over each secondary period, we used the average  $T_e$  as an environmental covariate. Average values of  $VO_{2\max}$  and body mass taken in the laboratory were used as individual covariates. With Pollock's robust design, capture–recapture models can be used to estimate conditional capture (and recapture) probabilities and population size for each primary period. Though not of specific interest to this study, patterns of capture across primary periods provide estimates of survival rates, and data from both primary and secondary periods can be used to estimate temporary emigration, i.e. absence during an entire primary sampling period (Kendall *et al.* 1997; Kendall 1999).

We hypothesized that models of capture–recapture parameters that included environmental temperature ( $T_e$ ) and the  $VO_{2\max}$  of individual Deer Mice would best explain conditional capture probabilities, which we used as a proxy for above-ground activity. We therefore composed models in which conditional capture probabilities were modelled as a function of the individual and group covariates against models without these functional relationships to assess these hypotheses. We used Program MARK to calculate parameter estimates for each of our candidate models (White & Burnham 1999). All models included one or more of the following parameters: survival ( $S_i$ ), temporary emigration ( $\gamma_i$ ), conditional probability of capture ( $p_{ij}$ ) and probability of recapture ( $c_{ij}$ ), where  $i$  refers to the primary trapping period and  $j$  refers to the secondary trapping period (a list of candidate models is shown in Table 1). Because our experiment did not contain a large sample size of individuals, we set  $c_{ij}$  and  $p_{ij}$  equal to each other in all models. Parameters were estimated as time-dependent and time-independent. If a parameter specific to a primary period (e.g.  $\gamma_i$ ) was run as time-dependent, time variation was with respect to days; if a parameter specific to a secondary period was run, time variation was with respect to a 2-h interval (e.g.  $c_{ij}$ ). Temporary emigration was modelled as both Markovian and non-Markovian, where Markovian emigration was modelled as if an animal's decision to temporarily emigrate (or immigrate) was dependent on its decision during the previous time period, whereas non-Markovian emigration was not dependent on an individual's previous decision. Temporary emigration was included in our models because closed capture models assume that emigration is permanent. In our study, mice may have been unavailable for capture because they were voluntarily inactive in underground burrows, or because the placement of traps in our grid did not allow equal capture probability among times (*sensu* Bailey, Simons & Pollock 2004). Thus, because temporary emigration is controlled for, conditional probability of capture (i.e. capture probabilities contingent on an animal being available for capture)

**Table 1.** Candidate models were ranked by the quasi likelihood corrected Akaike Information Criterion (QAICc) to examine the effect of time, operative temperature, individual  $VO_{2max}$  and individual mass on capture probabilities. The model with highest support is shown in bold text

Model	QAICc	$\Delta$ QAICc	QAICc weight	Model likelihood	Number of estimated parameters	QDeviance
<b>Non-Markovian</b>						
S(.) $\gamma(\cdot)$ p(t, $T_e$ , $VO_{2max}$ , mass)	1233.00	0.00	0.40241	1.000	10	1212.49
S(.) $\gamma(\cdot)$ p(t, $T_e$ , $VO_{2max}$ )	1233.66	0.67	0.28832	0.717	9	1215.25
S(.) $\gamma(\cdot)$ p(t, $T_e$ , mass)	1242.32	9.32	0.00381	0.010	9	1223.91
S(.) $\gamma(\cdot)$ p(t, $VO_{2max}$ , mass)	1246.90	13.90	0.00039	0.001	10	1226.40
S(.) $\gamma(\cdot)$ p(t, $VO_{2max}$ )	1247.88	14.89	0.00024	0.001	9	1229.47
S(.) $\gamma(\cdot)$ p(t, mass)	1255.69	22.69	0.00000	0.000	9	1237.27
S(.) $\gamma(\cdot)$ p(t, $T_e$ )	1274.57	41.57	0.00000	0.000	9	1256.16
S(.) $\gamma(\cdot)$ p(t)	1285.74	52.74	0.00000	0.000	8	1269.41
S(.) $\gamma(\cdot)$ p(.)	1297.30	64.29	0.00000	0.000	3	1291.23
<b>Markovian</b>						
S(.) $\gamma_m(\cdot)$ p(t, $T_e$ , $VO_{2max}$ , mass)	1234.87	1.87	0.15777	0.392	11	1212.26
S(.) $\gamma_m(\cdot)$ p(t, $T_e$ , $VO_{2max}$ )	1235.07	2.08	0.14250	0.354	10	1214.57
S(.) $\gamma_m(\cdot)$ p(t, $T_e$ , mass)	1242.32	9.32	0.00381	0.010	9	1223.91
S(.) $\gamma_m(\cdot)$ p(t, $VO_{2max}$ , mass)	1246.63	13.63	0.00044	0.001	10	1226.13
S(.) $\gamma_m(\cdot)$ p(t, $VO_{2max}$ )	1247.25	14.26	0.00032	0.001	9	1228.84
S(.) $\gamma_m(\cdot)$ p(t, mass)	1255.69	22.69	0.00000	0.000	9	1237.28
S(.) $\gamma_m(\cdot)$ p(t, $T_e$ )	1276.51	43.52	0.00000	0.000	10	1256.01
S(.) $\gamma_m(\cdot)$ p(t)	1287.80	54.81	0.00000	0.000	9	1269.39
S(.) $\gamma_m(\cdot)$ p(.)	1289.54	56.55	0.00000	0.000	4	1281.45



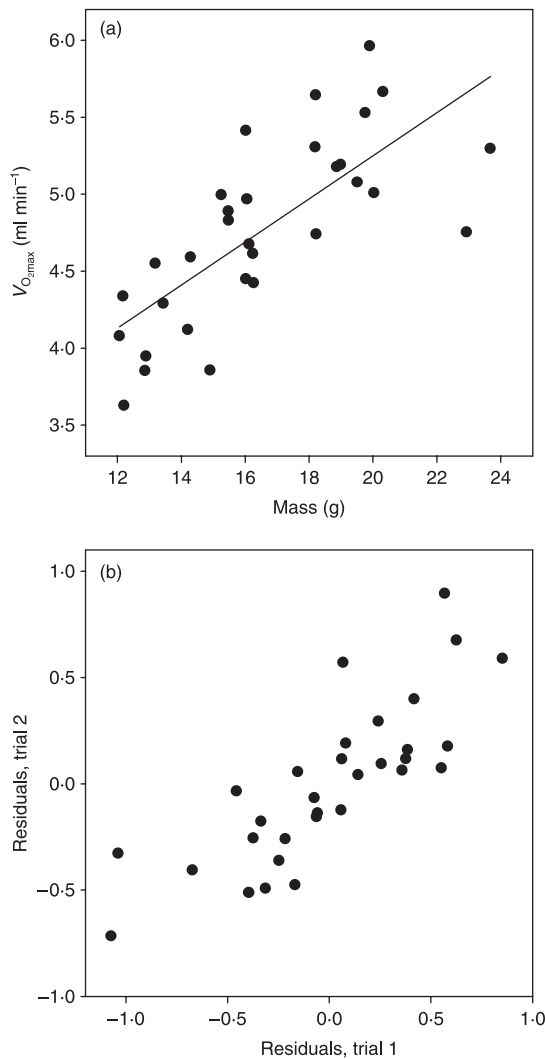
**Fig. 1.** Operative temperature ( $T_e$ ), air temperature ( $T_a$ ) and wind speed ( $V$ ) and corresponding deer mice captures during trapping nights.

should reflect the probability that an animal is above ground (and therefore is active). All covariates were converted to standard normal deviate. We used the logit link function to constrain parameter estimates between 0 and 1. Because a Goodness-of-Fit test is not available for robust design models that include individual covariates, we used the program RDSURVIV (Kendall *et al.* 1997) to obtain an estimate of  $\hat{c}$ . The estimate of  $\hat{c}$  was then used to correct the precision of our parameter estimates for overdispersal.

## Results

### ENVIRONMENTAL CONDITIONS

Typically, air temperatures decreased and wind speed increased over the course of a night (Fig. 1). Air temperatures ranged from an average nightly minimum of  $-5.4$  °C (95% CI:  $\pm 3.2$  °C; range:  $-14.4$  °C to  $-0.9$  °C) to a nightly maximum of  $-0.55$  °C (95% CI:  $\pm 2.2$  °C; range:  $-4.6$  °C to  $3.0$  °C). Wind speed ranged from an



**Fig. 2.** (a)  $VO_{2\max}$  increases with mass among individuals ( $\beta = 0.14$ , intercept = 2.45,  $r = 0.74$ ,  $P < 0.001$ ). Average mass ( $16.6 \pm 1.10$  g, mean  $\pm$  95% CI) and average  $VO_{2\max}$  ( $4.75 \pm 0.21$  ml  $O_2$   $min^{-1}$ , mean  $\pm$  95% CI) from two laboratory trials are plotted for our experimental deer mice. (b) Residuals of  $VO_{2\max}$  from mass are repeatable within an individual between trials.

average nightly minimum of  $1.8$  m  $s^{-1}$  (95% CI:  $\pm 0.6$  m  $s^{-1}$ ; range:  $0.8$  m  $s^{-1}$  to  $3.5$  m  $s^{-1}$ ) to an average nightly maximum of  $4.4$  m  $s^{-1}$  (95% CI:  $\pm 1.34$  m  $s^{-1}$ ; range:  $2.4$  m  $s^{-1}$  to  $6.4$  m  $s^{-1}$ ). Operative temperatures ranged from an average nightly maximum of  $-2.7$  °C (95% CI:  $\pm 1.8$  °C; range:  $-6.3$  °C to  $-0.1$  °C) to an average nightly minimum of  $-7.8$  °C (95% CI:  $\pm 3.7$  °C; range:  $-14.6$  °C to  $-3.9$  °C).

#### PHYSIOLOGICAL CHARACTERISTICS OF INDIVIDUALS

Among individuals,  $VO_{2\max}$  increased with mass for the 31 Deer Mice in our study (Fig. 2a), and was consistent with previous studies of Deer Mice (e.g. Hayes & O'Connor 1999). Furthermore, measurements of  $VO_{2\max}$  between days were repeatable: residuals of the regressions of  $VO_{2\max}$  on body mass were highly correlated

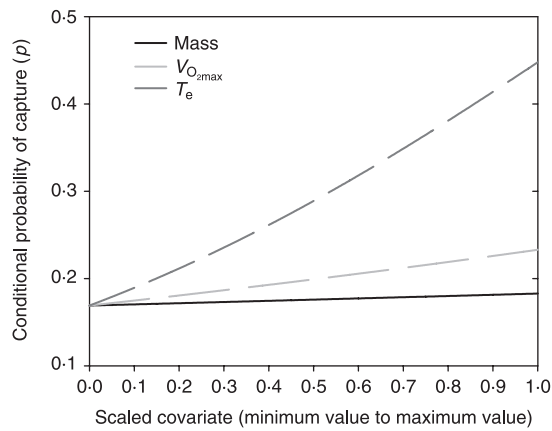
( $r = 0.81$ ,  $P < 0.001$ ; Fig. 2b).  $VO_{2\max}$ , not corrected for body mass, was also highly repeatable ( $r = 0.91$ ,  $P < 0.001$ ). Because of the high repeatability of estimates of  $VO_{2\max}$ , we used the average  $VO_{2\max}$  and average mass of both measurements in our mark–recapture analysis.

#### MODEL SELECTION AND CONDITION CAPTURE PROBABILITIES

To correct the precision of estimates of model parameters for potential overdispersion in the data, we used an estimate of  $c$ -hat (= 1.288) from program RDSURVIV, calculated as the Pearson chi-squared value divided by the model's degrees of freedom. Candidate models were subsequently ranked using QAICc values (Burnham & Anderson 2002), calculated in program MARK. Only 28 of the 31 mice that were entered into  $VO_{2\max}$  trials were included in the CMR analysis because 3 mice were presumed to have left the trapping area as they were never caught again after day 3. Because of the low numbers of mice in our study, these absent mice were excluded because their disappearance might overinfluence the estimation of CMR parameters in our models.

Capture–mark–recapture models that incorporated both environmental conditions ( $T_e$ ), time of night and individual characteristics ( $VO_{2\max}$  and mass) had the highest support for explaining the capture histories of mice in this study (Table 1). Because no one model in our set of candidate models had overwhelming support (i.e. model weight  $> 0.9$ ) compared with all other models, we used a multimodel inference approach (Burnham & Anderson 2002). We calculated average parameter estimates and their standard errors based on the top four models from all candidate models (including both Markovian and non-Markovian emigration) for averaging because the  $\Delta$ QAICc scores were approximately within 2, suggesting a high level of support for these models (Burnham & Anderson 2002).  $VO_{2\max}$  and  $T_e$  were included in all four top models, providing very strong support for an effect of  $VO_{2\max}$  and  $T_e$  on conditional capture probabilities. Models containing both variables had a summed QAICc weight of 0.991. Model-averaged estimates of  $\beta$  values linking  $p_{ij}$  and  $VO_{2\max}$  and  $T_e$  were  $\beta = 1.382 \pm 0.142$  (SE) and  $\beta = 0.401 \pm 0.012$  (SE), respectively. Mass was only included in two of the four models, with QAICc weights summing to 0.565, providing modest support for the effect of mass on conditional capture probabilities. For models where mass was included, the average  $\beta$  of mass was  $0.168 \pm 0.006$  (SE), while the averaged  $\beta$  across all models was  $0.0949 \pm 0.010$  (SE).

Conditional capture probabilities increased both with increasing  $T_e$ , increasing  $VO_{2\max}$ , and increasing mass (Fig. 3). Over the range of operative temperatures experienced during the study, conditional capture probabilities varied from 0.168 to 0.448. Individuals were 165% more likely to be captured at the warmest temperature than the coldest temperature during the trapping periods. Individuals with the highest  $VO_{2\max}$



**Fig. 3.** The influence of operative temperature ( $T_e$ ),  $VO_{2max}$  and body mass on conditional capture rates derived from multimodel logit parameter averages are plotted (relative to the intercept =  $-1.59$ ).

were 38% more likely to be captured than individuals of the lowest  $VO_{2max}$ . Conditional capture probabilities increased only 8% over the full range of masses for individuals in this study.

## Discussion

Much is known about the physiological processes that produce heat in animals, but relatively little is known about how individual variation in heat production affects the ability to survive cold in nature. This dearth of information is probably a result of the difficulty of simultaneously conducting physiological, behavioural and life-history studies. Mark-recapture studies that incorporate individual and environmental covariates may prove useful for improving our understanding of the ecological links between physiological performance, behaviour (e.g. microenvironmental selection) and life history.

Because Deer Mice at our study site sometimes experience directional selection for high  $VO_{2max}$  (the physical environment is quite cold), and because Deer Mice may operate close to their maximal thermogenic capacities (Hayes 1989a,b; Hayes & O'Connor 1999), we expected that variation in thermogenic capacity might influence rates of activity in these mice. Indeed, all top-ranked models included  $T_e$  and  $VO_{2max}$  as determinants of conditional capture probability (our proxy for activity). Colder temperatures retarded activity and higher  $VO_{2max}$  and mass favoured increased activity (Fig. 3). Our results are among the first to show a direct link between individual variation in physiological capacity and activity of mammals in nature.

Small mammals can be active only in environments in which their rates of heat loss and heat gain are equal over the long term; otherwise, their body temperature will change. In cold environments, small mammals must produce heat rapidly and limit heat loss. In warm environments, small mammals need to limit external heat gain and dissipate heat rapidly. Small mammals

can modify their behaviour and physiology to regulate body temperatures during activity. Behaviourally, rodents often choose microhabitats that reduce the need for physiological thermoregulation, and they often choose to be active during times of the day or night that are least thermally stressful. In hot environments, diurnal rodents adjust the timing of their activity to avoid the hottest parts of the day (Chappell & Bartholomew 1981; Vispo & Bakken 1993; Sharpe & Van Horne 1999; Kenagy *et al.* 2004). In cold environments (e.g. during winter), small nocturnal mammals tend to be active closer to sunset rather than later in the night (Seabloom *et al.* 1994). Hence, their activity tends to occur during the part of the night when temperatures are warmer. However, data for mammal activity during particularly cold periods are not as readily available as are data for mammal activity during particularly hot periods.

A major difference between this study and previous studies that link above-ground activity with environmental conditions is that our analysis incorporates data on individual physiological capacities. Animals with higher physiological capacities for heat production may remain active in extreme cold when animals with lesser capacities are unable to do so. The survival of individuals living in cold environments may depend critically on their thermogenic capacity because mammals that cannot produce sufficient heat will become hypothermic, and they may die as a result. In a test of a related hypothesis, non-shivering thermogenesis (the noradrenalin-elicited increase in heat production over resting heat production) was not associated with overwinter survival in Short-Tailed Field Voles (Jackson, Trayhorn, & Speakman 2001). However, field studies of both birds and mammals suggest indirectly that there may be viability selection on thermogenic capacities. For example, severe weather or winter conditions have been associated with increased mortality in Bighorn Sheep, Cliff Swallows, Cotton Rats, European Rabbits, Pronghorn Antelope and wild horses (Barrett 1982; Berger 1983; Langley & Shure 1988; Brown & Brown 1998; Portier *et al.* 1998; Rödel *et al.* 2004). Increased capture probabilities of deer mice in this study suggest that high  $VO_{2max}$  may directly contribute to higher activity rates that would likely confer higher survival if foraging (while avoiding predators) during cold portions of the year is required.

Another means by which small mammals could maintain body temperature in cold conditions is by reducing their conductance (i.e. increasing their insulation). Animals with better insulation (i.e. lower conductance) should be better able to survive cold conditions because the rate at which they lose heat to the environment would be reduced. We did not measure conductance of the mice we studied, and indeed there is a paucity of studies in the literature that attempt to relate thermogenic capacity or conductance to the activity or survival of individuals in nature. In one of the only experimental field studies conducted, Kenagy & Pearson (2000) increased the thermal

conductance of Meadow Voles (*Microtus californicus*) by shaving off their fur. In shaved voles, energy expenditure was expected to increase and survival was expected to decrease. Compared with unshaved voles, shaved voles expended approximately 10% more energy, but their survival was not reduced during the 3 weeks of the study. It would be interesting to repeat this experiment with high-altitude Deer Mice during a cold time of the year and with a larger sample size. Owing to the cold temperatures experienced at night by mice at high altitude, we predict that the behaviour of mice lacking fur would be drastically altered and that above-ground activity would decline substantially or else mortality would occur.

In summary, this study demonstrated that individual variation in an ecologically relevant metric of physiological performance (thermogenic capacity) affected above-ground activity (estimated as capture probabilities) of Deer Mice. Capture–recapture studies that incorporate individual covariates for physiological performance are a valuable tool for investigating the complex interrelationships among physiology, behaviour and life history in the wild. Our results demonstrate that individual variation in physiological performance may constrain behaviour in nature. Besides contributing to our understanding of interactions in the multivariate phenotype, our results also suggest that it may be possible to elucidate the mechanistic factors influencing capture probabilities. Such information could be valuable to ecologists, life historians and wildlife managers seeking to understand individual and environmental factors that influence variation in survivorship.

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