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# Individual consistency of maximal oxygen consumption in deer mice

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**Abstract.** Individual physiological performance is often assumed to be consistent and repeatable. We examined the individual consistency of maximum oxygen consumption ( $\dot{V}O_2\text{max}$ ) in deer mice (*Peromyscus maniculatus* Wagner). Correlations of repeated measures on individuals were studied over time, short-term captivity, long-term cold acclimation to 3°C, and acclimation to low (340 m) and high (3800 m) altitudes. The latter three treatments are known to induce significant changes in  $\dot{V}O_2\text{max}$ . Two measurement protocols, severe cold exposure and intense exercise, were used to elicit  $\dot{V}O_2\text{max}$ . The  $\dot{V}O_2\text{max}$  as elicited by exercise and cold exposure were strongly and significantly correlated for all experimental treatments. Individual correlations across experimental treatments were generally strong for whole-animal  $\dot{V}O_2\text{max}$  data, using both the exercise and cold exposure protocols. Correlations were weaker, but usually remained significant, when effects of body mass were removed. Across-altitude correlations were significant in most cases but correlation coefficients were lower than for other treatments. Our results suggest that in many cases, individual  $\dot{V}O_2\text{max}$  measurements in one experimental situation are useful indicators of performance relative to the group mean in other situations or acclimation regimes.

**Key-words:** Deer mice, high altitude, maximal aerobic metabolism, phenotypic plasticity, physiological performance, repeatability, within-individual variation

## Introduction

A major focus of organismal physiology has been the determination of performance limits (e.g. maximum running speed or endurance, minimum and maximum tolerable temperatures, maximal

rates of oxygen consumption, etc.). These measurements are intrinsically interesting to mechanistic and comparative physiologists and they are frequently of critical importance for investigations of the ecology and evolution of physiological traits. For many such studies, a fundamental assumption is that performance as measured at one time or in one set of conditions can be usefully extrapolated to performance at other times or in different conditions. This assumption has some important limitations. Performance is usually described as species or group means, an approach that tends to mask the magnitude and evolutionary significance of individual variation (Bennett, 1987; Pough, 1989). Moreover, many physiological parameters show substantial within-individual variation (i.e. phenotypic plasticity) related to age, reproductive status, seasonality, acclimation, conditioning, or other factors. Therefore, it is often unclear whether performance estimates based on one or a few measurements in one set of conditions are useful predictors of performance in other situations. The utility of such extrapolations will be enhanced, particularly for studies of selection on physiological traits, if individual differences in performance can be shown to be repeatable across diverse experimental, ontogenetic and/or environmental conditions. Few such studies have been reported.

In this paper we use data sets collected during a long-term study of aerobic metabolism in deer mice (*Peromyscus maniculatus* Wagner) to examine the within-individual consistency of maximal oxygen consumption ( $\dot{V}O_2\text{max}$ ). This is one of the most frequently used indices of overall performance, particularly in endothermic vertebrates. Previous work (Chappell, 1984) suggested that the  $\dot{V}O_2\text{max}$  of individual deer mice is highly correlated across different measurement protocols (cold exposure vs intense exercise). The purpose of the present study was to determine if individual  $\dot{V}O_2\text{max}$  remain correlated over long time periods and across several acclimation regimes and environmental conditions that induce substantial changes in mean  $\dot{V}O_2\text{max}$ . While our analyses have obvious relevance for our own work on deer mice (Chappell & Snyder, 1984; Chappell, Hayes &

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Snyder, 1988; Hayes, 1989a,b) we believe they are also germane to other studies that involve the consistency and predictability of individual performance.

## Materials and methods

### Animals

Deer mice used in this study fell into three general categories. Some were captured from wild populations and held in captivity for substantial periods (months to years) prior to measurements. These (subspecies *sonoriensis* and *rufinus*) were collected from California, Utah and Colorado. Additional animals came from laboratory-bred strains derived from subspecies *sonoriensis*, *rufinus*, *gambelii* and *nebrascensis*. Strains were also derived from populations in California, Utah and Colorado, and were periodically outbred to wild-caught mice from the source populations. A final group was captured immediately prior to measurements of  $\dot{V}O_2\text{max}$ ; these mice were obtained from *sonoriensis* populations in eastern California. Animals were housed in plastic mouse cages, provided with wood shavings for bedding and given *ad libitum* water and rodent chow, occasionally supplemented with fresh fruit or vegetables.

### Measurements of maximum oxygen consumption

Aerobic performance was measured using two standardized protocols previously shown to reliably elicit  $\dot{V}O_2\text{max}$ : severe cold exposure in a wind tunnel and intense exercise in an enclosed treadmill. The treadmill and wind tunnel were connected to open circuit respirometry systems incorporating an Applied Electrochemistry S3-A oxygen analyser interfaced to a computer. During cold exposure measurements, mice were subjected to a 4–5  $\text{ms}^{-1}$  wind at ambient temperatures ( $T_a$ ), low enough to induce hypothermia in approximately 15 min. Treadmill exercise measurements were made during 6 min of running at tread speeds higher than the maximum sustainable aerobic running speed.  $\dot{V}O_2\text{max}$  was calculated as the highest 1 and 2 min of oxygen consumption during exercise and cold exposure, respectively. Details of the protocols have been published elsewhere (Chappell, 1984; Chappell & Snyder, 1984).

### Experimental protocols

We examined the consistency of individual  $\dot{V}O_2\text{max}$  across four acclimation regimes.

The reproducibility of  $\dot{V}O_2\text{max}$  over time in unchanging environmental conditions was tested using control animals ( $n = 25$ ) from the cold acclimation experiment described below (Hayes & Chappell, 1986). These mice were laboratory bred and were maintained at constant temperature ( $T_a = 23^\circ\text{C}$ ) and photoperiod (14L:10D). Cold exposure and exercise  $\dot{V}O_2\text{max}$  were measured at the beginning and end of a 3-month acclimation period.

We determined the effect of short-term captivity with 29 mice captured during June 1987 near the Barcroft Laboratory of the White Mountain Research Station in eastern California (elevation 3800 m). Mice were captured in Sherman live traps that were checked several times each night. The animals were taken to the laboratory, housed in standard plastic mouse cages and provided with rodent chow, water and a slice of fresh apple. One group of mice ( $n = 13$ ) had cold exposure  $\dot{V}O_2\text{max}$  measured on the day immediately following capture (day 1) and again the next day. The  $\dot{V}O_2\text{max}$  of a second group of mice ( $n = 16$ ) was measured on the second day after capture and again 8 or 9 days after capture.

The effect of cold acclimation was assessed using 86 laboratory-bred mice. Both cold exposure and exercise  $\dot{V}O_2\text{max}$  were determined prior to and at the conclusion of an acclimation period of approximately 3 months at  $T_a = 3^\circ\text{C}$  and a photoperiod of 14L:10D. Means for both cold exposure and exercise  $\dot{V}O_2\text{max}$  increased substantially and significantly after cold acclimation (Hayes & Chappell, 1986).

We evaluated the effect of acclimation to low and high altitude (340 and 3800 m, respectively) using data from Chappell & Snyder (1984) and Chappell *et al.* (1988). During these studies about 540 laboratory-reared and wild-caught individuals were tested at both altitudes. In all cases, mice were acclimated to the test altitude for at least 2 months before  $\dot{V}O_2\text{max}$  was measured with the cold exposure or exercise protocols (usually both). Sample means for  $\dot{V}O_2\text{max}$  were significantly reduced at high altitude relative to the low altitude results. A number of distinct  $\alpha$ - and  $\beta$ -haemoglobin genotypes were represented among the tested mice. The  $\beta$ -globin genotype does not measurably influence  $\dot{V}O_2\text{max}$  (Chappell *et al.*, 1988). However,  $\alpha$ -globin genotype significantly affects  $\dot{V}O_2\text{max}$  (Chappell & Snyder, 1984), so these animals

were analysed according to genotype (see Statistical procedures).

#### Statistical procedures

The data were analysed with the Statistical Analysis System (SAS). Because mean  $\dot{V}O_{2\max}$  and mass often changed between replicate measures, we used the interclass correlation coefficient (Pearson's  $r$ ) rather than the intraclass correlation coefficient to index repeatability (i.e. we measured individual performance relative to the mean, not absolute performance; Falconer, 1989; van Berkum *et al.*, 1989). Two different procedures were used to account for any influence of body mass. First, we used simple correlations to test whether whole-animal performance of individuals was consistent across experimental treatments. Rates of oxygen consumption are profoundly affected by body size (Heusner, 1982; Calder, 1984; Schmidt-Nielsen, 1984), so significant correlations could result from individuals having consistent  $\dot{V}O_{2\max}$  relative to their mass, or from individuals showing consistent trends in body mass between measurements, or both. Accordingly, we performed a second set of analyses. The  $\dot{V}O_{2\max}$  was regressed on body mass and residuals from the regression were calculated. The correlation of residuals across experimental treatments was then determined. In one case (day 1 to day 2 for short-term captivity), there was no significant correlation of  $\dot{V}O_{2\max}$

with body mass. For both analytical approaches, a significant positive correlation indicates that individuals show consistent performance relative to the overall performance mean.

Additional analyses were performed for the altitude-acclimation experiments. The  $\alpha$ -globin genotype affects  $\dot{V}O_{2\max}$  and there is an interaction of genotype with altitude such that the relative ranking of genotypes at low altitude is reversed at high altitude (Chappell & Snyder, 1984; Chappell *et al.*, 1988). In order to examine across-altitude consistency independent of genotypic effects, we calculated the correlation of residuals from an ANOVA by  $\alpha$ -globin genotype. To account for the combined effects of  $\alpha$ -globin genotype and body mass, we calculated the correlation of residuals from an ANCOVA by  $\alpha$ -globin genotype (the class or 'treatment' variable) and body mass (the covariate). The common slope estimate for body mass was fit after establishing that there was no heterogeneity of slopes among genotypes.

## Results

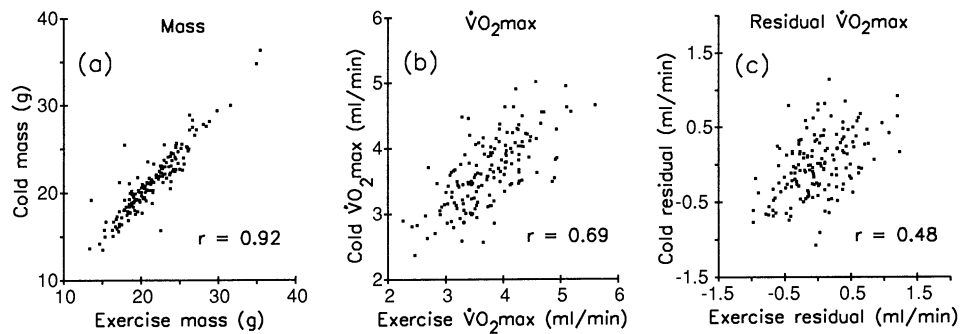
### Measurement technique and body mass

Whole-animal  $\dot{V}O_{2\max}$  measured via cold exposure and whole-animal  $\dot{V}O_{2\max}$  measured via treadmill exercise were strongly and significantly correlated in all experiments that employed both techniques (Fig. 1 and Table 1). Residuals from regressions of exercise and cold exposure  $\dot{V}O_{2\max}$

**Table 1.** Correlation of individual body mass and  $\dot{V}O_{2\max}$  as elicited by exercise and cold exposure. The  $\dot{V}O_{2\max}$  is expressed as whole-animal data and as residuals from the regression of  $\dot{V}O_{2\max}$  on body mass. The whole-animal  $\dot{V}O_{2\max}$  and residual columns show the correlation coefficient  $r$ , with the associated probability value in parentheses. Correlations significant at  $P < 0.05$  are in bold type. A significant positive value indicates that individuals are consistent in their performance rankings relative to the group mean.

Treatment group	Body mass	Whole-animal $\dot{V}O_{2\max}$	Regression residual	$n$
CONST-B	<b>0.99</b> (0.0001)	<b>0.74</b> (0.0001)	<b>0.59</b> (0.0017)	25
CONST-A	<b>0.88</b> (0.0001)	<b>0.52</b> (0.0074)	0.35 (0.0899)	25
COLD-B	<b>0.98</b> (0.0001)	<b>0.86</b> (0.0001)	<b>0.64</b> (0.0001)	86
COLD-A	<b>0.95</b> (0.0001)	<b>0.83</b> (0.0001)	<b>0.65</b> (0.0001)	86
$\alpha$ -high	<b>0.95</b> (0.0001)	<b>0.64</b> (0.0001)	<b>0.53</b> (0.0001)	267
$\alpha$ -low	<b>0.92</b> (0.0001)	<b>0.69</b> (0.0001)	<b>0.48</b> (0.0001)	158
$\beta$ -high	<b>0.98</b> (0.0001)	<b>0.53</b> (0.0001)	<b>0.47</b> (0.0001)	80
$\beta$ -low	<b>0.88</b> (0.0001)	<b>0.70</b> (0.0001)	<b>0.55</b> (0.0001)	115
REC-high	<b>0.98</b> (0.0001)	<b>0.72</b> (0.0001)	<b>0.53</b> (0.0001)	99
REC-low	<b>0.94</b> (0.0001)	<b>0.75</b> (0.0001)	<b>0.44</b> (0.0001)	75

Abbreviations for treatment group: CONST-B, constant conditions, before 3-month acclimation; CONST-A, constant conditions, after 3-month acclimation; COLD-B, before 3-month cold acclimation; COLD-A, after 3-month acclimation;  $\alpha$ -low,  $\alpha$ -globin genotypes at low altitude;  $\alpha$ -high,  $\alpha$ -globin genotypes at high altitude;  $\beta$ -low,  $\beta$ -globin genotypes at low altitude;  $\beta$ -high,  $\beta$ -globin genotypes at high altitude; REC-low,  $\alpha$ -globins including rare recombinants at low altitude; REC-high,  $\alpha$ -globins including rare recombinants at high altitude.



**Fig. 1.** An example of individual correlations for measurements made during cold exposure and treadmill exercise for (a) body mass, (b)  $\dot{V}O_{2max}$  and (c) residuals from regressions of  $\dot{V}O_{2max}$  on body mass. All correlations are significant at the  $P = 0.0001$  level. The data ( $n = 158$ ) are for  $\alpha$ -globin genotypes measured at low altitude (the  $\alpha$ -low treatment group in Table 1).

on body mass were significantly correlated in every analysis except one ( $P = 0.0899$ ; final measurements from the constant conditions experiment), for which the data set was relatively small ( $n = 25$ ). Replicated measures of body mass of individuals showed highly significant correlations in every experimental treatment ( $r$  from 0.41 to 0.99; Tables 1–3).

#### *Effect of time*

For individuals subjected to approximately 3 months of acclimation to constant environmental conditions, initial and final  $\dot{V}O_{2max}$  for both exercise and cold exposure were significantly correlated (Fig. 2 and Table 2). Residuals from regressions on body mass were also significantly correlated. The exercise and cold exposure correlation coefficients were not significantly different for either the raw data or the residuals.

#### *Effect of short-term captivity*

In 13 recently captured wild deer mice at high altitude, mean cold exposure  $\dot{V}O_{2max}$  increased by 11.2% (paired  $t = 5.33$ ,  $P = 0.0002$ ) between days 1 and 2 after capture. Body mass also increased significantly over this interval. For another group of 16 mice, both  $\dot{V}O_{2max}$  and body mass increased between days 2 and 8 or 9, but neither increase was significant. Individual values of  $\dot{V}O_{2max}$  were significantly correlated between days 1 and 2, and between days 2 and 8 or 9 (Table 2). Residuals from regressions on body mass were not correlated between days 2 and 8 or 9 (similar correlations were not obtained for days 1 and 2 because regressions on body mass were not significant).

#### *Effect of cold acclimation*

Individual values of cold exposure  $\dot{V}O_{2max}$  before cold acclimation were significantly correlated with cold exposure  $\dot{V}O_{2max}$  after cold acclimation (Table 2). Pre- and post-acclimation measurements of exercise  $\dot{V}O_{2max}$  were also individually correlated, even though the acclimation-induced increase in  $\dot{V}O_{2max}$  was only  $\frac{1}{3}$  as large for exercise as for cold exposure. Pre- and post-acclimation residuals from regressions of  $\dot{V}O_{2max}$  on body mass were significantly correlated for both exercise and cold exposure.

#### *Effect of altitude*

Individual values of whole-animal  $\dot{V}O_{2max}$  at low and high altitude were significantly correlated in all cases except for exercise  $\dot{V}O_{2max}$  for  $\beta$ -globin strains (Fig. 3 and Table 3). Residuals from regressions on body mass were significantly correlated in two out of three data sets for cold exposure  $\dot{V}O_{2max}$ . For exercise  $\dot{V}O_{2max}$ , the correlation of residuals between low and high altitude was not significant in any of three data sets. If ANCOVA is used to account for the combined influence of  $\alpha$ -globin and body mass, residuals for all cold exposure data sets show significant individual correlations and one correlation for exercise approaches significance.

## **Discussion**

Using physiological performance as measured in one set of conditions (e.g. the laboratory) to predict performance in another set of conditions (e.g. the natural habitat) is a routine extrapolation for physiologists and ecologists. Frequently the seminal issue is the average performance of a species

**Table 2.** Correlation across acclimation regimes of individual  $\dot{V}O_{2max}$  and body mass.

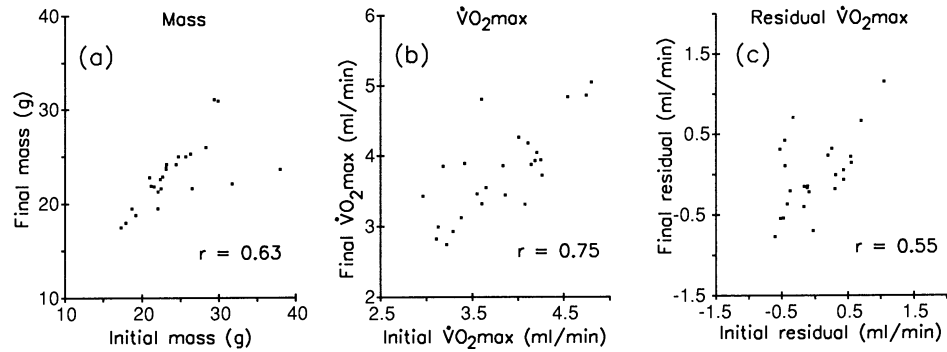
Treatment group	Protocol	Body mass	Whole-animal $\dot{V}O_{2max}$	Regression residual	n
TIME	C	<b>0.63</b> (0.0007)	<b>0.75</b> (0.0001)	<b>0.55</b> (0.0046)	25
TIME	E	<b>0.53</b> (0.0070)	<b>0.67</b> (0.0002)	<b>0.68</b> (0.0002)	25
COLD	C	<b>0.82</b> (0.0001)	<b>0.66</b> (0.0001)	<b>0.46</b> (0.0001)	86
COLD	E	<b>0.80</b> (0.0001)	<b>0.80</b> (0.0001)	<b>0.65</b> (0.0001)	86
CAP-A	C	<b>0.88</b> (0.0001)	<b>0.87</b> (0.0001)	—	13
CAP-B	C	<b>0.83</b> (0.0001)	<b>0.56</b> (0.0237)	0.16 (0.5643)	16

Numbers and symbols as in Table 1. Abbreviations for treatment group: TIME, 3 months in constant conditions: COLD, 3-month cold acclimation; CAP-A, days 1 to 2 following capture; CAP-B, days 2 to 8 or 9 following capture (see text for details). Abbreviations for protocol: C, cold exposure; E, exercise.

**Table 3.** Correlation of individual  $\dot{V}O_{2max}$  and body mass across acclimation from low (340 m) to high (3800 m) altitude.

Treatment group	Protocol	Body mass	Whole-animal $\dot{V}O_{2max}$	Regression residual	n
$\alpha$	C	<b>0.68</b> (0.0001)	<b>0.36</b> (0.0001)	0.10 (0.2268)	162
$\alpha$ -GT	C		<b>0.42</b> (0.0001)	<b>0.16</b> (0.0361)	
$\alpha$	E	<b>0.59</b> (0.0001)	<b>0.32</b> (0.0001)	0.06 (0.3655)	213
$\alpha$ -GT	E		<b>0.36</b> (0.0001)	0.13 (0.0582)	
$\beta$	C	<b>0.49</b> (0.0001)	<b>0.52</b> (0.0001)	<b>0.54</b> (0.0001)	73
$\beta$	E	<b>0.41</b> (0.0001)	—0.13 (0.2066)	—0.09 (0.3789)	97
REC	C	<b>0.57</b> (0.0001)	<b>0.47</b> (0.0001)	<b>0.22</b> (0.0055)	164
REC-GT	C		<b>0.46</b> (0.0001)	<b>0.19</b> (0.0169)	
REC	E	<b>0.69</b> (0.0001)	<b>0.49</b> (0.0001)	0.06 (0.6281)	66
REC-GT	E		<b>0.60</b> (0.0001)	0.15 (0.2112)	

Numbers and symbols as in Table 1. Abbreviations for protocol as in Table 2. Abbreviations for treatment group:  $\alpha$ , pooled  $\alpha$ -globin genotypes;  $\alpha$ -GT,  $\alpha$ -globin genotypes after accounting for genotype effects;  $\beta$ , pooled  $\beta$ -globin genotypes; REC, pooled  $\alpha$ -globin genotypes including rare recombinants; REC-GT,  $\alpha$ -globin genotypes including rare recombinants and after accounting for genotype effects (see text for details).



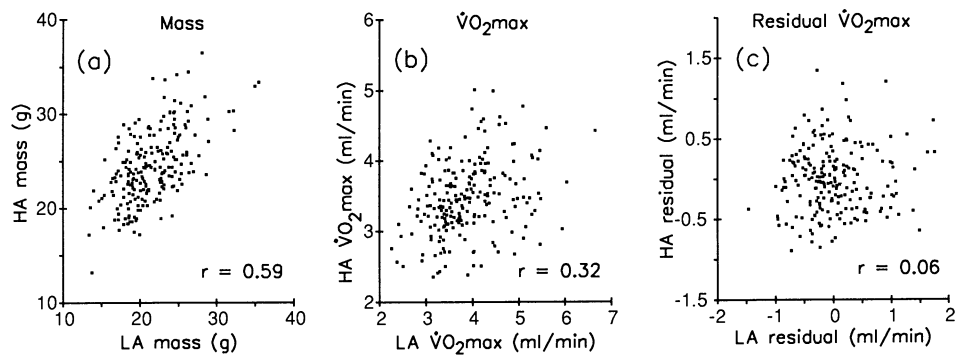
**Fig. 2.** An example of individual correlations for cold exposure and measurements made 3 months apart for (a) body mass, (b)  $\dot{V}O_2\text{max}$  and (c) residuals from regressions of  $\dot{V}O_2\text{max}$  on body mass. All correlations are significant at the  $P = 0.005$  level. The data ( $n = 25$ ) are for control animals measured at low altitude (the time treatment group with cold exposure protocol in Table 2).

or the mean value for some other group and the repeatability of individual performance is of lesser interest. However, many studies make the fundamental assumption that individual performance relative to the group mean remains repeatable and consistent over long time periods or across a range of environmental conditions or acclimation regimes. This assumption is particularly pertinent to studies dealing with questions involving the genetics, selective value or evolution of physiological traits.

Despite its importance, the repeatability and consistency of individual performance has received surprisingly little attention from physiological ecologists (Bennett, 1987). Many of the existing studies concern various aspects of locomotor performance. The repeatability of speed and endurance has been examined in lizards (Huey & Hertz, 1984; Garland, 1985; Garland & Else, 1987) and domestic and wild mammals (Ryan, 1975;

Tolley, Notter & Marlowe, 1983; Djawdan & Garland, 1988). In one study, Huey & Dunham (1987) demonstrated that sprint speed of wild *Sceloporus merriami* adults is repeatable across years. This work is particularly interesting because it revealed consistent performance in a trait, which presumably has considerable selective significance, for animals living in natural situations over periods comprising a substantial fraction of expected life-span. By contrast, van Berkum *et al.* (1989) showed moderate short-term repeatability but relatively low long-term repeatability for speed, stamina and size in *S. occidentalis* during the first year of life. Additional studies are needed to examine the consistency of other ecologically relevant physiological characters in other taxa.

For birds and mammals,  $\dot{V}O_2\text{max}$  is perhaps the most useful and widely employed index for integrated metabolic performance. It describes the



**Fig. 3.** An example of individual correlations for treadmill exercise measurements at low (340m) and high altitude (3800m) for (a) body mass, (b)  $\dot{V}O_2\text{max}$  and (c) residuals from regressions of  $\dot{V}O_2\text{max}$  on body mass. The correlations of body mass and  $\dot{V}O_2\text{max}$  are significant ( $P = 0.0001$ ), but the correlation of the residuals is not ( $P = 0.3655$ ). The data ( $n = 213$ ) are for  $\alpha$ -globin genotypes measured at low altitude and high altitude (the  $\alpha$ -treatment group with exercise protocol in Table 3).

upper limit to aerobic power generation, and hence is particularly relevant to environment or behavioural contexts where intense and sustained power output is crucial (e.g. Wickler, 1980; Seeherman *et al.*, 1981; Dawson & Dawson, 1982; Hochachka, 1985; Dawson & Smith, 1986). Our considerable database on the  $\dot{V}O_2\text{max}$  of deer mice (*P. maniculatus*) provides a convenient opportunity to investigate individual performance consistency for this important physiological trait.

Perhaps the simplest (and most trivial) test of the consistency of individual performance is to examine performance over time for animals held in constant environmental conditions. Unless there are effects of circannual rhythms or ontogeny (e.g. maturation or senescence), little change is expected in population means for the variable in question. Over the course of a 3-month period in an unchanging environment, deer mice exhibited small (*c* 2–4%) but significant changes in  $\dot{V}O_2\text{max}$  as elicited by both exercise and cold exposure. Nevertheless, the performance of individuals relative to the mean was very repeatable over a 3-month period. Results were similar for both exercise and cold exposure protocols (Table 2). Individual correlations were highly significant for both whole-animal  $\dot{V}O_2\text{max}$  and for the residuals of regressions of  $\dot{V}O_2\text{max}$  on body mass.

A more rigorous and meaningful test of consistency is to examine individual correlations before and after a condition change or acclimation regime known to affect population means of the variable in question. We used two protocols that change thermogenic  $\dot{V}O_2\text{max}$  in deer mice: short-term captivity and long-term cold acclimation. The capacity for metabolic heat production has been shown to change rapidly following capture in a number of vertebrate endotherms. This phenomenon is probably of little consequence ecologically (except that it probably reflects differences between field and laboratory environments), but it may be very important for the correct interpretation of experimental results. In some species (e.g. winter-acclimatized finches; Dawson & Smith, 1986), cold exposure  $\dot{V}O_2\text{max}$  declines sharply in the few days following capture. In summer-acclimatized deer mice it increases (this study), but despite the rapid change in mean  $\dot{V}O_2\text{max}$ , whole-animal performance of recently captured individuals remains consistent (Table 2).

Long-term cold acclimation provides a robust and ecologically relevant test of performance consistency. In many small mammals and birds, seasonal acclimatization to winter conditions or acclimation to a cold laboratory environment

induces substantial increases in thermogenic  $\dot{V}O_2\text{max}$  (Rosenmann, Morrison & Feist, 1975; Heimer & Morrison, 1978; Wickler, 1980; Heldmaier *et al.*, 1986; Dawson & Smith, 1986; Dawson & Olson, 1987; Hayes, 1989a). We subjected deer mice to a 3-month acclimation to 3°C, which induced a 31% increase in mean cold exposure  $\dot{V}O_2\text{max}$  and a 9% increase in mean exercise  $\dot{V}O_2\text{max}$  (Hayes & Chappell, 1986). Individual performance showed high consistency during cold acclimation, for both whole-animal  $\dot{V}O_2\text{max}$  and residuals from regressions (Table 2). Individual performance was also highly correlated between cold exposure and exercise measurements, despite the three-fold difference between the two protocols in the magnitude of  $\dot{V}O_2\text{max}$  change (Table 2).

A somewhat different question concerning individual performance consistency arises in situations where the variable of interest is constrained by the imposition of an extrinsic limiting factor. Previous work (Chappell & Snyder, 1984; Chappell *et al.*, 1988) demonstrated that the mean  $\dot{V}O_2\text{max}$  of deer mice held at an altitude of 3800 m is substantially lower than the mean  $\dot{V}O_2\text{max}$  of the same animals held at 340 m, even after acclimation periods of 2 months or longer. Presumably the decrease in  $\dot{V}O_2\text{max}$  at 3800 m is due to reduced  $PO_2$  (104 Torr compared to 155 Torr at 340 m). We examined individual correlations of  $\dot{V}O_2\text{max}$  between low and high altitudes in mice from three haemoglobin genotype groups: common  $\alpha$ -globin polymorphisms,  $\alpha$ -globins including rare 'recombinant'  $\alpha$ -globin haplotypes, and  $\beta$ -globin polymorphisms.

Results from the across-altitude tests were roughly comparable to results from the across-time and cold acclimation experiments, but there were some important qualitative and quantitative differences. Whole-animal  $\dot{V}O_2\text{max}$  showed highly significant individual correlations between low and high-altitude measurements in all three groups, except for exercise measurements in  $\beta$ -globin genotypes. The correlations generally improved if the effects of genotypic differences were taken into account using ANCOVA. Nevertheless, whole-animal correlation coefficients for altitude experiments were considerably lower than for the other acclimation regimes we employed, averaging less than 0.40 as opposed to about 0.72 (Tables 2 and 3). Individual correlations of residuals from regressions of  $\dot{V}O_2\text{max}$  on body mass were significant for cold exposure measurements in all three genotype groups, but not for any of the exercise measurements. As we found for the whole-animal data, *r*-values were



low, even for correlations that were statistically significant. Hence, these correlations have relatively little predictive value and account for only a small fraction of the variance in  $\dot{V}O_2\text{max}$ .

To summarize, the aerobic performance of individual deer mice is repeatable across several acclimation regimes and for different measurement protocols. Correlations are highest for whole-animal  $\dot{V}O_2\text{max}$  data, but usually remain significant if the effects of body mass are removed. Within individuals, thermogenic  $\dot{V}O_2\text{max}$  is highly correlated with exercise  $\dot{V}O_2\text{max}$ , even following acclimation to cold or to different altitudes. Across-altitude correlations for individual  $\dot{V}O_2\text{max}$  are significant in most cases but correlation coefficients are lower, perhaps because low  $PO_2$  at high altitude constrains aerobic metabolism. Nevertheless, the overall repeatability of  $\dot{V}O_2\text{max}$  in deer mice is as high or higher than the repeatabilities of sprint speed and endurance in lizards (Bennett, 1980; Huey & Dunham, 1987; van Berkum *et al.*, 1989), and racing performance in racehorses (Tolley *et al.*, 1983) and greyhounds (Ryan, 1975). We conclude that a single measurement of an individual deer mouse's  $\dot{V}O_2\text{max}$  ranking relative to the population mean does provide a useful indicator of that individual's  $\dot{V}O_2\text{max}$  ranking in many other acclimation regimes. However, correlations between substantially different altitudes are frequently too weak for measurements at one altitude to provide much indication about relative performance at a vastly different altitude.

Previous work (Chappell & Snyder, 1984; Chappell *et al.*, 1988) showed that deer mice carrying different haemoglobin genotypes have different  $\dot{V}O_2\text{max}$  and that the rankings of genotypes are a function of altitude. These studies supported Snyder's (1981) hypothesis that haemoglobin polymorphisms in *P. maniculatus* evolved as a result of selection for maximal aerobic performance at different native altitudes. The consistency of  $\dot{V}O_2\text{max}$  found in the present study provides additional support for that hypothesis; it suggests that the single measurements of  $\dot{V}O_2\text{max}$  (upon which those earlier conclusions were based) are indicative of aerobic performance throughout a mouse's lifetime. The low correlations we found for across-altitude comparisons are less relevant to the hypothesis, since individual mice probably occupy a fairly restricted range of altitudes during their lifetimes.

It has been suggested that individuals can achieve physiological versatility and perform reasonably well across a range of conditions only

at the expense of maximal performance in specialized conditions (the 'jack-of-all-trades is a master-of-none' hypothesis; Huey & Hertz, 1984; Jackson & Hallas, 1986). One way to test this hypothesis is to examine individual performance across different conditions or environments. Negative correlations are predicted if the hypothesis is correct, since specialists that perform well in one set of circumstances should perform poorly in contrasting situations, while less specialized performers should show similar intermediate rankings in all conditions. Huey & Hertz (1984) found no evidence in favour of the hypothesis in their study of sprint speeds of lizards at different body temperatures. Our results also do not support the hypothesis. We observed no significant negative correlations of individual performance, but instead found many significant positive correlations. Moreover, deer mice that are good performers during exercise are likely to be good performers during the rather different enterprise of metabolic heat production. This is somewhat surprising, since in many respects exercise and thermogenic  $\dot{V}O_2\text{max}$  appear to be relatively independent traits; they respond unequally to conditioning programmes and thermal acclimation, and frequently differ substantially within individuals (Seeherman *et al.*, 1981; Conley *et al.*, 1985; Hayes & Chappell, 1986). However, some interdependence is expected because exercise and thermogenesis utilize common effector organs (skeletal muscle) and share major components of the oxygen transport system (Weibel, 1984).

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