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MULTIVARIATE ANALYSIS OF GOLDEN MARMOT MAXIMUM RUNNING SPEED: A NEW METHOD TO STUDY MRS IN THE FIELD[1]

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Abstract. I develop a multivariate technique permitting the study of variation in the maximum velocity of animals. The method was applied to study maximum running speed (MRS) of adult golden marmots (*Marmota caudata aurea*). Subjects were encouraged to run to home burrows after being livetrapped, and were timed while running over a randomly selected distance between 1.7 and 36.0 m. Body mass, sex, distance run, substrate, and incline the individual ran across for 52 different subjects were entered into a linear model, which implicitly modeled MRS as a function of the running time. Body mass did not significantly explain variation in running time and was deleted. A new model fitted to the remaining variables significantly explained variability in time, and therefore MRS. The model did not violate any of the assumptions of linear models, and appeared to be robust. Intrayear repeatability of individual MRS was small, suggesting that environmental factors may account for much of the variation in MRS in golden marmots. The model predicts that the four significant variables (sex, distance run, substrate, incline) should influence space use and patch selection in golden marmots since they influence the speed at which an alarmed marmot can reach a refuge. The general method developed here can be applied to other species and should shed light on patch use and foraging behavior of refuging species.

Key words: habitat use; Khunjerab National Park; linear model; Marmota; *maximum running speed; method; MRS; multivariate; Pakistan; patch choice; repeatability; Sciuridae.*

INTRODUCTION

Many animals use refugia to escape predators. For instance, some birds may fly to a bush, fish may swim beneath an overhanging rock, insects may retreat to a hole, and ground squirrels may enter burrows when being pursued by a predator. The behavior of these animals may be described as being patterned in space around their refugia (e.g., Barash 1973, Frase and Armitage 1984). For refuging animals, the estimated minimum time it would take them to return to a refuge from a point in space should be an important factor that influences how they use their habitat (sensu Ydenberg and Dill 1986, Dill 1990). Thus, knowledge of maximum escape velocities in natural settings should permit a better understanding of space use.

Reports of maximum running speed (MRS) are often based on anecdotal reports of animals running in the field (see Garland 1983) or on experimental field studies (e.g., Trombulak 1989), or are the results of carefully controlled and measured studies of velocity in the laboratory (e.g., Huey et al. 1984, Djawdan and Garland 1988, Garland et al. 1988). Anecdotal reports often fail to measure and study variables that may significantly affect MRS (e.g., the slope of terrain the animals are running on, sex, body mass, the distance over which the animal runs, etc.). Experimental field studies try to control for some of these variables by forcing animals to run in unfamiliar but standardized settings (e.g., Djawdan and Garland 1988). Laboratory studies often control for extraneous variables (e.g., body mass, incline, age, etc.) that may be important determinants of velocity for animals under natural conditions. Artificial situations are thus created, which make extrapolation to field conditions difficult. A study of maximum running speed that addresses its multidimensional nature should shed light on space use and patch choice by refuging animals.

Golden marmots (*Marmota caudata aurea*) are an ideal species for such a study because they have well-defined refugia (burrows), often escape predators by running quickly to a burrow, and pattern their behaviors in space around burrows (D. T. Blumstein, *personal observations*). I chose to study the influence of five variables (body mass, sex, distance run, incline, substrate) in explaining the variation in MRS of adult golden marmots. These variables were selected either because other researchers have suggested they may influence MRS in terrestrial mammals (substrate: Nelson and Mech 1985, Djawdan and Garland 1988; body mass: Garland 1983, Trombulak 1989; incline: Taylor et al. 1972, Reichman and Aitchinson 1981), or because I thought that they might influence MRS of marmots (sex, distance).

In the following sections I develop and apply a general statistical technique to measure the relative importance of different variables in explaining variation in maximum locomotor velocity of free-living animals.

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Additionally, I review assumptions of linear models and methods to test their robustness. Methods to qualitatively and quantitatively evaluate a linear model are described and later applied. Field repeatability of MRS is discussed. Throughout, I report the methods and results of an experimental multivariate study of MRS in golden marmots.

METHODS

Subjects and data collection

Application of this technique assumes properly collected data. In general, the objective is to have a set of independent time measurements of animals moving quickly between two points. To avoid pseudoreplication (e.g., Machlis et al. 1985), there should be no more than one observation in the final data set for each individual. The distance over which individuals are timed should be randomly selected and should include a range of distances. A uniform distribution of distances is required for a good estimate of observer response time. Other continuous independent variables should also be uniformly distributed and categorical independent variables should be approximately equally represented.

I studied the sprint speeds of adult golden marmots at Dhee Sar (36°81′ N, 74°95′ E) in Pakistan's Khunjerab National Park between 10 May and 7 September 1990. Golden marmots are large (3–5 kg) Old World sciurids found in the Karakoram mountains of Central Asia (Roberts 1977). Dhee Sar is a relatively flat high alpine meadow (elevation 4100–4300 m) surrounded by steep lateral glacial moraines and punctuated with hilly terminal moraines. Marmots tend to live beside or on the moraines. Over 100 individuals lived in the 17 marmot groups studied in 1990.

Marmots were trapped in Tomahawk livetraps set in burrow entrances. Once trapped, a marmot was transferred to a canvas handling bag in which it was processed (sexed, weighed to the nearest 50 g, eartagged, and measured, and its back was marked or remarked with Nyanzol dye). Following processing, the marmot was released and encouraged to run to a burrow by shouting and arm-waving. I assume these manipulated runs generated maximal sprint velocities, and discarded observations if they appeared slow. In a study of golden mantled ground squirrel (*Spermophilus saturatus*) running speeds, Kenagy and Hoyt (1989) reported no significant differences in velocities of naturally observed runs and runs that were encouraged following trapping.

One to three observers timed (to hundredths of a second) a marmot during an interval while the marmot was constantly running. Observers attempted to time the marmot over a randomly selected distance between 2 and 30 m that included neither the first few steps, nor the end of the marmot's run. The stopwatch was started after the marmot had run a metre or so and, I assumed, had accelerated to a constant velocity. The actual distance travelled between two recognizable landmarks was measured with a tape measure to the nearest 0.1 m. The incline the marmot travelled across was measured with a clinometer. It was not possible to randomize the inclines run across, and the majority of my observations were of marmots running along no incline or downhill. I defined three different substrate categories (dirt, stones, vegetation), and described a run by the predominant category crossed. Since I wanted to release marmots near the point of capture, no attempt was made to randomize the substrates they were run across.

Data for analysis

One consequence of having multiple observers is that for a given run, an individual may have been timed over a slightly different distance or incline, or run over a different substrate. Rather than averaging (e.g., Djawdan and Garland 1988) the times and distances from different observers (which might lose information and/or make unnecessary assumptions about the relationship between independent variables and MRS), I treated each observer's datum as a unique observation. Thus, an observation consisted of the time it took a marmot to run between two points, the distance, incline, and substrate between those points, and the sex, age, and body mass of the marmot. This assumes a high degree of interobserver reliability. In fact, interobserver reliability was good: when marmots were timed across nearly identical intervals, velocities calculated from measured times of different observers were similar ($n = 12$: Kendall's $\tau = 0.788$, $P < .01$; Wilcoxon signed-ranks z corrected for ties $= -0.432$, $P > .05$).

I discarded an observation if the marmot: was not an adult (<3rd summer of activity based on known and estimated age individuals); travelled over several different inclines within a single run; stopped running while it was being timed; seemed not to run. Observations were also discarded if an observer was not sure of the exact starting and stopping points, or if the observer was generally uncertain about the timing of the event.

From this set of observations, I randomly chose one datum per individual. This set of data was used in the following analysis.

Statistical analysis

I developed a linear model that can be used to study the effects of selected independent variables on maximum escape velocity. To do this, velocity was modelled implicitly as a function of distance travelled and time was used as the dependent variable. Linear models assume a linear relationship between dependent and independent variables. This assumption is really a working hypothesis: if the final model does not explain much variation in the dependent variable, a nonlinear model (or a linear model with different variables) may be justified.

To model velocity implicitly as a function of distance, I multiplied the distance in an observation by each of the independent variables and used these new values as independent variables to predict time. Since:

$$t = d(1/V) \quad (1)$$

(where t = time, d = distance, and V = velocity), new variables created by multiplying raw scores by distance can be used to predict time while simultaneously reflecting the relative importance of a variable in influencing variation in MRS. In other words, if a new independent variable failed to significantly explain variation in time, then it would not explain variation in velocity. I used time as the dependent variable to associate measurement error with the variable most likely to generate error.

I assumed that most of my measurement error would be associated with recording the running time of the marmot. This is likely because distance, body mass, sex, substrate, and incline are variables that can be observed and measured relatively carefully, or easily scored. In contrast, accurate measurements of time may be more difficult. For instance if a stopwatch or manually triggered event recorder is used, the response time of the investigator adds onto the actual time of the running animals. Two observer response times are involved in each measure: the response time when an animal crosses point *A*, and the response time when it crosses point *B*. Since it is not possible to make an a priori prediction about whether these response times will be additive or cancel each other out, total time may have considerable error associated with it.

The foregoing linear model permits study of the relative importance of different independent variables in explaining variation in MRS while simultaneously predicting the time it would take an individual to travel a certain distance, given certain parameters. Other variables of interest were entered into the model as well. The model is formally an analysis of covariance (ANCOVA), incorporating both categorical (sex, substrate) and continuous variables (distance, body mass, incline). Categorical variables were dummy coded (Cohen and Cohen 1983), and all raw independent variables were transformed by multiplying the value or category by the distance run in that observation. I chose an ANCOVA rather than a dummy variable regression because this method permitted an overall significance test for the categorical factors, whereas a dummy variable regression would essentially provide contrasts between each level of a categorical factor and the reference level.

A linear model was first fitted to all variables of interest. Given: μ = observer response time (specifically, the intercept of the linear model); d = distance; m = body mass; g = sex; s = substrate; i = incline; and ϵ = unexplained variance, then:

$$t = \mu + d(m) + d(d) + d(g) + d(s) + d(i) + \epsilon. \quad (2)$$

I used a backward stepping algorithm (SAS 1990) to delete variables with the least significant Type III sum of squares having a $P > .1$. A Type III sum of squares was used as observations of categorical variables and covariates were unbalanced, yet all covariates were present (SAS 1990). Variables deleted from the model are assumed to have an insignificant impact on MRS.

Descriptive univariate and bivariate statistics were computed using FASTAT (SYSTAT 1989); nonparametric descriptive statistics were computed using StatView 512+ (Abacus Concepts 1986); linear models were estimated using PROC GLM in SAS (SAS 1990). Unless otherwise noted, significance implies a two-tailed $P < .05$.

Statistical assumptions

Statistical assumptions associated with general linear models include independently and normally distributed independent variables with a constant variance (Fox 1984). Assumptions were tested by analyzing the residuals with the SAS procedure UNIVARIATE. Additionally, a strong correlation between independent variables (multicollinearity) would prevent interpretation of the results. Multicollinearity was checked by generating a bivariate correlation matrix of all independent variables and searching for correlations greater than the absolute value of 0.7 (Slinker and Glantz 1985).

Model evaluation

Because this is a new method to study MRS, I wished to evaluate its robustness. Ideally, models should be evaluated with a set of independent observations (e.g., observations on different individuals; Bowerman and O'Connell 1990). To do this, a set of independent observations must be divided. The first portion would be used to develop a model (i.e., determine which variables significantly explained variability in time and therefore velocity, and to estimate the coefficients of significant variables). The remaining portion of the data would be used to study the robustness of the model.

Models may be good at qualitative predictions (they include the correct variables; see Cohen and Cohen 1983) and/or quantitative predictions (they accurately predict the dependent variables; see Montgomery and Peck 1982, Bowerman and O'Connell 1990). To study the qualitative fit of a model, the model developed with the first data set is run with the second data set. If the same variables still significantly explained variability in the dependent variable, and no assumptions are violated, the model qualitatively fits. Additionally, the quantitative predictability of the model can be tested. In this case, the coefficients from the model are used to predict the times for the second data set. These predicted times can be compared to observed times and tested for goodness of fit.

I did not want to subdivide my initial set of independent observations, and because golden marmots are quite difficult to trap, I could not easily increase my sample size. However, many individuals were timed on different days during the study. For those individuals timed on >1 d, I created a second data set of randomly selected observations for the same individuals run on a 2nd d. This second data set was used to evaluate the model. Because this is a nonindependent sample (i.e., it consists of repeated measures on the same individuals), inference about the predictability of the model should be limited.

1. *Qualitative evaluation.*—The second data set consisted of observations of the same individuals in the first set but timed on different days. The linear model developed with the first data set was fitted to the second data set. Residuals were plotted against each independent variable in the model to search for a trend or heteroscedasticity. The difference between the time predicted using the coefficients from the first model, and the observed time in the second data set was also plotted against independent variables to search for a trend or heteroscedasticity. If either of these were found in either analysis, the model would not be adequate to explain the second data set, and I would conclude that the model was not qualitatively robust.

2. *Quantitative evaluation.*—I checked quantitative fit by studying the difference between predicted and observed scores, and by studying the root mean square error (root MSE) of the differences between the predicted and observed scores.

I defined percent difference as:

$$100(t_o - t_p)/t_o \qquad (3)$$

where t_o = observed time, t_p = predicted time. A low average difference would suggest the model was robust. Two difference estimates were calculated; the first used the initial data set, the second used the second data set. I used the initial data set's difference value to provide a frame of reference to the values calculated from the second data set.

Root MSEs of the differences for both data sets were generated. MSEs reflect the goodness of fit of a model (Bowerman and O'Connell 1990). Again, the root MSE calculated from the first data set provided a reference for the values in the second set.

3. *Repeatability.*—The multivariate nature of the data suggested that a study of repeatability (e.g., Huey and Dunham 1987, Van Berkum et al. 1989, Huey et al. 1990, Shaffer et al. 1991, Austin and Shaffer 1992) could provide unique information on field repeatabilities. Repeatability of individual performance is usually measured under controlled situations and does not incorporate natural sources of environmental variation. I studied repeatability two ways.

First, I compared the velocities of individuals measured on different days regardless of the substrate or inclines, etc., that they ran across. To do this, I calculated a Pearson correlation coefficient of the velocities in data sets 1 and 2. Austin and Shaffer (1992) and Van Berkum et al. (1989) justify the use of a Pearson correlation coefficient rather than an intraclass correlation (see Falconer 1981) in ecological studies of repeatability.

Second, I tested to see if there was consistency in whether an animal that ran faster than predicted on one day would also run faster than predicted on another day. Conversely, I wanted to see if an animal that was slower than predicted on a given day was also slower than predicted on another day. This analysis would account for those independent variables that significantly influenced MRS. I calculated a correlation coefficient for the difference between observed and predicted times from data sets 1 and 2. Times were predicted using the coefficients generated from the linear model.

4. *Simulations.*—To further study the quantitative importance of independent variables in influencing MRS, simulations were run. The inverse of the sum of the significant coefficients in the model equals the predicted velocity (see Eq. 1). I fixed all categorical variables and all but one continuous variable. Then, I solved for a range of values for the one continuous variable. Plots of the relationship between an independent variable and the predicted velocity permit a visual assessment of the importance of a continuous independent variable in influencing MRS, controlling for variation in other independent variables.

RESULTS

The model

Sixty-three different marmots were run and timed; over 50% of them were timed on >1 occasion. From these observations, 11 observations were discarded. I then randomly chose a single observation per marmot. The first data set consisted of observations of 52 different adult marmots (Table 1, Appendix). The model was first fitted with five independent variables: body mass, sex, distance run, substrate, and incline. Body mass did not have a significant Type III sum of squares and was deleted. When a new model was fitted, all independent variables had significant Type III sums of squares (Table 2). Ninety-three percent of the variance in observed time was explained with these two continuous and two dummy coded categorical variables. From this, I infer that sex, distance run, substrate, and incline significantly influenced the MRS of these marmots.

Using the coefficient estimates of significant variables (Table 2), I generated an equation that predicts running time. Where x^* is the intercept coefficient of the relationship $t = d(1/V)$ (i.e., the predicted time if all other predictors are 0, an unrealistic and unmeaningful term since it is outside the range of distance values used to develop the model), and where an asterisk indicates a coefficient estimate of the other variables defined in Eq. 2,

$$t = \mu + d[x^* + g_c^* + d(d^*) + s_c^* + i(i^*)] \qquad (4)$$

TABLE 1. Descriptive statistics for independent variables initially entered in the linear model of marmot running speeds as well as for observed running speeds. Number of observations is listed for each variable. See Appendix for raw data.

Variable (Category)	Mean	SE	Range	N
Substrate (Stones)				31
(Dirt)				18
(Vegetation)				3
Distance (m)	11.9	1.02	1.7–36.0	52
Incline (°)	−6.5	1.47	−35–+15	52
Body mass (g)	3229.8	104.48	1850–4900	52
Males	3349.1	147.81	1900–4900	29
Females	3079.4	142.52	1850–4025	23
Speed (m/s)	4.41	0.15	2.45–7.95	52
Males	4.20	0.18	2.45–5.70	29
Females	4.68	0.24	3.04–7.95	23

predicts the time it takes an animal in category c (e.g., male or female and running over dirt, stones, or vegetation) to run a given distance over a certain incline. For instance, assume a male marmot runs 10.0 m up a 10° dirt slope. By substituting the appropriate coefficients (from Table 2) into Eq. 4, and ignoring μ, time can be predicted:

$$\begin{aligned} t = 10.0\ \text{m}[&0.3713\ \text{s/m} + 0\ \text{s/m} \\ &- 10\ \text{m}(0.0030\ \text{s/m}^2) \\ &- 0.0548\ \text{s/m} + 10°(0.0032\ \text{s/°m})], \\ t = 3.19\ \text{s}.& \end{aligned} \tag{5}$$

Dividing the distance by the predicted time will generate a predicted velocity: in this case, 3.13 m/s.

Statistical assumptions

Residuals analysis failed to indicate significant departures from the assumptions of general linear models (Fox 1984). The residuals did not significantly depart from a normal distribution (Wilk-Shapiro test, P = .5913). Plots of the residuals vs. each continuous independent variable illustrated no consistent trends and fairly homogeneous variance. Plots of the residuals vs. the categorical variables showed variability related to the number of observations: the data were unbalanced.

Only one pair of independent variables (the substrate classes "dirt" and "stones") had a bivariate correlation coefficient >0.4. Thus, I conclude multicollinearity was not a problem with these data.

Qualitative evaluation

The model appears robust. The second data set consisted of 30 observations of some of the individuals in the first data set. Eq. 4 was used to calculate the predicted times for each observation in both data sets. Predicted times were subtracted from the observed times, and these residuals were used to test the robustness of the model. These residuals appeared to violate none of the assumptions of linear models.

Residuals were plotted against all independent variables in the model and body mass (excluded from the model). A trend in these residual plots or heteroscedasticity would suggest either additional variables were needed, or the data violated assumptions of linear models. Neither trends nor heteroscedasticity were noted in these residuals plots.

Quantitative evaluation

The average difference (residual) in the first data set was −1.69 ± 3.44 s ($\bar{X}$ ± 1 SE) and the second data set had an average difference of −1.95 ± 5.19 s. The model seems to predict the times in the second data set about as well as it predicts the times in the data set originally used to develop the model and calculate the coefficients.

The root MSE for the first data set was 0.532 s, while for the second data set the root MSE was 0.709 s. (Root MSE is expressed in the units of the original variables.) Thus, the model predicts time (and therefore MRS) to within ≈0.5 s on the first data set and a little less well with the second data set. The model seems to be quantitatively robust.

Repeatability

Neither the difference in velocity nor the difference between observed and predicted time was significantly repeatable between days (Fig. 1). The correlation between the velocities in the first and second data sets was small (r = 0.155, n = 30), and not significant. The relationship between observed and predicted times was also small (r = −0.208, n = 30), and nonsignificant. From this, I conclude that field measurements of MRS were not repeatable in the marmots studied.

Simulations

The relative influence of incline was studied by predicting velocities of adult marmots running 10 m over dirt and varying the incline between −30° and +30° (Fig. 2). For instance, to calculate the velocity of a male running 10 m up a 10° dirt slope, the appropriate coefficients from Table 2 are entered into the following equation (recall Eqs. 1 and 4):

TABLE 2. Linear model parameter estimates and their significance for the linear model of marmot running speeds fitted with SAS to predict running time. Overall, the model explained 93% of the variation in running time and was highly significant ($P < .001$).

Variable	df	Type III ss	F	Estimates†	Category‡	SE
Intercept	1	0.4815	1.58NS	−0.3064NS		0.2439
x§	1	22.3582	73.30***	0.3713***		0.0370
Sex	1	2.7384	8.98**	−0.0385*** 0‖	F M	0.0128
Substrate	2	6.6801	10.95***	−0.0734** −0.0548*** 0‖	W D S	0.0342 0.0126
Distance	1	2.4096	7.90**	−0.0030**		0.0011
Incline	1	8.3542	27.39***	0.0032***		0.0006

NS $P > .05$; ** $.001 < P < .01$; *** $P < .001$.

† These coefficient estimates are used to predict the time it takes a certain sex marmot to run a specified distance and incline over a particular substrate. The coefficients presented here are unstandardized and are used to predict running time. Standardized coefficient estimates (created by setting the mean of the variables to 0 and the SD to 1.0) are: $\text{Sex}_F = -0.0528$; $\text{Substrate}_W = -0.0128$; $\text{Substrate}_D = -0.2859$; Distance = −0.0768; Incline = 0.0936.

‡ "Category" refers to the different possible states of the categorical variables (F = female; M = male; D = dirt; S = stones; W = vegetation).

§ The variable "x" is the intercept for the relationship $t = d(1/V)$. Thus, $1/x$ would be the predicted velocity in the hypothetical case where all other predictors are 0.

‖ A result of SAS's parameterization whereby dummy variable categories are 1 less than the total number of categories. SAS sets one category to 0 and solves for the remaining categories.

$$V = 1/[x^* + g_c^* + d(d^*) + s_c^* + i(i^*)],$$

$$V = 1/[0.3713\ \text{s/m} + 0 + 10\ \text{m}(-0.0030\ \text{s/m}^2) - 0.0548\ \text{s/m} + 10°(0.0032\ \text{s/m°})],$$

$$V = 3.14\ \text{m/s}. \tag{6}$$

The range of velocities predicted falls within the range of observed velocities. The slope of this line varies: an adult marmot running downhill appears to gain velocity at a faster rate than one running uphill loses it. This nonlinear relationship between an independent variable and velocity is predictable since the linear model was developed using the reciprocal of velocity. The reciprocal of a linear relationship, by definition, is nonlinear. Since the linear model was significant, this nonlinear relationship should also be significant.

The influence of distance run was studied by predicting velocities of adult marmots running across level dirt and varying the distance between 3 and 32 m (Fig. 1b). Marmots may accelerate when running longer distances. Again, the slope of the line seems to vary: the marginal gain in velocity is greater with greater distances.

DISCUSSION

Alternative statistical analyses

There are several other potential ways to study how different independent variables influence maximum velocity. A univariate analysis might lump all observations (regardless of the incline, distance, sex of marmot, etc.) to generate an average maximum velocity, or compare the means of sums of individuals from the same category (e.g., sex). Bivariate correlations between independent variables (e.g., body mass, sex, distance, substrate, incline) and the dependent variable, velocity (distance/time), might be used to look for trends between independent and dependent variables. However, neither univariate nor bivariate analyses permit the study of the independent influence of one variable, controlling for all other variables. Thus, a nonmultivariate analysis is not particularly useful to analyze such a heterogeneous data set. A multivariate method that would account for the unique influence of independent variables is warranted.

An intuitively obvious, but methodologically flawed, multivariate analysis would regress each independent variable against the velocity. The problem with such a method is that it prevents the study of distance's effect on MRS. If velocity were the dependent variable and distance were an independent variable, then a ratio-correlation problem might arise (Atchley et al. 1976, Schoener 1988). Ratio correlation arises when a dependent variable is calculated from an independent variable and there is error in one or both of the measurements. Ratio correlation creates a spurious correlation that may not reflect the true relationship between the variables. If velocity were the dependent variable, and distance an independent variable, a spurious correlation would be likely. The method developed in this paper addresses the above problems by incorporating multiple variables in a way that avoids the ratio-correlation problem.

Marmot MRS

Over the range of values measured, golden marmot MRS is independent of body mass, but is influenced by the: (1) sex of the marmot; (2) distance run; (3) substrate type; and (4) incline over which it runs.

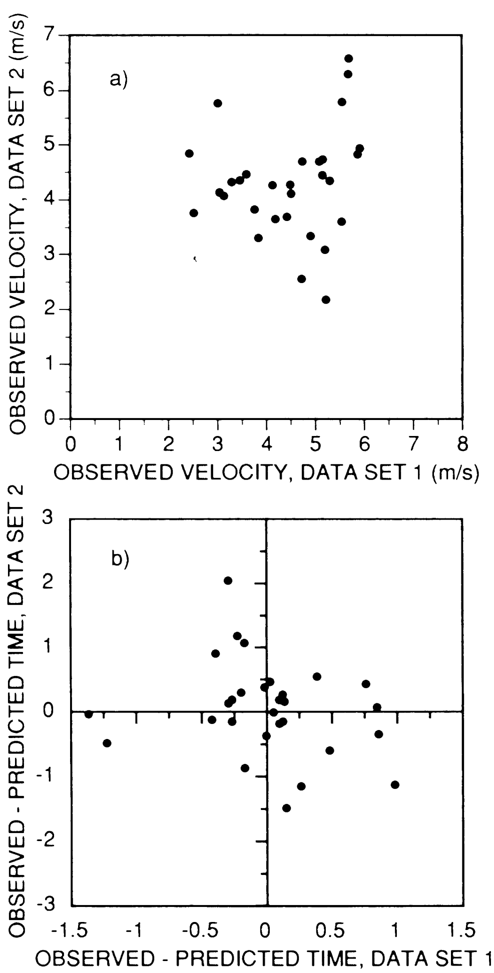

FIG. 1. Plots of repeatability of golden marmot sprint speeds displayed two ways. Part (a) illustrates the repeatability of raw velocity scores from data sets 1 and 2. Part (b) illustrates the relationship of the difference between observed and predicted (using the linear model) times for the two data sets. Each data point is a different marmot, timed on two separate days.

There are conflicting reports of the relative importance of body mass' influence on MRS in terrestrial mammals. Based on an interspecific literature survey, Garland (1983) concluded that in rodents, MRS is independent of adult body mass. Djawdan and Garland (1988) observed no significant relationship between MRS and body mass in any of 25 species of rodents they studied. Recently, Trombulak (1989) studied the relationship between body mass and running speed in Belding's ground squirrels (*Spermophilus beldingi*) to test the hypothesis that body fat influences locomotor ability. He found a significant negative relationship between body mass and running speed and inferred that this explained seasonal fattening strategies. Because velocity is impaired by increased body mass, hyperphagy immediately prior to hibernation, rather than fattening early in the summer and maintaining body mass, becomes the best strategy to minimize the time exposed to predators while in a state of impaired locomotor ability.

Surprisingly, body mass did not significantly influence MRS in adult golden marmots, another hibernating sciurid. This directly conflicts with Trombulak's (1989) observation in Belding's ground squirrels, and is consistent with conclusions based on anayses of different rodent species with different life histories (Garland 1983, Djawdan and Garland 1988). Trombulak (1989) studied squirrels during hyperphagia and could be certain that differences in body mass were due only to fat. I studied adult marmots throughout their active season, and assume that much of the difference in body mass in adult marmots is a function of seasonal fattening patterns. Indeed, marmots generally lose mass after emerging from hibernation and begin gaining mass

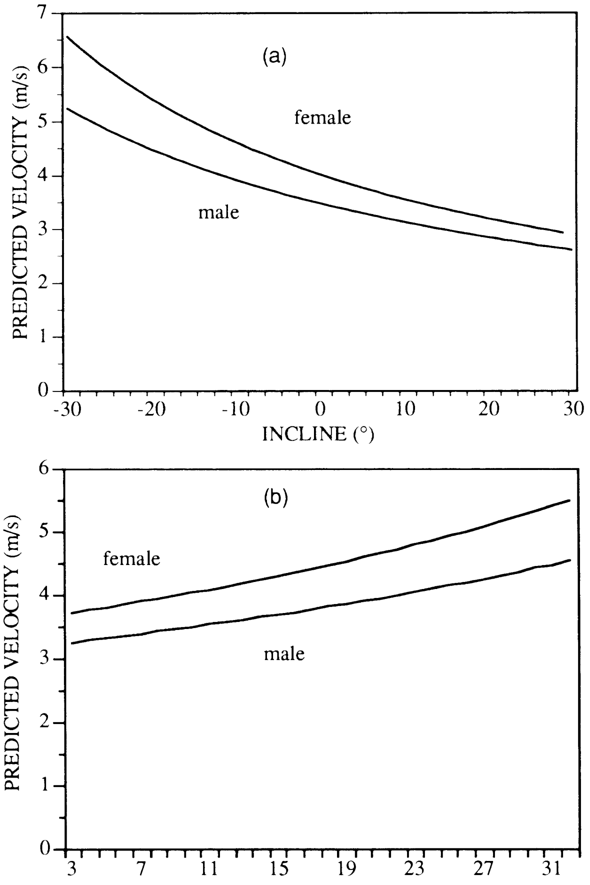

FIG. 2. Illustration of the influence of independent variables on maximum running speed (MRS) in golden marmots. Both graphs are the result of simulations where all but one independent variable was set, and one continuous independent variable was varied. Predicted observer response time, μ, was not included in the equations used to generate these predicted times. Part (a) illustrates the relationship between simulated incline and predicted MRS. Part (b) illustrates the relationship between simulated distance run and predicted MRS.

following the disappearance of snow (D. T. Blumstein, *personal observation*). A large but not obese animal has more muscle with which to locomote, while an obese individual may have its locomotor ability compromised by its increased mass. Furthermore, Trombulak timed animals when they may have been accelerating (during the 1st s of their run), while I timed animals after I assumed their initial burst of acceleration was completed. Body mass or obesity may influence acceleration more than maximum sustainable speed. Nevertheless, this study suggests further research in other hibernating sciurids is required before Trombulak's suggestion that changes in body mass influence the ability to escape, and thus influence fattening strategies, is generalized to other species.

It is interesting that sex, independent of body mass, influences MRS in adult marmots. In all age classes, male golden marmots are significantly heavier than females (P. Ebenhöh and D. T. Blumstein, *unpublished data*). Perhaps there are intersexual differences in motivation, physiology, or muscle mass that account for different MRSs.

The positive relationship between distance run and predicted velocity (Fig. 2b) was unexpected. Because the distance an individual marmot was run was randomized between 2 and 30 m, the model was generated using a large range and fairly uniform distribution of distance values. Usually, uniformly distributed independent variables should provide a descriptive model as there should be no outliers with excessive leverage (Rousseeuw and Leroy [1987] discuss leverage in multiple-regression models). If this positive relationship between distance and velocity is true, then it suggests golden marmots can run for >30 m without appreciably fatiguing. This conclusion is suspect since some marmots timed for a short distance were closer to holes than those timed over a longer distance. Marmots close to holes may have either not run as fast or slowed before we stopped timing them. This is likely since some of the short observations were aborted longer runs (i.e., we hoped to time a marmot running 15 m, but it was only 10 m from a burrow so we timed it for <10 m). However, Dill (1990) found no significant relationship between the distance to a refuge and escape velocity in an African cichlid fish. Nevertheless, I conclude that qualitatively distance is an important variable that influences MRS for golden marmots, but the actual quantitative relationship requires further study.

Anecdotal evidence supports the conclusion that substrate influences locomotor ability. Marmots running on certain substrata (wet dirt or loose stones) appear to slip more and move more slowly than individuals running on a more solid surface. Nelson and Mech (1985) mention other instances of an individual's locomotor efficiency being influenced by substrate.

Anecdotal evidence supports the conclusion that incline is important to golden marmots. It was difficult to encourage marmots to run uphill. Often, they would pause and either run downhill in the opposite direction, or run along, but not up the slope. Pattie (1967) reported that startled yellow-bellied marmots (*Marmota flaviventris*) fled by running downhill. Thus, for a marmot-sized mammal, incline may be an important determinant of MRS (cf. Taylor et al. 1972).

The asymmetrical shape of the predicted velocity curve (Fig. 2a) implies marmots running downhill gain velocity at a faster rate than marmots running uphill lose it. Thus, the marginal risk of predation associated with a unit change in distance from the refuge depends on the incline. The effects of slope on velocity violate assumptions of some foraging models, which assume predation risk increases linearly with distance from a refuge (e.g., Valone and Lima 1987, Devenport 1989).

The linear model generated predicted times that compared favorably to the observed times for both data sets. The predictive ability of the model might be improved if the categorical data were balanced and the continuous variables were collected so that all values were equally represented. Unfortunately, the nature of the question prevented me from collecting such data. Recall, it was very difficult to get the marmots to run uphill, so the data set was biased towards those observations of marmots running downhill and on flat sections. Additionally, all substrate types were not evenly distributed across the study area, thus substrate types are unbalanced in the data set.

Repeatability

Repeatability calculated two ways was quite low. If I have correctly estimated the true repeatabilities, I would need sample sizes of 90 (for $r = -0.208$) or 200 (for $r = 0.155$) to have enough power to permit me to say that there was zero repeatability (Rohlf and Sokal 1981). Thus I am unable to distinguish between a low value and a truly zero value with existing data.

Significant repeatabilities of locomotor performance measured in controlled conditions have been found in other species (e.g., Garland and Else 1987, Huey and Dunham 1987, Van Berkum et al. 1989, Shaffer et al. 1991, Austin and Shaffer 1992). Exceptions include low or nonsignificant repeatabilities between several years (Huey et al. 1990, Austin and Shaffer 1992) or metamorphic stages (Shaffer et al. 1991).

Repeatability could have been low or zero in marmots if the experimental protocol was inconsistent. Certainly, the environmental variables (e.g., substrate type, incline) varied between measurements. Despite this natural variation, it was possible to fit a highly significant linear model that explained 93% of the variance in running time to the data. Thus, I do not feel that the experimental protocol was inconsistent enough to explain the observed low repeatability.

Assuming the low repeatabilities reflect a real biological situation, then the low values suggest that nongenetic factors may greatly influence the MRS of marmots. A fast individual in one set of circumstances might not be relatively fast in another set of circumstances. Repeatability places an upper limit on heritability estimates (Falconer 1981, Boake 1989). Low repeatabilities of MRS could come about in two ways: environmental factors could be very important in determining MRS, and/or there could be little additive genetic variance for MRS. Low repeatabilities suggest a selective force (such as pursuit predators) may no longer be able to generate a response to selection on MRS. Perhaps extant selective forces are working on other behavioral correlates that minimize the necessity of escaping (e.g., the patterning of behavior in space with respect to refugia).

Importance of observer response time

This method enables the study of the importance of human response time when timing running animals. Human response time (estimated by μ) can potentially bias measurements of MRS. If response time is large, measured velocities may be less than predicted velocities because the time used to calculate measured velocity will be excessively large. This is not only a problem when timing events with a stopwatch, but also when a stopwatch is used to calibrate a more precise measuring device (e.g., a Doppler radar gun; Blake et al. 1990). There is a relationship between human response time, the distance an animal is timed, and the difference between predicted and observed scores. As the distance over which a subject is timed increases, the relative influence of human response time decreases. Knowledge of μ should enable studies of MRS that are minimally biased by human response time. The statistical technique presented here can be used to estimate μ.

The estimate of μ, or the intercept of this linear model, was not significantly different from zero (Table 2) and was within the range of response times reported by other investigators doing similar tasks. Barnes (1980) and Meister (1985) reported 0.1–0.3 s response times for humans responding to visual stimuli that do not require complex cognitive processing. Another investigator doing a similar task reported a response time of $\approx$0.3 s (Belkin 1961). If significant, the negative value of the intercept would imply we tended to anticipate the marmots crossing visual lines when timing them.

This model is very sensitive to the range of distances over which subjects are run; the intercept estimate can change appreciably if there are outliers. To obtain a representative intercept, the distribution of distances run by the subjects should be as uniformly distributed as possible and should include short distances.

Conclusions

Similar studies of maximum escape velocity in other species are needed to better understand the influence of extrinsic environmental and intrinsic variables on escape velocity. Further study is required to understand repeatability in nature. If other species show similarly low or nonexistent field repeatabilities for MRS, then we may have to revise our way of thinking about current selection operating on locomotor performance. Variables that influence escape velocity may influence the perception of predation risk. Theory predicts, and empirical studies support, the hypothesis that predation risk is often traded-off against the benefits of engaging in an activity or choosing a patch (Lima and Dill 1990). Thus, the perception of predation risk can influence relative patch quality. A better understanding of the perceptual world of animals should permit significant variables to be incorporated into foraging and habitat choice models, increasing their realism and hopefully predictive ability.

I predict sex, distance run, substrate, and incline influence space use and patch selection in golden marmots. These specific hypotheses can be tested by quantifying how marmots pattern their behavior with respect to refugia. Testing these hypotheses will provide new insight into the perceptual world of marmots.

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APPENDIX

Data set number 1 used to generate the linear model to study MRS in golden marmots.* Statistical summary is given in Table 1.

ID	SEX	SUB	SLPE (°)	DIST (m)	TIME (s)	VEL (m/s)	WT (g)
12	F	D	−5	19.00	3.63	5.23	3075
6	F	D	−15	12.50	2.25	5.56	3950
24	F	D	0	1.70	0.41	4.15	3525
38	F	D	−5	3.30	0.93	3.55	3300
50	F	D	3	6.10	1.18	5.17	2375
61	F	D	2	8.80	1.69	5.21	2825
76	F	D	−12	16.20	2.73	5.93	3625
147	F	D	−35	7.00	0.88	7.95	3175
8	F	S	−10	12.00	2.31	5.19	2325
20	F	S	−15	4.60	1.42	3.24	3475
22	F	S	−5	15.00	3.59	4.18	2675
27	F	S	−10	10.00	2.25	4.44	3575
43	F	S	10	17.40	5.72	3.04	2675
59	F	S	−10	14.40	2.82	5.11	2525
112	F	S	0	5.70	1.63	3.5	3825
114	F	S	12	22.80	6.89	3.31	2525
117	F	S	0	21.30	5.16	4.13	1875
124	F	S	−11	10.00	3.24	3.09	1850
129	F	S	−13	6.00	1.05	5.71	2325
130	F	S	−15	13.00	2.64	4.92	4000
132	F	S	−8	11.10	2.46	4.51	3725
9	F	V	−8	4.30	0.73	5.89	3575
104	F	V	0	11.00	2.43	4.53	4025
10	M	D	−35	4.80	0.86	5.58	3725
11	M	D	−5	3.30	0.76	4.34	4900
21	M	D	0	13.20	3.49	3.78	4000
29	M	D	−3	5.00	0.94	5.32	2575
30	M	D	5	13.00	3.09	4.21	2800
52	M	D	−20	13.50	2.57	5.25	3850
95	M	D	−12	6.50	1.87	3.48	4075
100	M	D	10	6.00	2.45	2.45	3400
108	M	D	−10	9.20	1.76	5.23	4025
115	M	D	−4	32.00	6.23	5.14	2875
2	M	S	0	4.30	0.83	5.18	1900
4	M	S	−5	11.40	2	5.7	2225
23	M	S	−5	28.00	7.27	3.85	2050
28	M	S	−15	5.80	1.54	3.77	3725
39	M	S	−15	16.20	5.14	3.15	4025
40	M	S	15	4.40	1.73	2.54	3650
41	M	S	−5	12.20	2.95	4.14	3925
44	M	S	−20	10.40	2.84	3.66	3625
69	M	S	−10	3.90	1.08	3.61	3450
78	M	S	−15	17.20	5.62	3.06	4125
79	M	S	−15	19.00	5.61	3.39	2550
80	M	S	10	9.10	1.91	4.76	3575
92	M	S	−15	4.50	0.88	5.11	4025
97	M	S	8	17.00	5.2	3.27	2375
105	M	S	−18	17.40	3.68	4.73	4225
107	M	S	−10	9.00	1.72	5.23	2625
109	M	S	13	21.00	8.01	2.62	2425
131	M	S	−10	36.00	7.62	4.72	2375
42	M	V	0	12.00	2.58	4.65	4025

* Columns are: ID = marmot identification number; SEX = sex of marmot; SUB = substrate marmot ran across; SLPE = incline of slope marmot ran across; DIST = distance marmot was timed; TIME = duration of run timed; VEL = velocity of marmot run; WT = body mass of marmot immediately prior to run.