

Age Effects on Yellow-Bellied Marmot (*Marmota flaviventris*) Maximum Running Speed

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Abstract

Age effects on maximum running speed (MRS) in yellow-bellied marmots (*Marmota flaviventris*) were examined to see whether this performance trait varied with age. Individuals were trapped in Tomahawk livetraps, then released and encouraged to run to burrows by yelling and chasing over varying distances. Factors possibly affecting the MRS including incline, distance run, age, sex, and substrate were recorded and controlled for in a general linear model that sought to explain variation in run time. I found that distance run and substrate have significant effects on run time, while age, incline, and sex had insignificant effects on run time. However, younger marmots ran over a wider range of speeds than older marmots. This suggested that yellow-bellied marmots did not experience somatic senescence although there appeared to be natural selection for locomotor ability.

Introduction

Yellow-bellied marmots (*Marmota flaviventris*) tend to live in grass-forb meadow habitats with boulders or talus slopes, where they can dig burrows and forage (Armitage 2003). The burrows provide a refuge for marmots to run to when threatened by predators. Calculating the maximum running speed (MRS) of marmots may aid in the study of marmot behavior, especially in regards to understanding foraging and anti-

predator behavior. These behaviors have the potential to affect survival and population demographics.

Several factors may contribute to MRS. The effect of age, body mass, distance run, incline, substrate, and sex on run time and speed will be examined. Previous studies have shown or suggested that these factors may affect running speed (Blumstein 1992; Blumstein et al. 2004). My study will examine age effects on MRS. Ageing and senescence have been found to affect species differently. Studies have shown a wide range of species from Richardson's and Columbian ground squirrels to fallow deer to brown bears to experience reproductive and/or somatic senescence (Broussard et al. 2003, Broussard et al. 2005, McElligott et al. 2002, Schwartz et al. 2003). Other species appear not to experience reproductive and/or somatic senescence (Slade 1995). Many studies on somatic senescence use either mortality rates as a measure (Promislow 1991, Slade 1995) or physical measures such as MRS (Van Berkum et al. 1989).

Yellow-bellied marmots do not appear to experience reproductive senescence (Blumstein, unpublished data), producing an average of 4 to 5 pups per litter throughout their reproductive lives, although middle-aged females are more likely to wean litters. Survivorship is highest for middle-aged females suggesting marmots may experience somatic senescence (Blumstein, unpublished data). Studying age effects on MRS will show if marmots experience somatic senescence on a performance trait that is likely to be under direct selection.

Methods

Marmots were caught in Tomahawk live traps baited with Omalene 100 horse feed set facing burrows. Traps were set early in the morning and in the afternoon, then checked after approximately three hours. Trapping was rotated among several sites so that each site was trapped for several sessions approximately every two weeks. Standard measurements were taken from trapped marmots (Ozgul et al. 2006). Blood samples were taken the first time an individual was trapped in a week. If a blood sample was taken, the marmot was not run. If the marmot was a recapture for the week and no blood was taken then the marmot was run.

To run the marmot, it was taken a distance approximately five to thirty meters from the burrow. The marmot was then released from the trap bag and chased and yelled at until it reached a burrow or otherwise moved out of view. The run time, run distance, incline, substrate, individual ID, and body mass were recorded. The marmot was assumed to be running at its maximum speed when chased and yelled at. Run time and distances were measured when the marmot was running constantly and consistently in a straight line. Timing did not include the starting and ending steps of a run in order to minimize measuring acceleration and deceleration. Distance was measured to the nearest 0.1 m using a tape measure against stakes dropped during timing or noted landmarks. The incline was measured using a clinometer. For analysis, observations were discarded if the marmot did not appear to run at its maximum speed, if data such as substrate was missing, or if the observer was very unsure of the timing and distances of the run.

My data set includes those data I collected as well as data collected since 2002. If a marmot had been run more than once in a single year, I randomly selected a single

observation per year so as to avoid excessive pseudoreplication. I assume that MRS of subjects was independent across year. My data set consisted of 182 observations, on 149 subjects. Individuals were run an average of 1.221 times (SD 0.5030, range 1 to 3).

The statistical software package SPSS 11.0 (SPSS, Inc. 2005) was used to isolate the effects of age on maximum running speed, after controlling for effects of distance run, incline, substrate, and sex. To avoid the ratio-correlation problem (Blumstein, 1992), I fitted a general linear model to statistically model run time, the time it took a subject to run a given distance. Independent variables included, the distance run, age, sex, incline and substrate. I log-10 transformed run time and distance run to normalize these variables. I infer significance when $p\text{-values} < 0.05$, and I calculated partial eta-square values as a measure of effect size. I visually examined the residuals of the general linear model to check for normality.

To study whether there was selection on MRS, I fitted a model without age, calculated the residuals, and plotted age against these residuals. The plot showed how each individual run time varied from the predicted log-10 run time against the age of the individual. If there was selection in MRS over age, the plotted residuals would show a trend toward certain values. If there was no selection in MRS over age, the plotted residuals would be randomly distributed across age.

Results

After controlling for other variables that may influence locomotor ability, I found no significant effect of marmot age on run time (Table 1). Body mass is correlated with age, and marmots were not run when they reached their pre-hibernation ‘obese phase’ so

mass was not included in the model. As expected, distance run had the greatest effect on run time ($p < 0.001$, partial eta-square = 0.531). The substrate a marmot ran across also significantly influenced run time (marmots ran fastest on dirt and short vegetation and slowest on talus, overall $p < 0.001$, partial eta-square = 0.118). I found no significant effects of other potentially important variables (Table 1).

Table 1: Parameter predictors and significance values for the linear model.

Parameter	Factor	B-value	p-value	partial-eta squared
Sex			0.122	0.014
	Female	-0.104	0.008	
	Male	-0.312	<0.001	
Substrate			<0.001	0.118
	D	-0.07457	0.004	
	S	-0.003176	0.912	
	SV	-0.06576	0.005	
	T	0.07046	0.071	
	TV	0	-	
Age Exact			0.232	0.008
Incline			0.429	0.004
Log10rundist			<0.001	0.531

There appeared to be evidence for selection in MRS. The plot of standardized residuals for log-10 run time against age showed a trend in which younger marmots ran over a wider range of times, and therefore speeds, than older marmots (Figure 1).

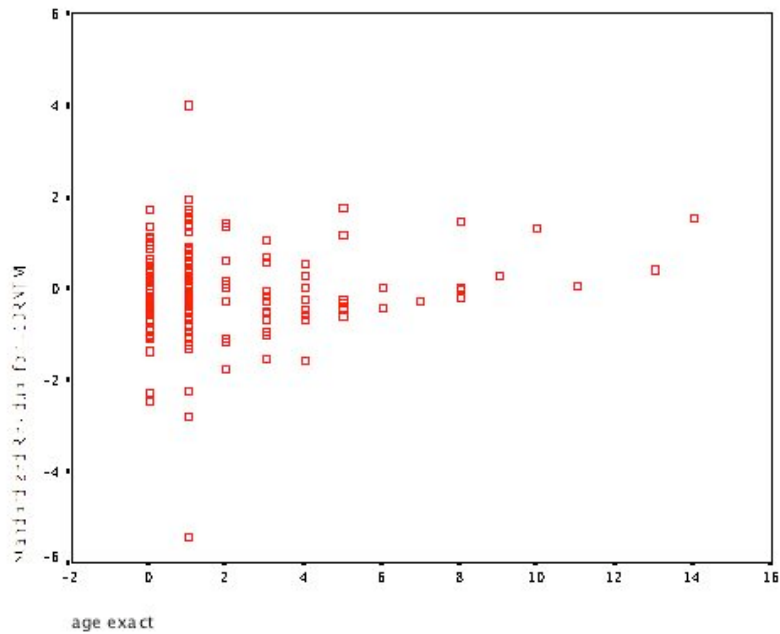


Figure 1: Standard residuals of log-10 run time by age, on a model that did not include age as an independent variable.

Discussion

I found that age had no significant effect on running speed. Other variables affected MRS more than age. Therefore it appears that marmots do not experience somatic senescence for this performance trait. This is supported by previous studies that showed that yellow-bellied marmots did not appear to experience somatic senescence (Schwartz 1998). Age appears to affect physical performance measures such as MRS and aerobic performance for many species such as rats, mice, and lizards (Carter et al. 2003, Chappell et al. 2003, Van Berkum et al. 1989) while few other studies have concluded that some species of rodents do not show an age effect (Dohm et al. 1995). Some of these differences may be caused by different sampling conditions, such as measurements on lab animals versus wild caught animals. In Slade's study (1995) no evidence of senescence was found in wild rodents, as measured by survival, but it was noted that wild

rodents rarely lived as long as laboratory-raised animals. It is also much more difficult to control variables that may affect physical performance, such as substrate, in field experiments than in laboratory experiments. It may be possible that older animals experiencing physical declines are preyed upon, resulting in a very low probability of trapping and running and experiment with them.

Our population has a greater number of younger animals than older animals. Thus, I had more data for younger animals than older animals. Run time over distance run was used as a measure of MRS. Given available data, the plot of age against standard residuals of run time showed that younger marmots ran at a wider range of speeds while older marmots ran at a narrower range of speeds (Graph 1). The distribution of run time changed with age even though the residual run time did not change significantly. This suggests that locomotor ability was under stabilizing selection; older marmots ran a narrower range of speeds. One explanation of this stabilizing selection is that slower animals were preyed upon, while faster animals suffered an energetic cost.

As expected, distance run was the variable with the greatest effect on run time, since animals running a longer distance would require more time to cover it. However, after controlling for other important factors that influenced locomotor ability, it appeared that marmots of all ages would cover the same distance in approximately the same amount of time.

Substrate also significantly affected run time and therefore MRS. With tall vegetation arbitrarily set as a baseline, marmots ran faster on dirt and short vegetation. These two types of substrate provided a more stable footing than talus, and may have contained fewer obstacles than in tall vegetation. Stones also allowed marmots to run

faster although the difference from tall vegetation was insignificant, possibly because stones were more slippery to run on. Talus slowed down run speed, likely because of its instability. The type of substrate the marmots ran on clearly affected running speeds, most likely because of the stability and obstacles present.

Although incline has been found to affect running speed in other species such as the golden marmot (Blumstein 1992), no significant effect has been found in yellow-bellied marmots in past studies (Blumstein et al. 2004). No significant effects were found in this study either. The insignificant effect of incline on running speed was unexpected, since a steep uphill run would be expected to be slower than a downhill run. Marmots were observed to prefer running downhill or along the slope (personal observation, Blumstein 1992), resulting in a data set with unevenly distributed inclines. A more significant effect may be found with more runs at different inclines especially uphill. Age may predispose individuals to run along or downhill to prevent a decrease in MRS, although this was not examined.

The sex of the marmot also did not have a significant effect on running speed. Although both were insignificant, females ran slightly slower than males. However, most older marmots were females while the younger marmots were more evenly distributed between males and females. A larger number of data points for older males would provide a better comparison of age effects on MRS.

Conclusions

Of the factors considered for effects on yellow-bellied marmot MRS, run distance and substrate significantly affected run time. Run time over a distance run was used as a

measure for MRS. Age, incline, and sex were not significant influences. Further data should be collected especially on older and male marmots since the sample sizes were small compared to younger and female marmots. Current results supported the hypothesis that yellow-bellied marmots did not experience somatic senescence in regards to MRS although they do experience selection.

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