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Cover photo: A vigilant yellow-bellied marmot (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory, Colorado, USA. Blumstein *et al.* (pp. 879–887) report that the time allocated to anti-predator vigilance in marmots is heritable and is weakly correlated with locomotor performance. Interestingly, faster marmots allocate more time to vigilance while slower marmots allocate less time. Photo: Arpat Ozgul.

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Heritability of anti-predatory traits: vigilance and locomotor performance in marmots

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Abstract

Animals must allocate some proportion of their time to detecting predators. In birds and mammals, such anti-predator vigilance has been well studied, and we know that it may be influenced by a variety of intrinsic and extrinsic factors. Despite hundreds of studies focusing on vigilance and suggestions that there are individual differences in vigilance, there have been no prior studies examining its heritability in the field. Here, we present one of the first reports of (additive) genetic variation in vigilance. Using a restricted maximum likelihood procedure, we found that, in yellow-bellied marmots (*Marmota flaviventris*), the heritability of locomotor ability ($h^2 = 0.21$), and especially vigilance ($h^2 = 0.08$), is low. These modest heritability estimates suggest great environmental variation or a history of directional selection eliminating genetic variation in these traits. We also found a significant phenotypic ($r_P = -0.09 \pm 0.04$, $P = 0.024$) and a substantial, but not significant, genetic correlation ($r_A = -0.57 \pm 0.28$, $P = 0.082$) between the two traits (slower animals are less vigilant while foraging). We found no evidence of differential survival or longevity associated with particular phenotypes of either trait. The genetic correlation may persist because of environmental heterogeneity and genotype-by-environment interactions maintaining the correlation, or because there are two ways to solve the problem of foraging in exposed areas: be very vigilant and rely on early detection coupled with speed to escape, or reduce vigilance to minimize time spent in an exposed location. Both strategies seem to be equally successful, and this 'locomotor ability-wariness' syndrome may therefore allow slow animals to compensate behaviourally for their impaired locomotor ability.

Introduction

To avoid predators, prey must first detect them; thus, prey must allocate some proportion of their time to anti-predator vigilance. Studies on anti-predator vigilance have revealed a remarkable degree of sophistication and phenotypic plasticity. In birds and mammals, we know that vigilance may be influenced by a variety of intrinsic (e.g. species (Blumstein & Daniel, 2005), stress hormone levels (Mateo, 2007), body condition (Bachman, 1993), body size (Caro, 2005)) and extrinsic factors (e.g. habitat

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type (Frid, 1997), visibility (Ebensperger & Hurtado, 2005; Bednekoff & Blumstein, 2009), group size (Beauchamp, 2008) and time of year (Metcalfe & Furness, 1984)). Animals often decrease their vigilance when they are in groups (Beauchamp, 2008), and an individual in an exposed position (within the group) is likely to increase its vigilance (di Blanco & Hirsch, 2006). The presence of predators influences vigilance (Creel *et al.*, 2008), as does the degree to which prey can detect predators (Bednekoff & Blumstein, 2009). Although most studies have focused on extrinsic environmental factors that explain variation in vigilance, vigilance may be state dependent in some species. For instance, in Belding's ground squirrels (*Spermophilus beldingii*), individuals in poor body condition are less vigilant (Bachman, 1993), and body condition and recent experience in feeding

influence a particular type of vigilance – sentinel behaviour – in some mammals (Clutton-Brock *et al.*, 1999) and birds (Wright *et al.*, 2001; Bednekoff & Woolfenden, 2003). Reproductive status could also affect vigilance strategies; females with young are more vigilant than females without young (Rieucau & Martin, 2008). Despite this phenotypic plasticity, vigilance may have a heritable basis. Indeed, some heritable components of personality in birds are based, indirectly, on measures of vigilance (e.g. Dingenmanse *et al.*, 2002; van Oers *et al.*, 2004).

We studied vigilance behaviour in yellow-bellied marmots, a socially plastic, seasonally active, sciurid rodent. Much is known about marmot anti-predator behaviour. For instance, vigilance is influenced by an individual's ability to detect terrestrial predators; marmots with their peripheral visibility experimentally blocked were more vigilant than those with unimpaired visibility, and blocked marmots increased their vigilance when they left the blocked area (Bednekoff & Blumstein, 2009). In nature, peripheral visibility is reduced in areas of high vegetation and steep slopes, two factors that influence population persistence. Marmot colonies in poor-visibility habitats are more likely to go extinct (Blumstein *et al.*, 2006).

Blumstein *et al.* (2004) found that about 26% of the variation in the time marmots allocate to vigilance can be explained by both extrinsic and intrinsic factors and vigilance patterns are repeatable within an individual ($r_{IC} = 0.29$); this repeatability suggests that vigilance may be heritable (Boake, 1989). Given the substantial amount of unexplained variation and a modest amount of repeatability, we estimated directly the heritability of anti-predator vigilance as well as additional genetic factors that might influence an individual's vigilance.

Animals may use vigilance to compensate for shortcomings in other traits; hence, we investigated the genetic relationship between vigilance and locomotor performance. Individuals unable to escape predators because of intrinsic factors (such as impaired locomotor ability caused by pregnancy (Cooper *et al.*, 1990) or excessive body mass (Garland, 1983)) should be at a greater risk of predation, and this vulnerability should influence vigilance. For refuging animals (i.e. those that must leave a protected area to forage), individuals with impaired performance could reduce their predation risk in at least two ways; they could be more vigilant when foraging, and thus detect approaching threats at greater distances, or they could be less vigilant while foraging, and thus forage faster and spend less time exposed to predators. In yellow-bellied marmots, we see a positive phenotypic correlation between maximum running speed and time allocated to vigilance (Blumstein *et al.*, 2004), suggesting that slow individuals compensate for their running performance shortcomings by adopting the latter strategy (i.e. look less and minimize exposure time). In our study, we quantified the genetic relation-ship between locomotor performance and vigilance to further understand the evolutionary potential of these anti-predatory traits.

Methods

Study site and population monitoring

All measurements and samples were collected at the Rocky Mountain Biological Laboratory (RMBL; 38°57′N, 106°59′W), Gunnison County, Colorado, USA. At RMBL, habitats range from open meadow and forest clearings to steep talus slopes. Substrates include a variety of vegetation types and heights, as well as dirt and stones. Vegetation changes throughout the marmots' active season (Blumstein *et al.*, 2004).

Marmots from the study population were routinely live trapped during the summer months. Trapped individuals were transferred to cloth handling bags where weight, sex and reproductive status were determined. Marmots were marked with fur dye (for observation from a distance) and given permanent ear tags (for long-term individual identification) (Armitage, 1982). Behavioural observations were systematically recorded throughout the summer. From this set of behavioural observations, we extracted information on probable mothers and fathers for offspring born from 2001 to 2008.

Genotyping

Hair samples were plucked from marmots and stored in clean envelopes at −20 °C. We extracted DNA from these hair samples using a QIAamp® Mini Kit (Qiagen Inc., Valencia, CA, USA). All samples were extracted according to manufacturer's instructions and subsequently stored at −20 °C. Polymerase chain reactions (PCR) were used to amplify the following polymorphic loci: BIBL31, BIBL18, BIBL4, MA018, MS47, GS22, IGS6, SGS14, 2G2, MA091, ST10 and SGS25 (May *et al.*, 1997; Stevens *et al.*, 1997; Gossens *et al.*, 1998; Hanslik & Krukenhaüser, 2000; da Silva *et al.*, 2003; Floyd *et al.*, 2005). The amplified region was sized using an ABI 3730 Prism DNA sequencer (Applied Biosystems, Foster City, CA, USA). Electropherogram peaks were analysed using GENEMAPPER software (version 3.0; Applied Biosystems, Foster City, CA, USA).

Pedigree

Genotypes were analysed using CERVUS 3.0 (Kalinowski *et al.*, 2007). This program considers all candidate mother–father possibilities for a given offspring and calculates a likelihood score for each trio. The score of the most likely trio is compared to a simulation-generated critical value, and parentage is assigned at the appropriate confidence level. To determine critical values, we ran a simulation accounting for allele frequencies, the

number of candidate parents of each sex, the proportion of parents sampled, the proportion of loci typed, the proportion of highly ($R > 0.4$) related mothers and the proportion of loci mistyped (Jones & Arden, 2003). The strict confidence level was set at 95% and the relaxed at 80%. Marmots at RMBL are well trapped and observed, and we therefore assumed a sampling proportion of 99% for candidate mothers and 96% for candidate fathers. The proportion of loci typed was 0.948, and the proportion mistyped was set at 0.01.

A list of candidate mothers was selected for each offspring using nipple size measurements (an index that reflects pregnancy and nursing) that were routinely recorded when marmots were trapped. Candidate fathers were selected more broadly: male marmots were grouped into two distinct geographical areas, separated by approximately 5 km, which represent a natural break in the marmot population. All offspring from each geographical group were given the same list of potential fathers.

As adult female yellow-bellied marmots are largely philopatric (Armitage, 1984), females in the same geographical group are often highly related. Close relatives within the list of candidate parents can make it more difficult for CERVUS to assign the most likely parent for an offspring (Jones & Arden, 2003). To control for this, we calculated the proportion of female marmots related at a level of $R > 0.4$ or higher for each year. Parentage was then analysed by year, with the appropriate relatedness value and proportion of related candidate parents included.

Parentage links of 873 offspring were assigned at 95% confidence level using 8 (n = 85) to 12 (n = 788) loci. Parentage links for five more individuals were estimated with eight loci at 80% confidence level. Finally, in 17 cases where genetic samples were missing, parentage was assigned based solely on behavioural observations. The final pedigree included 968 individuals, of which 890 had full parentage (both mother and father), 73 had no parents, four had only a sire and one had only a dam. Our entire pedigree encompassed five generations, and each individual had at least one pedigree link. It should be noted that a restricted pedigree containing only links assigned at the 95% confidence level generated similar results for all analyses.

Measuring maximum running speed

Adult, yearling and juvenile marmots (weighing more than 700 g) were run during the summer months of 2002–2008. A run began when a marmot was released from the handling bag and chased by a shouting, arm-waving researcher towards a burrow. Using a digital stopwatch, an observer timed and marked the run distance. The precise distance run, incline (measured in degrees), substrate category and straight distance to burrow were then measured and recorded. Substrates were categorized as type I (stones and talus), type II (dirt and short vegetation) or type III (tall vegetation). Anything above the marmot's head was considered tall vegetation.

Unsuccessful runs were eliminated from analysis. Marmots often curved their running path or unexpectedly changed their target burrow, making a straight run distance impossible to measure. If an observer was unsure of a measured time or distance, the run was eliminated. Runs that occurred across heterogeneous substrates and inclines were not included in the final data set. We also eliminated runs that were <1.5 s, because these short runs are susceptible to enhanced error effects (Blumstein, 1992). Our final data set consisted of 187 individuals; each individual was measured between 1 and 10 times for an average of 1.82 measures per individual.

Measuring time allocated to vigilance

Focal observations were conducted during times of peak activity (sunrise to 10:00 h and 16:00 h to sunset) throughout the summer months of 2003–2008. We did not observe animals on rainy or excessively windy days, as these extreme weather conditions would likely affect visibility and foraging behaviour. We observed foraging marmots for a maximum of 2-min using 15–45× spotting scopes and recorded the following behaviours: quadrupedal and bipedal foraging, quadrupedal and bipedal looking (hereafter, vigilance), locomotion and out of sight (Blumstein *et al.*, 2004). When the marmot being watched left the immediate area, focal observations were truncated, and focal duration was noted. Observers were positioned far from marmots, and their presence did not obviously affect the animals' behaviour.

Observers dictated observations into microcassette recorders and later scored them using JWATCHER 1.0 (Blumstein & Daniel, 2007). Observers practised entering information into JWATCHER until intra-observer reliability was ≥0.95. We also noted the number of conspecifics within 10 m of the focal subject (group size may affect time allocation), incline category (0–10°, 10–30° and >30°) and substrate category as described previously. All observers were trained to identify each behaviour, slope category and substrate type with 100% accuracy. In total, repeated measures of vigilance were made on 315 individuals. Each individual was measured between 1 and 24 times for an average of 5.23 measures per individual.

Estimating quantitative genetic parameters

The animal model (a type of mixed model) uses both fixed and random effects to explain phenotypic variation. This modelling approach allows for incomplete and multigenerational pedigrees, making it particularly useful for studies on natural populations (Kruuk, 2004). Furthermore, it is less likely than parent–offspring

regressions to be biased by assortative mating, inbreeding, selection and shared environment (Kruuk, 2004). We used the program ASREML 2.0 (Gilmour *et al.*, 2004) to fit the following animal model:

$$y = Xa + Zb + c$$

In this model, fixed effects (*a*), random effects (*b*) and residual errors (*c*) explain phenotypic measures of a quantitative trait (*y*). *X* and *Z* represent corresponding design matrices relating data records to the appropriate fixed and random effects (Kruuk *et al.*, 2000). Individual identity (linked to a pedigree) is included as a random effect to determine an animal's additive genetic value (hence the name 'animal model').

We used univariate animal models to partition phenotypic variance into several fixed and random components. Significance of random terms was assessed using a log-likelihood ratio test in an additive stepwise manner. Random effects were added to the model in the following order: location (i.e. colony site), year, individual variation that was divided into permanent environment and additive genetic, maternal environment, maternal genetic, paternal environment and paternal genetic components. According to Kruuk & Hadfield (2007), environmental effects were retained in the model, even if nonsignificant, when genetic effects were tested to properly account for the structure of the data. To evaluate parental effects (environmental and genetic), individuals with no parental information in the pedigree were excluded from all models in the stepwise analysis (see Table 1 for a summary of data structure). However, when parental effects were not significant, heritability estimates were computed using all individuals. Similar heritability estimates were obtained using dataset including or excluding individuals with no parental information.

Modelling maximum running speed with a regression of velocity (distance/time) as a function of distance run creates a ratio-correlation problem (Atchley & Anderson, 1978; Blumstein, 1992). In this case, the dependent variable would be calculated from an independent variable, creating a false correlation between the two. Furthermore, any measurement error would affect both variables (Blumstein, 1992). Considering that run time = distance run * speed^{-1}, we modelled maximum running speed using a regression of run time as a function of distance run multiplied by fixed effects (see Blumstein, 1992 for a full description of the method). Our model included substrate category (dummy variable) and incline as fixed effects. Note that by modelling maximum running speed to explain variation in run time, short duration run time residuals would be associated with faster subjects, and a negative correlation between run time and vigilance would suggest that slow marmots allocated less time to vigilance, whereas fast marmots allocated more time to vigilance. The vigilance model included three fixed effects (days since 1 January of that year, number of conspecifics within 10 m and incline category) to explain the proportion of time in sight an individual allocated to vigilance (angularly transformed).

Using a bivariate model that incorporated all data for both vigilance and running speed, we estimated the phenotypic and genetic covariance between vigilance and running speed. Covariance significance was tested using a log-likelihood ratio test (LRT) between a model with and without the covariance term constrained to zero. Fixed effects structure for both traits was similar to univariate analyses. Location was fitted as a random term for vigilance only. We first estimated permanent environment (co)variance structure by adding a permanent environment random term for both traits. Because maximum running speed and time allocated to vigilance were not simultaneously measured, we could not estimate residual covariance within this analysis; the residual covariance was therefore fixed at 0. However, because both traits were measured on the same individuals, permanent environmental covariance represented the covariance between the traits at the individual level and was considered equal to phenotypic covariance. The phenotypic correlation was then estimated as permanent environment covariance divided by the square root of the product of the phenotypic variance for each trait.

We estimated the genetic correlation by fitting an additive genetic and a permanent environment random term for both traits. The genetic correlation (cov(XY)/$\sqrt{V_{AX}V_{AY}}$) between the two traits was estimated by dividing the genetic covariance by the square root of the product of the additive genetic variances of traits *A* and *B* (i.e. the product of the two standard deviations). The genetic correlation is therefore dependent on the genetic covariance estimated by the bivariate model.

	Locomotor performance		Vigilance	
	All individuals	Individuals with full parentage only	All individuals	Individuals with full parentage only
Number of observations	341	238	1237	983
Number of unique individuals	187	147	315	258

Table 1 Summary of data sets used to estimate quantitative genetic parameters.

*Some individuals were observed across multiple years in more than one age category.

Fitness consequences and additional analyses

Following Hadfield's (2008) suggestions, we investigated the fitness consequences of locomotor performance and vigilance using bivariate models that incorporated the traits under study as well as two fitness proxies-lifetime reproductive success (LRS) and longevity. LRS was estimated as the total number of offspring produced over the lifetime of each individual that survived to reproductive age (≥2 years). LRS was estimated directly from the pedigree, which incorporated genetic samples from an estimated 96% of the population (see sampling proportions listed in pedigree methods). It is incredibly rare for a marmot to go un-trapped within a given year, unless it has died or dispersed beyond our study site; therefore, individuals trapped in the summer of 2008 were thought to be still living and were not included in the analysis. Longevity estimates were based on a few direct observations of predation, but mostly on regular observations and trappings (if an adult was not seen for a year, it was assumed dead). Marmots at RMBL are well trapped and observed, and most residents are tracked from birth to death. Female marmots are philopatric and tend to remain at their natal colony; however, yearling male marmots often disperse to nearby colonies (Armitage, 1984), and dispersal may be mistaken for death when individuals do not immigrate to a colony within the study site. We assumed that male yearlings of all running speeds and vigilance types dispersed at equal rates; therefore, the ambiguity surrounding this particular age sex class would not bias analysis. LRS estimates were available for 710 individuals (mean: 7.19; range: 0–143), and the longevity of 677 individuals (mean: 3.38; range: 0–14) was known.

We evaluated the directional and stabilizing selection differential, S and C, respectively, for vigilance and locomotor performance using both longevity and lifetime reproductive success (LRS) as fitness proxies. S was calculated as the covariance between the trait and relative individual fitness (Lynch & Walsh, 1998). C was evaluated as the covariance between the orthogonal quadratic trait and relative individual fitness (Lande & Arnold, 1983). Covariances were estimated using bivariate models with a permanent environment effect. Residual covariance was set to 0, and permanent environment variance was considered as the phenotypic covariance. Covariance significance was assessed using a LRT statistic. Both longevity and LRS were corrected for sex in the bivariate analyses because of sexual differences in mortality rate and reproductive strategy. Vigilance and locomotor performance were corrected for the same fixed effects as previously mentioned.

We also estimated the correlation between an individual's locomotor performance and its exposure time while foraging; this analysis allowed us to test the hypothesis that slower marmots (with reduced vigilance while foraging) minimize time spent in exposed locations.

Focal duration (N = 664) was used as a proxy for exposure time while foraging. By doing so, we assume that marmots that have longer bouts of foraging are more exposed to predation than those that forage in very short bouts.

Results

Final models of both maximum running speed and vigilance included permanent environment and additive genetic random effects (MRS: LRT = 15.162, $P < 0.001$; vigilance: LRT = 7.760, $P = 0.005$). The vigilance model also included location as a random effect (LRT = 86.080, $P < 0.001$). We found parental (both maternal and paternal) environment and genetic effects to be nonsignificant for both vigilance and locomotor performance (all $P > 0.21$). Vigilance estimates of additive genetic variance and heritability were small but detectable (Table 2); estimates for locomotor performance were more substantial (Table 2). For both vigilance and running speed, most of the variance at the individual level can be attributed to additive genetic effects (Table 2).

We found a significant phenotypic covariance and correlation between vigilance and locomotor performance (LRT = 5.06, $P = 0.024$, $cov_P = -0.01 \pm 0.003$;. $r_P = -0.09 \pm 0.035$), and a substantial, but not significant, genetic correlation (LRT = 3.02, $P = 0.082$, $cov_G = -0.01 \pm 0.004$;. $r_G = -0.57 \pm 0.276$). Because locomotor performance was modelled as run time adjusted for run distance, a negative correlation with vigilance implied that fast marmots were also more vigilant (Fig. 1). When estimating the genetic correlation, we fixed the permanent environment covariance at zero to allow model convergence. Small and nonsignificant components of variance associated with the permanent environment for both traits in univariate analyses suggest a negligible permanent environment covariance. Other variance components from the bivariate model were similar to those from univariate analysis and are not reported.

None of these heritable anti-predator behaviours seemed to be under selection (Fig. 2). Maximum running speed was neither related to longevity ($S = -0.0311 \pm 0.0537$, LRT = 0.27, $P = 0.599$; $C = -0.1080 \pm 0.4067$, LRT = 0.12, $P = 0.729$), nor lifetime reproductive success (log ($x + 1$) transformed; $S = -0.00119 \pm 0.00718$, LRT = 0.15, $P = 0.697$; $C = -0.4591 \pm 0.5801$, LRT = 0.81, $P = 0.368$). Vigilance was also not related to longevity ($S = -0.00123 \pm 0.0107$, LRT = 0.02, $P = 0.882$; $C = -0.000921 \pm 0.00808$,. LRT = 0.22, $P = 0.639$), nor lifetime reproductive success ($S = 0.000845 \pm 0.00146$, LRT = 1.00, $P = 0.317$; $C = -0.00726 \pm 0.01264$, LRT = 0.36, $P = 0.548$).

From the analysis of exposure time, we found that focal duration is significantly shorter in slower marmots ($r = -0.13 \pm 0.045$, LRT = 6.06, $P = 0.014$).

|	Locomotor performance		Vigilance	
	Variance	Ratio	Variance	Ratio
Raw phenotypic*	**0.331 (0.025)**	–	**0.035 (0.001)**	–
Conditional phenotypic†	**0.287 (0.024)**	–	**0.035 (0.003)**	–
Permanent environment	0.000 (0.001)	0.00 (0.001)	0.001 (0.001)	0.01 (0.027)
Additive genetic‡	**0.059 (0.022)**	**0.21 (0.070)**	**0.003 (0.001)**	**0.08 (0.041)**
Location	–	–	0.004 (0.003)	0.14 (0.086)

Table 2 Estimates (with SE) of variance components and proportion of variance from univariate animal models.

*Phenotypic variance estimated directly from the data as suggested by Wilson (2008).
†Phenotypic variance conditional on fixed effects estimated as the sum of variance components of the animal model. Fixed effects included in the model of locomotor performance were substrate categories (A (estimate ± SE): 0.901 ± 0.126; B: 0.704 ± 0.105 and C: 0.945 ± 0.113; $P < 0.001$) and incline (estimate: $4.42e{-}3 ± 2.07e{-}3$, $P = 0.003$). Model of vigilance included days since 1 January (estimate: $1.05e{-}3 ± 0.31e{-}3$, $P = 0.003$), number of conspecifics within 10 m (estimate: $-0.017 ± 0.003$, $P < 0.001$) and incline category ($<10°$: $0.511 ± 0.058$; $10–30°$: $0.497 ± 0.059$ and $>30°$: $0.459 ± 0.059$; $P < 0.001$) as fixed effects.
‡Heritability (h^2) is the additive genetic proportion of variance estimated as additive genetic variance divided by the conditional phenotypic variance.
Estimates significantly different from zero are in bold.
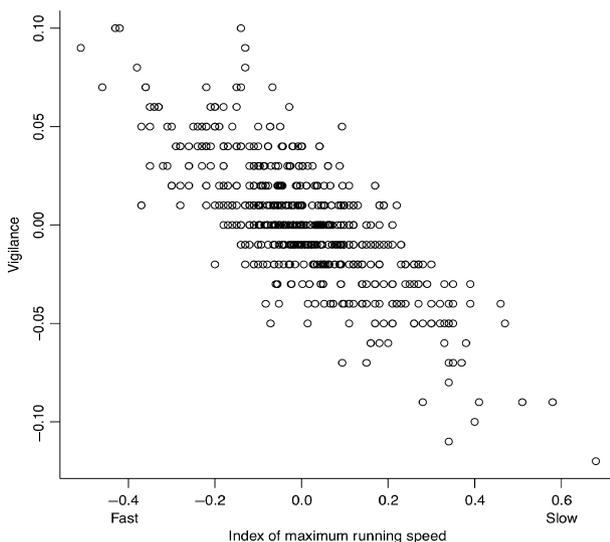
Fig. 1 Additive genetic correlation between vigilance and maximum running speed in yellow-bellied marmots. Predicted breeding values (PBVs) obtained from BLUPs of the bivariate animal model of vigilance and maximum running speed are used illustratively.

Discussion

This is one of the first studies to estimate the heritability of vigilance (see Rogers *et al.*, 2008 for a captive study); we found it was low ($h^2 = 0.08$). On the one hand, our estimate is not surprising because traits closely associated with fitness often exhibit low heritability (Roff, 1997). We expect strong selection on animals to be vigilant because nonvigilant animals would be quickly preyed upon. In such a case, alleles closely associated with the fitness-related trait may be rapidly fixed by selection and individual genetic variation depleted. However, we did not find any evidence for selection on vigilance over the study period; predation rates in our study population may be too low to allow any detectable selection on such anti-predator behaviour. We may also expect low heritability estimates for vigilance because this behaviour may depend on an individual's state (Bachman, 1993; Rieucau & Martin, 2008) or fluctuating immediate environment. Although we found permanent environmental effects to be minimal, high environmental variation contributed to our low heritability estimates.

On the other hand, the relatively small heritability is surprising given that multivariate studies on vigilance typically explain only 20–30% of anti-predator vigilance. We hypothesized that individual genetic differences might be the 'magic bullet' that explains a substantial amount of the remaining variation but found that this was not the case. Given all that is known about anti-predator vigilance, it is surprising that multivariate models seldom explain much variation in the time an individual allocates to anti-predator vigilance (Blumstein, 1996; Blumstein *et al.*, 2004). Aggregated analyses (with categories such as group size) explain substantially more variation in vigilance (Blumstein & Daniel, 2005), but the results from un-aggregated analyses leave us wondering what other factors explain individual variation in vigilance.

Our estimates of heritability were typically based on multiple measurements of both vigilance and maximum running speed. Multiple measurements of variable behavioural traits provide more robust heritability estimates (e.g. Arnold & Bennett, 1984; Arnold, 1994). Indeed, in some cases, estimating heritability using average values (which is always better than estimating heritability using a single value) leads to heritability
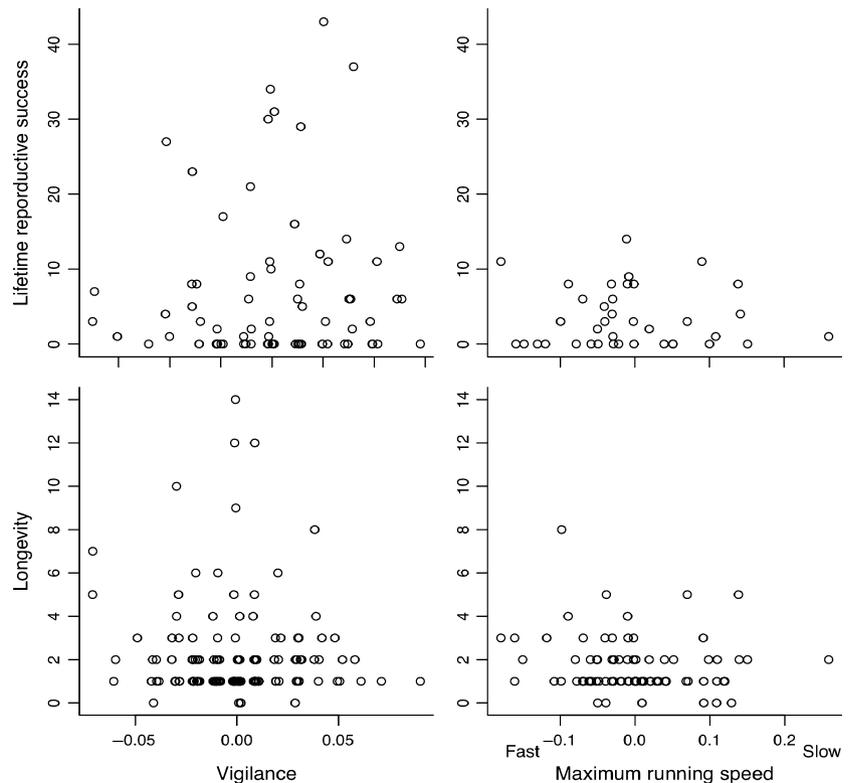
Fig. 2 Relationship between vigilance and maximum running speed with fitness proxies (longevity and lifetime reproductive success). Individual BLUPs of vigilance and maximum running speed from a phenotypic bivariate model are illustrated. Data on vigilance and running speed were not available for all individuals.

estimates that exceed repeatability estimates (Arnold & Bennett, 1984).

Running speed, while clearly a behavioural trait, is also a direct measure of performance (Irschick *et al.*, 2008). Many studies have documented significant heritable differences in performance (Bennett & Huey, 1990), which is surprising given that performance is likely to be under strong selection. Although we may expect selection on performance (especially in a refuging species), we found no relationship between maximum running speed and either fitness proxy during the study period. The presence of heritable genetic variation ($h^2 = 0.21$) indicates that some opportunity for evolution still exists, but any directional selection to increase running speed might be constrained by its weak genetic correlation with vigilance.

The significant phenotypic and considerable (Roff, 1997), but insignificant, genetic correlation between vigilance and running speed suggests two different strategies: fast animals are wary, and slow animals are less wary, while foraging. This positive relationship (because locomotor performance was modelled as running time adjusted for running distance, a negative correlation with vigilance shows that fast marmots were also more vigilant) is somewhat unexpected, given that many studies have identified negative genetic correlations between fitness-related traits [e.g. fecundity and wing dimorphism (Roff & Brandford, 1996), offspring

number and quality (Mappes & Koskela, 2004), and age at first reproduction and senescence (Charmantier *et al.*, 2006)].

In our efforts to understand the surprising direction and size of this correlation, we hypothesized three different ways in which this locomotor performance-wariness syndrome may be present in the population. First, environmental heterogeneity and genotype-by-environment interactions could maintain variation. Thus, there may be variation in the environment, such that slow/less vigilant marmots do better in certain environments for which the fast/more vigilant genotype does worse. Second, the variation may be maintained because there are two equally valid ways to survive while foraging – be vigilant, detect predators, and outrun them or reduce time spent foraging by being less vigilant, thereby minimizing exposure. Third, the genetic correlation may arise with genetic drift and persist because neither trait is under selection.

Although we might expect a fast/more vigilant marmot to outcompete a slow/less vigilant one, we found no evidence for fitness consequences in either measured trait. We also found that slow marmots had shorter focal durations, suggesting that they spent less time foraging or foraged in shorter bouts. Slow/less vigilant marmots might compensate behaviourally for their seemingly inferior qualities by spending less time foraging in

exposed areas than fast/more vigilant marmots. Further studies on covariance selection and behavioural compensation of speed–vigilance correlation would increase our understanding of this counterintuitive anti-predatory trait association.

Acknowledgments

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