Proximate Causes of Intraspecific Variation in Locomotor Performance in the Lizard *Gallotia galloti*

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ABSTRACT

To understand the evolution of biological traits, information on the degree and origins of intraspecific variation is essential. Because adaptation can take place only if the trait shows heritable variation, it is important to know whether (at least) part of the trait variation is genetically based. We describe intra- and interindividual variation in three performance measures (sprint speed, climbing, and clambering speed) in juvenile *Gallotia galloti* lizards from three populations and examine how genetic, environmental (incubation temperature), and ontogenetic (age, size) effects interact to cause performance variation. Moreover, we test whether the three performance traits are intercorrelated phenotypically and genetically. Sprint speed is highest in juveniles incubated at the lowest temperature (26°C) irrespective of population. Climbing speed differs among populations, and the differences persist at least until the lizards are 30 wk old. This suggests that the three populations experience different selective pressures. Moreover, mass, snout-vent length, and hindlimb length seem to affect climbing performance differently in the three populations. The variation in sprinting and climbing ability appears to be genetically based. Moreover, the two performance traits are intercorrelated and thus will not evolve independently from each other. Clambering speed (i.e., capacity to climb up an inclined mesh) varies among individuals, but the origin of this variation remains obscure.

Introduction

Information on the degree and origins of intraspecific variability is essential to our understanding of the evolution of biological characteristics. In natural populations, most traits show at least some degree of variation. Since evolutionary responses to selective pressures can be expected only when the trait under consideration shows heritable interindividual variation, it is important to know whether (at least) part of the trait variation is genetically based.

Locomotor abilities of squamate reptiles are among the best-studied performance traits in vertebrates. Many species show surprisingly high intraspecific variation in these traits, and students have used different approaches to trace the sources of this variation (reviews in Bennett 1989; Garland 1994).

Longitudinal studies have shown that within individual lizards and snakes, locomotor performance may vary with external factors such as temperature (e.g., John-Alder and Bennett 1981; Marsh and Bennett 1986; van Berkum et al. 1986; Huey et al. 1989; Van Damme et al. 1989*a*; Swoap et al. 1993; Autumn et al. 1994; Xiang et al. 1996) and internal factors such as hormone levels (Klukowski et al. 1998), stomach contents (e.g., Garland and Arnold 1983; Ford and Shuttlesworth 1986), and reproductive condition (e.g., Bauwens and Thoen 1981; Van Damme et al. 1989*b*; Sinervo et al. 1991; Miles et al. 2000). On a larger time scale, performance also changes ontogenetically (e.g., Huey 1982; Garland 1985; Carrier 1996).

Cross-sectional studies have centered on correlates of among-individual variation in performance (review in Garland and Losos 1994). Design features that explain variation in performance in squamates include morphological (e.g., Bauwens et al. 1995; Bonine and Garland 1999; Zani 2000), physiological (e.g., Bennett and Huey 1990; Autumn et al. 1994; Bonine et al., in press), and biochemical (e.g., Abu-Ghalyun 1995) elements. A number of studies have addressed the question of whether the interindividual variation in design and performance traits is genetic or phenotypic (e.g., van Berkum and Tsuji 1987; Tsuji et al. 1989; Bennett and Huey 1990; Jayne and Bennett 1990; Brodie and Garland 1993; Garland 1994; Sorci et al. 1995). Although in most cases the traits do show significant broad-sense heritability, other tests show that environmental effects (e.g., incubation temperature, humidity) may play a surprisingly important role (e.g., Van Damme et al. 1992;

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Shine and Harlow 1996; Elphick and Shine 1998; Finkler 1999; Braña and Ji 2000). Whether these effects are transient or influence the animal's phenotype throughout substantial parts of its life is still unclear (Burger 1989; Philips et al. 1990; Elphick and Shine 1998).

One way to assess whether interindividual variation in a trait has evolutionary significance is by comparing populations under different selection pressures (Arnold 1981; Garland and Adolph 1991; Garland and Losos 1994). Several studies have revealed significant interpopulational differences in locomotor performance among squamate populations (e.g., Crowley 1985*a*, 1985*b*; Snell et al. 1988; Huey et al. 1990; Sinervo and Losos 1991; Van Damme et al. 1997). Interpretation of these differences often implies a trade-off between different aspects of locomotion. Negative genetic correlations are considered the prime cause of evolutionary trade-offs among performance traits. However, there is no empirical support for such genetic correlations in squamate reptiles (e.g., Tsuji et al. 1989; Jayne and Bennett 1990; Brodie and Garland 1993; Garland 1994; Sorci et al. 1995).

Most studies have examined the effects of one of the above-mentioned factors in isolation. In this study, we describe intra- and interindividual variation in three performance measures (sprint speed, climbing speed, and clambering speed [defined as the ability to climb up an inclined mesh]) in juveniles of the lizard *Gallotia galloti* from three populations and examine how genetic, environmental, and ontogenetic effects interact to cause this variation. Within each individual, we tested for ontogenetic changes by measuring the performance ability of each individual lizard at the three tasks every 4 wk from 6 until 30 wk of age. Among individuals, we tested whether incubation temperature and morphology (snout-vent length, hindlimb length, and mass) affect locomotor performance and whether sprinting, climbing, and clambering ability are intercorrelated, both phenotypically and genetically. Furthermore, we tested whether differences in locomotor performance are genetically based by comparing hatchlings with known relatedness. Finally, we tested whether locomotor performance differed among three populations and whether locomotor ability was differentially affected in the three populations by the above mentioned variables.

Material and Methods

Animals and Their Maintenance

We caught 15 adult *Gallotia galloti* (10 females, five males) from each of three populations on Tenerife (Canary Islands, Spain). The first site, near San Isidro, is situated in the south of the island of Tenerife at an altitude of 500 m, the second is in the middle of the island (Las Cañadas) at 3,500 m, and the third is in the north (Icod) at sea level. The climate in San Isidro is drier and hotter; at Las Cañadas, temperatures fluctuate drastically; and at Icod, it is cooler and more humid (Thorpe and Baez 1987; Thorpe and Brown 1991). Microhabitat does not differ greatly among populations; lizards were caught on low walls at San Isidro, on rocky outcrops at Las Cañadas, and on stone walls and among leaf litter in a banana plantation at Icod. All animals were transported to the lab at the Institute for Nature Conservation in Brussels, Belgium, and housed in 100 × 40-cm cages with a sandy substrate and some stones. Each cage contained two females and one male, with populations kept apart.

Eight females from the first, eight from the second, and seven from the third population reproduced successfully. As soon as clutches were laid, the eggs were removed from the cages and incubated separately in moist vermiculite (10 : 8 g vermiculite : water). Each clutch was split, and eggs from the same clutch were randomly assigned to the three different incubation temperature treatments (26°, 28.5°, 31°C).

After hatching, juveniles were kept individually in 25 × 20-cm cages with a sandy substrate covered by leaf litter. When their weight exceeded 5 g, juveniles were moved to cages twice as large. In total, 54 juveniles from the San Isidro population, 18 from the Las Cañadas population, and 35 from the Icod population were used in this study.

Both adults and juveniles were fed live crickets and banana dusted with calcium once every 2 d. Water was always present. A 150-W spotlight provided heat and light for 10 h/d, which allowed lizards to thermoregulate.

Experimental Setup

From the age of 6 wk, all 107 juveniles were tested for maximal sprint speed and climbing speed on two substrates: (1) on smooth slates to mimic climbing on rocks and (2) on mesh to mimic climbing through the vegetation. Hereafter, we refer to these performance measures as climbing and clambering, respectively. The tests were repeated every 4 wk until the lizards were 30 wk old (see Table 1 for raw data).

Maximal sprint speed was obtained by chasing an animal down a 150-cm-long × 10-cm-wide racetrack with a cork substrate. Six photocells positioned at 25-cm intervals registered when a lizard passed. Elapsed time between the passing of successive cells was stored in a computer, and sprint speed over every 25-cm interval was calculated. Each individual was tested five times. As a measure of maximal sprint speed, we used the highest attained speed over any 25-cm interval of the five trials.

Maximal climbing speed was obtained in a similar setup, only in this case, a 100-cm-long × 10-cm-wide racetrack tilted to an angle of 70° was used. Six photocells were positioned 15 cm apart. Each individual was tested three times. As a measure of maximal climbing speed, we used the highest attained speed over any 15-cm interval of the three trials. The same setup was used to measure maximal clambering speed, but the slates were replaced by a copper mesh (mesh width, 2 mm; spacing, 5 mm).

Table 1: Raw data for different age groups of juvenile *Gallotia galloti* from three populations

Age	Mass (g)	Snout-Vent Length (mm)	Hindlimb Length (mm)	Sprint Speed (cm/s)	Climbing Speed (cm/s)	Clambering Speed (cm/s)
6 wk:						
Population 1	2.80 ± .18	42.11 ± .41	18.32 ± .27	120.10 ± 7.35	32.52 ± 2.93	77.89 ± 4.73
Population 2	2.19 ± .11	41.76 ± .54	17.31 ± .25	127.45 ± 10.50	34.98 ± 3.52	85.11 ± 4.37
Population 3	2.80 ± .33	40.42 ± .36	17.68 ± .64	119.41 ± 8.43	41.32 ± 3.05	92.68 ± 6.08
10 wk:						
Population 1	3.51 ± .16	46.19 ± .40	19.71 ± .30	97.23 ± 6.35	30.67 ± 2.59	78.91 ± 4.96
Population 2	2.94 ± .25	43.28 ± .44	18.81 ± .48	99.05 ± 8.73	31.42 ± 2.42	84.85 ± 7.97
Population 3	2.88 ± .17	43.14 ± .53	18.28 ± .36	114.63 ± 7.30	31.56 ± 3.30	75.25 ± 6.77
14 wk:						
Population 1	4.42 ± .61	47.27 ± .46	20.35 ± .45	114.97 ± 9.31	42.39 ± 3.86	94.25 ± 7.46
Population 2	3.17 ± .17	45.69 ± .77	19.60 ± .39	81.73 ± 8.13	36.01 ± 1.90	88.29 ± 5.01
Population 3	4.62 ± .82	46.62 ± .69	20.48 ± .80	114.58 ± 7.22	39.38 ± 3.64	75.25 ± 6.77
18 wk:						
Population 1	4.22 ± .18	49.72 ± .59	20.69 ± .21	114.67 ± 7.11	41.26 ± 3.52	72.20 ± 4.82
Population 2	3.76 ± .29	46.03 ± 1.28	20.26 ± .41	104.33 ± 16.33	41.93 ± 6.52	84.75 ± 9.96
Population 3	3.45 ± .14	47.63 ± .73	19.59 ± .26	117.64 ± 10.76	35.29 ± 4.10	87.04 ± 7.86
22 wk:						
Population 1	4.77 ± .18	52.05 ± .58	21.93 ± .25	107.03 ± 5.41	39.70 ± 2.17	75.56 ± 4.43
Population 2	4.09 ± .20	49.05 ± .69	20.88 ± .34	92.26 ± 7.99	35.94 ± 3.74	73.97 ± 7.16
Population 3	4.07 ± .17	49.30 ± .63	20.79 ± .23	109.04 ± 6.50	39.18 ± 3.43	85.39 ± 5.01
26 wk:						
Population 1	5.36 ± .23	54.33 ± .69	22.99 ± .33	105.31 ± 7.71	34.98 ± 2.93	77.35 ± 5.21
Population 2	4.52 ± .33	51.13 ± 1.04	21.78 ± .53	89.45 ± 11.41	36.37 ± 4.94	66.14 ± 6.91
Population 3	4.68 ± .25	52.69 ± 1.04	21.82 ± .41	118.94 ± 5.84	41.97 ± 4.37	87.28 ± 8.30
30 wk:						
Population 1	6.78 ± .43	57.25 ± .96	24.44 ± .38	107.30 ± 13.85	38.75 ± 5.91	91.18 ± 13.06
Population 2	4.95 ± .51	52.67 ± 1.72	22.09 ± .59	106.81 ± 11.65	30.07 ± 10.03	86.81 ± 24.52
Population 3	5.77 ± .49	56.22 ± 1.80	23.10 ± .56	124.28 ± 10.63	42.06 ± 5.63	97.83 ± 9.54

Note. Population numbers correspond to the following: 1 = San Isidro, 2 = Las Cañadas, and 3 = Icod. All values are mean ± SE.

Before experimentation and in between trials, lizards were kept for at least 1 h in an incubator at 35°C. We used the average preferred body temperature for other species of *Gallotia* because no preferred body temperatures of *G. galloti* are reported in the literature (Márquez et al. 1997). Sprint, climbing, and clambering speeds were measured 1 d apart.

After each series of experiments (sprinting, climbing, and clambering), we measured snout-vent length and total hindlimb length (measured from the pelvis-femur joint to the metatarsus–third toe joint) with digital calipers (Mitutoyo, CD-15DC; 0.01 mm). All juveniles were weighed on an electronic balance (KERN 444; 0.01 g; see Table 1 for raw data).

Statistical Analysis

Prior to statistical analyses, all morphological and performance variables were logarithmically (log 10) transformed. The logarithms of the morphological variables (snout vent length, hindlimb length, mass) were entered in a principal component analysis to obtain one or a number of mutually independent morphological summary variables.

For each of the performance variables, we estimated linear mixed models, which included fixed effects, random effects, and correlated error terms (SAS Proc Mixed [Littell et al. 1996] and DFREML [Meyer 1991]). Different models were compared in order to obtain a minimum adequate model (MAM; Crawley 1993). As fixed effects, we introduced incubation temperature, population of origin, age, the morphological summary variable, and the interactions between the factors and the continuous variables. Mother, individual, and random slopes of the regression per mother and per individual for the age dependence were used as random effects. By including the slopes of the regressions, we could test for genetic variance in age dependence for each performance measure. In some models, we allowed for different genetic variances for the different source populations. The fathers of the individuals were not known, but we assumed that one clutch is from one father. Therefore, within a clutch, the random effect (and random slope) per mother accounted for part of the genotypic contribution to the phenotype plus common maternal environmental effects (Lynch and Walsh 1998). The individual effect (or slope) predicted the random deviation introduced by Mendelian segregation of maternal and paternal genotypes (Lynch and Walsh 1998) plus a constant individual environmental effect.

For each trait, we first fitted a global model using the restricted maximum likelihood (REML) approach (Littell et al. 1996). Starting from this global model, we first did a random effect model and error covariance structure selection. We used Akaike information criteria (AIC) for model comparison (Burnham and Anderson 1998). Subsequently, model simplification was carried out for the fixed effects using traditional hypothesis testing by means of F statistics. We switched to maximum-likelihood parameter estimation when selecting fixed effects to make sure that the correct likelihoods were compared (Venables and Ripley 1999). When an interaction effect is found to be significant, this means that at least one interaction effect differs from zero. To get a better idea of which groups then actually experience different effects, pairs of groups were lumped until all pairwise contrasts between the remaining groups were found to be significant.

After the model selection procedure, the final models are minimum adequate models (Crawley 1993). The AIC difference is the difference in AIC between models with and without the random parameter or between models with correlated or uncorrelated errors. A negative difference means that the model with an additional parameter describes the data better. Reported parameter estimates for fixed and random effects are obtained using REML optimization of the MAM selected model.

We originally planned to select a single multivariate linear mixed model, but the time necessary for numerically fitting a single model for the three performance measures made us change plans. In the DFREML software (Meyer 1991), we fitted a number of bivariate models for all pairs of performance traits and compared them with the corresponding univariate models we had fitted in SAS Proc Mixed (Littell et al. 1996). The genetic correlations between traits in DFREML always appeared to agree with the correlations calculated between predictions of random effects in the univariate models. We therefore report correlations between the predictions of random effects from univariate models and treat them as if they were estimated correlations in a multivariate model.

The breeding design did not allow for separating out the maternal from the genetic effects (Falconer and Mackay 1997; Lynch and Walsh 1998; Mousseau and Fox 1998). In reptiles, the most obvious environmental maternal effects include feeding rate of the mother, density, and incubation temperature (e.g., Shine and Harlow 1996; Sorci and Clobert 1997). To avoid at least these factors from influencing our results, we housed and fed each female in the same way and assigned each egg from the same clutch randomly to one of the three incubation temperature treatments (see "Animals and Their Maintenance"). Moreover, in most cases, maternal effects occur through changes in juvenile body size and mass (e.g., Sinervo 1990). We accounted for potential maternal effects, through juvenile size, by summarizing the morphological variables in a principal component and including it as a predictor variable in the analyses. In doing so, we also accounted for a common underlying phenotypic effect on the different performance traits. Often two traits that are genetically correlated share a common underlying phenotype (e.g., body size in case of locomotor performance traits). In a quantitative genetic approach, it cannot be decided whether this underlying phenotype actually exists unless it is explicitly considered as a predictor (or independent) variable.

Results

Principal Component Analysis

The principal component analysis on the three morphological variables (snout-vent length, hindlimb length, mass) yielded one new variable that accounts for 98% of the morphological variation. This principal component showed high positive loadings for all three morphological variables (0.58, 0.58, and 0.57, respectively). Therefore, it can be considered a global measure for the size of an individual and is hereafter referred to as "size." We introduced it as a fixed effect into the linear mixed model for each performance measure.

Maximal Sprint Speed

Sprint speed differed significantly between juveniles incubated at 26°C and juveniles incubated at 28.5° or 31°C; juveniles from the former group were faster than juveniles from the two other temperature treatments (estimate ± SE: incubation at 26°C, 127.7 ± 6.24 cm/s; incubation at 28.5° and 31°C, 100.15 ± 6.66 cm/s; $P = 0.001$). All other fixed effects (age, population, size, and interaction effects) were nonsignificant.

Mother and individual effects were retained in the mixed model as random effects (variance and AIC difference: mother, 202.01 and -6.1; individual, 595.73 and -13.7). In other words, juveniles with the same mother resemble each other more in maximal sprint speed than juveniles with different mothers. An autoregressive error correlation structure was preferred in the model selection procedure (Littell et al. 1996). The autoregressive first order correlation equalled 0.35 (AIC difference $= -9.6$), which implies that subsequent observations on the same individuals were significantly correlated.

Maximal Clambering Speed

Clambering speed did not differ significantly among populations or ages or with size (all $P > 0.05$). Only "individual" was retained in the mixed model as a random effect (variance and

AIC difference: 440.94 and −21.0). There is no significant mother effect. Therefore, juveniles with the same mother do not resemble each other more in clambering ability than juveniles with different mothers. The error structure selection procedure preferred uncorrelated error terms.

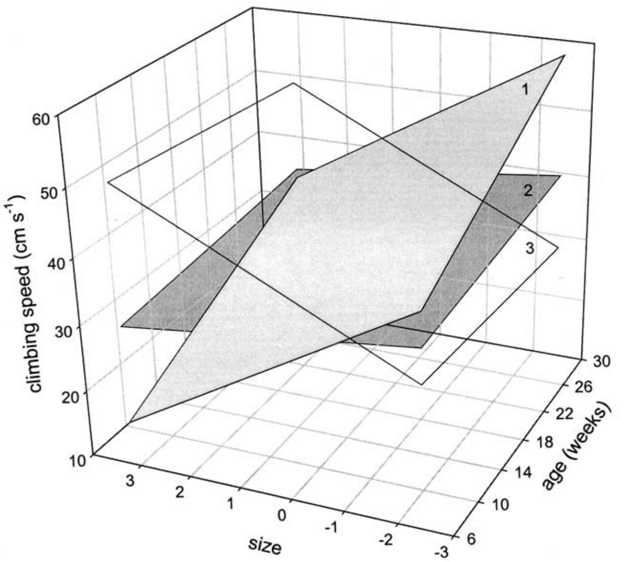

Figure 1. Three-dimensional surface plot of climbing speed against the factor scores of the first principal component (*size*) and age in the three populations of *Gallotia galloti*. Population 1 (San Isidro, *light grey*) differs from populations 2 (Las Cañada, *dark grey*) and 3 (Icod, *white*); for a given age, small, light, and short-limbed juveniles from San Isidro are the best climbers, while the opposite is true for juveniles from the two other populations.

Maximal Climbing Speed

Climbing speed differed significantly among populations; juveniles from the San Isidro population were faster at climbing than juveniles from the other two populations (estimate ± SE: San Isidro, 61.16 ± 18.44 cm/s; Las Cañadas and Icod, −25.05 ± 16.34 cm/s; $P = 0.001$). We found a significant age-population interaction effect; climbing speed increased with age in juveniles from San Isidro (estimate ± SE: 0.26 ± 0.15 cm/s), but it did not change with age in the other populations (estimate ± SE: −0.60 ± 0.25 cm/s; $P = 0.014$; Fig. 1). The size-population interaction effect was also significant; large juveniles from the San Isidro population were worse at climbing than small ones (estimate ± SE: −2.25 ± 5.44 cm/s), while the opposite was true for both other populations (estimate ± SE: 43.4 ± 11.93 cm/s; $P = 0.001$; Fig. 1).

Both mother and individual were retained in the model as random effects (variance and AIC difference: mother, 32.16 and −5.7; individual, 117.15 and −22.1). Therefore, juveniles with the same mother resemble each other more in climbing speed than juveniles with different mothers. The error structure selection procedure preferred uncorrelated error terms.

Correlations among Performance Measures

Among mothers, maximal sprint speed and maximal climbing speed are positively correlated (Pearson's correlation coefficient; $r = 0.61$, $P = 0.002$). This suggests that running and climbing are genetically correlated or depend on a strong common maternal effect in *Gallotia galloti* lizards.

Among individuals, maximal sprint speed is positively correlated with both climbing and clambering ($r = 0.61$, $P = 0.0001$; $r = 0.72$, $P = 0.0001$, respectively). The latter two are positively correlated with each other ($r = 0.72$, $P = 0.0001$). All three performance measures are thus correlated within individuals of *G. galloti*. These correlations stem from genetic correlations, common maternal effects (as supported by the presence of significant variance between mothers), or simply a persistent phenotypic individual factor that affects all performance measures in the same way.

Discussion

Unexpectedly, of the factors investigated in this study, only incubation temperature appeared to affect sprint speed. Juveniles from the low (26°C) incubation temperature regime were faster sprinters than juveniles from warmer (28.5° and 31°C) incubation treatments. Juvenile *Podarcis muralis* lizards showed the same response (Van Damme et al. 1992; Braña and Ji 2000), but the opposite effect has been found in other lizard families (e.g., scincids; Elphick and Shine 1998). During the first 30 wk of their lives, the effect of incubation temperature apparently overrides the effect of age, size, or population of origin in *Gallotia galloti* juveniles. Also, the interaction between incubation temperature and population of origin proved nonsignificant, which implies that juveniles from all three populations sprint fastest when incubated at low temperatures. This is striking considering the thermal environment differs among the three populations: San Isidro is a very dry and hot habitat, Las Cañadas lies at high altitudes where temperatures can fluctuate drastically, and Icod is cooler and more humid (see Thorpe and Baez 1987; Thorpe and Brown 1991). If these differences in environmental temperatures are reflected in the actual nest temperatures, the lack of population differentiation in incubation temperature at which juveniles with the highest sprinting abilities are produced supports the idea that the thermal physiology of lizards is evolutionarily conservative (Bogert 1949; Hertz et al. 1983; Crowley 1985*b*; Van Damme et al. 1989*a*, 1990; Autumn et al. 1994). Nest temperatures in the field, however, might not differ among the three sites if females of the three populations select the same thermal habitat in which to lay their eggs. At the moment, we cannot test this hypothesis explicitly as we do not have data on nest temperatures and/or nest selection in the field. As indicated by the nonsignificant interaction between age and incubation temperature, the differences in sprint speed among the *G. galloti* juveniles persisted until the end of the experiments, at which time the lizards were 30 wk old (cf. *Sceloporus occidentalis* and *Bassiana duperreyi* hatchlings; van Berkum et al. 1989; Elphick and Shine 1998).

Although clambering speed appeared to vary among individuals (only "individual" retained in model), none of the factors we included in the model could explain any of this variation. Clambering speed in juvenile *G. galloti* does not seem to depend on age, incubation temperature, size, or population of origin. The lack of population differentiation might indicate that the three populations do not experience different selection pressures in regard to clambering speed.

Climbing speed differed significantly among the juveniles from the three populations. Lizards from San Isidro were faster climbers than lizards from Las Cañadas and Icod, which suggests that selective pressures on climbing ability differ among populations and have caused populations to evolve in divergent ways. Moreover, the idea is substantiated by the fact that differences in climbing ability persist, and even become larger, when the juveniles grow older; climbing speed increases with age in juveniles from the San Isidro population, while it did not change in juveniles from Las Cañadas and Icod (significant age × population interaction effect). Not finding a significant age effect in juveniles from the Las Cañadas population might be due to low statistical power for this population as sample size is rather low; however, we did not find a change in climbing speed with age in juveniles from the Icod population either.

Interpopulational differences in locomotor performance have been shown to exist in other lizard species (Crowley 1985*b*; Snell et al. 1988; Huey et al. 1990; Sinervo and Losos 1991; Van Damme et al. 1997, 1998). In some studies, these differences have been linked to variation in predation pressure, prey density, or climatic factors (Crowley 1985*b*; Snell et al. 1988; Bennett and Huey 1990; Huey et al. 1990; Van Damme et al. 1998). Lizard populations with high rates of predation are often fast compared to populations with low rates of predation (Crowley 1985*b*; Snell et al. 1988; Bennett and Huey 1990; but see Huey et al. 1990). Moreover, it has been suggested that predator pressure and diversity are reduced at high altitudes (Crowley 1985*b* and references therein), and therefore lizards at Las Cañadas might not need to be fast climbers. At Icod, food might be more abundant than at San Isidro because the climate is cooler and more humid and the lizards occur on a banana plantation. In this context, climbing speed might not be determinant for the survival of the animals. At the moment, both hypotheses remain largely speculative because no quantitative data on predation pressure or prey density variation among the sampled populations are available.

For a given age, large, heavy, and long-limbed juveniles from the San Isidro population were worse at climbing than small, light, and short-limbed ones from the same population. The opposite was true for juveniles from both other populations. Biomechanical considerations predict that good climbers should be small, light animals (Hill 1950; Taylor et al. 1972; Huey and Hertz 1982; Cartmill 1985). Moreover, short limbs are beneficial when moving up steep inclines as they bring the center of gravity closer to the substrate and thereby reduce the potential to topple back (Sinervo and Losos 1991; Losos et al. 1994; Van Damme et al. 1997; Vanhooydonck and Van Damme 2001). Our data on climbing speed of juveniles from the San Isidro population substantiate these predictions, but data on climbing speed in both other populations do not. It is possible that lizards can alter their functional limb length by changing the degree of sprawling. Thus lizards with long limbs and a high degree of sprawling might be as good at climbing as lizards with short limbs (see also Van Damme et al. 1997, 1998; Vanhooydonck and Van Damme 2001).

Juveniles with the same mother resembled each other more in sprinting and climbing ability than juveniles with different mothers, which indicates that the variation in sprint speed and climbing speed is (at least partly) genetically based. This finding is consistent with results from studies on heritability of performance variation in reptiles (van Berkum and Tsuji 1987; Tsuji et al. 1989; Bennett and Huey 1990; Jayne and Bennett 1990; Brodie and Garland 1993; Garland 1994). Moreover, the population divergence in climbing speed substantiates this idea.

Our results show that among *G. galloti* individuals, all three performance measures are phenotypically correlated in a positive way. Thus fast sprinters appear to be good climbers and clamberers. This substantiates earlier findings that within the family of lacertid lizards, no trade-off exists between level and near vertical locomotion among conspecific populations (Van Damme et al. 1997) or among species (Vanhooydonck and Van Damme 2001; but see Sinervo and Losos 1991 and Macrini and Irschick 1998 on *Anolis* and *Sceloporus* lizards). Furthermore, among mothers, sprint speed and climbing speed appeared to be positively correlated. This result suggests that sprinting and climbing ability are genetically correlated, and direct selection on one of these performance measures will lead to simultaneous evolutionary changes in the same direction in both traits (cf. speed and stamina in garter snakes; Jayne and Bennett 1990; Brodie and Garland 1993; Garland 1994). A possible positive genetic correlation between sprinting and climbing ability in this case substantiates the positive phenotypic correlation and might explain why we did not find the expected relation between morphology and performance in all cases.

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