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Colin Donihue

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Abstract:
Microgeographic variation in fitness-relevant traits may be more common than previously appreciated. The fitness of many vertebrates is directly related to their locomotor capacity, a whole-organism trait integrating behavior, morphology, and physiology. Because locomotion is inextricably related to context, I hypothesized that it might vary with habitat structure in a wide-ranging lizard, Podarcis erhardii, found in the Greek Cyclade Islands. I compared lizard populations living on human-built rock walls, a novel habitat with complex vertical structure, with nearby lizard populations that are naive to human-built infrastructure and live in flat, loose-substrate habitat. I tested for differences in morphology, behavior, and performance. Lizards from built sites were larger and had significantly (and relatively) longer forelimbs and hindlimbs. The differences in hindlimb morphology were especially pronounced for distal components – the foot and longest toe. These morphologies facilitated a significant behavioral shift in jumping propensity across a rocky experimental substrate. I found no difference in maximum velocity between these populations, however females originating from wall sites potentially accelerated faster over the rocky experimental substrate. The variation between these closely neighboring populations suggests that the lizards inhabiting walls have experienced a suite of trait changes enabling them to take advantage of the novel habitat structure created by humans.

Keywords:
Introduction:

Animal locomotion integrates a suite of morphological, behavioral, and physiological attributes and impacts an individual’s fitness (Irschick and Garland 2001, Calsbeek and Irschick 2007, Irschick et al. 2008). Furthermore, locomotor behavior and performance is of necessity closely tied to an individual’s immediate ecological setting (Losos 1990, Toro et al. 2004, Kohlsdorf and Navas 2007). While traits associated with locomotion are often considered typological for a species, emerging evidence suggests that microgeographic variability in ecological context can result in considerably more intraspecific variation in fitness-relevant traits than previously appreciated (Richardson et al. 2014).

Other studies have demonstrated that the substrate and structure of a habitat are consistently related to a lizard species’ behavior, morphology, and performance (Vanhooydonck and Van Damme 2003, Calsbeek and Irschick 2007 Kohlsdorf and Navas 2007, Losos 2011). Lizards in more complex habitats tend to more often jump from branch-to-branch or rock-to-rock (Kohlsdorf and Navas 2007, Harrison et al. 2015). Additionally, jumping performance in lizards is often associated with longer hind limbs, particularly in the distal segments between the ankle and the tip of the longest toe (Moermond 1979, Losos 1990, Toro et al. 2004).

Laboratory tests of lizard locomotion typically employ a single experimental substrate. Moreover, the types of substrates used may (e.g. sand) or may not (e.g. cork or sandpaper) reflect naturally occurring substrates that have given rise to different adaptations for locomotion. Comparing lizard locomotion across multiple substrates is increasingly the focus of new studies (Tulli et al. 2012, Vanhooydonck et al. 2015), but these studies have yet to investigate performance of conspecifics living in different habitats and test predictions of associated...
morphological and behavioral differences according to those habitats.

Humans are ecosystem engineers, creating novel habitat structure across landscapes and exerting strong adaptive pressure on the organisms in those landscapes (Jones et al. 1994, Donihue and Lambert 2014). In the Greek islands, stone walls and terraces crisscross the landscape, and the eponymous Aegean Wall Lizard, *Podarcis erhardii*, can readily be found throughout (Valakos et al. 2008). However, *P. erhardii*, can also commonly be found dashing between bushes in nearby wall-less habitats with sand or loose-soil substrates. *Podarcis erhardii* living on stone walls experience a more structurally complex habitat than their conspecifics in non-wall habitats (Fig. 1). Based on other research showing that lizard traits change to accommodate new demands for locomotor performance in rocky habitats (Goodman 2007, Kohlsdorf and Navas 2007, Revell et al. 2007), I hypothesized that human alteration of the landscape should affect behavioral and morphological traits associated with locomotion. I tested for differences in jumping behavior, limb morphology, and sprinting performance between lizards living in areas with walls and areas without walls. The research demonstrates that human alteration of the environment can result in considerable microgeographic variation in important whole-organism traits such as locomotion.

**Methods:**

I collected 324 adult *P. erhardii* from 10, 50 m by 50 m sites within 15 km of each other on Naxos, a large island in the Greek Cyclade Islands. Five sites had stone walls, the other five were characterized by sandy substrate with interspersed *Juniperus oxycedrus* shrubs or a loose jumble of soil and Mediterranean phrygana (Fig. 1). All sites were selected for having a high density of lizards, and non-wall sites for being more than 200 m from the nearest built stone structure. While *P. erhardii* home range has not been investigated, sister species have reported...
home ranges no larger than 120 m² (Brown et al. 1995, Swallow et al. 1996) suggesting it is highly unlikely lizards from non-wall sites had originated on walls. For all lizards, I recorded sex and measured snout-to-vent length (SVL), and the length of each segment of the right fore and hind limb using digital calipers (Frankford Arsenal 672060).

I constructed two tracks for assessing lizard locomotion. Each track was 50 cm wide and 2 m long, with walls approximately 50 cm tall, constructed from heavy-duty plastic sheeting. One track had a sandy substrate (5 cm depth) reflecting the homefield of the five non-wall lizard populations, and the other was paved with large flagstones (averaging approximately 20 cm in diameter) from nearby walls. These flagstones were placed so each abutted the next, resulting in haphazard small (1 to 4 cm) gaps between uneven rock edges, mimicking the position and spacing of stones on top of local rock walls. The arrangement of rocks did not change through the entirety of the experiment. The track was not heated and conditions were kept consistent for all trials.

Before each trial, all lizards were allowed to thermoregulate at will for at least 30 minutes along a temperature gradient radiating from a suspended lamp (sand temperature 45C to 25C). Immediately before running the lizard, I recorded their temperature using a cloacal thermometer (Miller and Webber T6000). The sprinting temperatures selected by males and females between wall and non-wall sites did not significantly differ (Males: wall: 29.7±1.2C, non-wall: 30.3±1.9C; Females: wall: 29.3±1.2C, non-wall: 29.2±2.2C). Lizards were stationary in the same start position at the beginning of each trial. Each sprint was recorded with a video camera (Sony HDRPJ260V; 1920 x 1080 px; 50 Hz) suspended directly over the track using a tripod. The camera’s field of view encompassed the first 1.5 m of track and had a full dorsal perspective of
the running lizard. As motivation impacts sprint speed performance (Losos et al. 2002, Irschick et al. 2005), if the lizard did not seemingly run maximally I discarded their trial during analysis.

I calculated the position of the lizard frame-by-frame relative to a tape measure in the field of view using a custom-built JavaScript program (code: https://github.com/bkazev/savra).

To calculate velocity and acceleration, I fit a quintic spline to the position data (Walker 1998) with the SPAPI function in MatLab (MathWorks Inc., 2014). This spline function was then differentiated such that the maximum of the first derivative yielded maximum velocity, the second derivative, maximum acceleration. Finally, I watched each stone-substrate trial and counted the number of times the lizards jumped (body and all limbs simultaneously in the air) from rock to rock. The Yale IACUC office approved all experiments involving animals (permit: 2013-11548). All work was conducted with permission from the Greek Ministry of Environment, Energy, and Climate Change (Permit 11665/1669).

**Statistical analyses**

To test for differences in morphology between populations I used linear mixed effects models, evaluated using the LME command within the NLME (v3.1-121; 2015) package in R (v3.1.2; 2014). As the morphometric and performance traits were not normally distributed, each was Log transformation before analysis. Each morphometric was treated as a response variable with presence or absence of wall as fixed effects and with site of origin as a random effect. I tested for relative morphological differences by adding SVL as a covariate. To test for differences in performance response variables – maximum velocity and acceleration over each substrate – I again used wall presence or absence as a fixed effect and site of origin as a random effect with sprint temperature as an additional random effect. Finally, to determine whether there was a difference in propensity to jump between the wall and non-wall populations, I used the
count of jumps across the rocky experimental substrate as a fixed effect and included

temperature as a random effect. A Shapiro-Wilk test determined that jump counts were not
normally distributed (W=0.9435, P<0.0001), and so I Log_{10} transformed the jump counts for all
analyses. Whenever body size or temperature was used in a model, they were standardized to
have a mean of zero so as to make the estimates of each response variable directly interpretable
(standardized value = initial value – global mean value). In all cases, males and females were
analyzed independently to reduce interactions in the models. Finally, I used a type II ANOVA
(CAR package, v2.0-25) to calculate Wald chi-square values for the model fixed effects
and assign p-values appropriate for the unbalanced design (Langsrud 2003). Figures were made
in JMP (v11.2.0. SAS Institute Inc 2013.).

Results:

For clarity, all test statistics are related in the referenced tables. In-text, I instead present
the average trait value, plus and minus the standard error. Lizards, both males and females, from
wall sites had larger SVLs than lizards at non-wall sites (males: wall: 62.42±0.62 mm, non-wall
58.13±0.44 mm; females: wall: 59.23±0.74 mm, non-wall: 55.02±0.59 mm; Fig. 1; Table 1).
This pattern was consistent across both sexes for multiple limb measurements (Fig. 1). In
particular, the distal portions of the hindlimbs – the length between the ankle joint and the tip of
the longest toe, and the longest toe itself – were relatively (standardized by SVL) longer among
wall populations (Table 1). All together, lizards living on walls had proportionally longer hind
limbs than lizards in non-wall habitats (Fig. 2a, Table 1).

I found no difference in maximum velocity among lizards from either habitat of origin
across either experimental substrate (male maximum velocity on rock: wall: 1.99±0.45m/s, non-
wall 1.98±0.6m/s; female maximum velocity on rock: wall: 1.83±0.44m/s, non-wall
male maximum velocity on sand: wall: 1.98±0.6m/s, non-wall: 1.82±0.42m/s;
female maximum velocity on sand: wall: 1.73±0.47m/s, non-wall 1.67±0.34m/s; Table 2). While I found no difference in either population’s acceleration capacity over sand (see Table 2), I found that females from wall sites accelerated over the rocky experimental substrate faster than lizards from non-wall sites (Fig 2b, Table 2).

In contrast to other studies, I found that individual SVL was not a significant predictor of maximum velocity or acceleration across either substrate for either sex (Supplemental Table 1). Similarly, hindlimb length and the length of the longest toe did not significantly explain variation in sprinting performance (Supplemental Table 1).

Both males and females from wall populations exhibited a strong behavioral shift: the lizards accustomed to walls consistently traversed the rocky experimental substrate by jumping rock-to-rock (see supplemental video files 1 and 2). Non-wall lizards jumped significantly fewer times crossing the same experimental track (males: wall: 3.4±1.2 jumps, non-wall: 2.5±1.2 jumps; females: wall: 3.4±1.2 jumps, non-wall: 2.0±1.1 jumps; Table 2, Fig. 2c). Differences in jumping propensity were not explained by SVL (Table 3), however jump counts were significantly informed by the length of the distal components of the hind limbs (male longest toe: \( p=0.0181 \); female longest toe: \( p=0.0108 \); Table 3).

Discussion:

I found consistent differences between close-proximity populations of *P. erhardii* inhabiting different habitat-structure contexts. Lizards originating on sites with walls were larger than lizards from non-wall sites. Furthermore, the absolute length of each component of the hind limbs, and the relative length of the hindlimb as a whole was proportionally larger among wall
populations of both sexes (Fig. 2a). The difference in relative hindlimb length was driven by proportional differences in the foot and longest toe of wall-inhabiting lizards (Table 1).

Morphological differences between lizard populations sometimes result in local, habitat-specific performance advantages (e.g. limb length determining motility across branches of different diameters in Anolis; Calsbeek and Irschick 2007, Losos 2011). Long limbs in Lacertids are in some species an adaptation for fast sprints over loose substrates (Bauwens et al. 1995, Bonine and Garland Jr. 1999). However, I found no inter-population differences in sprinting ability across sand. Alternatively, long hind limbs are also associated with jumping capacity and propensity (Moermond 1979, Losos 1990, Toro et al. 2004), particularly in rocky habitats (Goodman 2007, Kohlsdorf and Navas 2007, Revell et al. 2007). Indeed, I found that lizards from wall sites (with longest hind limbs) jump 1.5 times more often than non-wall populations on the same experimental track (Fig. 2c; supplemental video files 1 and 2). While there was no difference in the maximum sprint velocity of either population across either substrate, I found that females from rock wall populations accelerated more quickly than those from the non-wall habitats over the rocky experimental substrate (Fig. 2b).

Motivation will considerably affect measurements of an animal’s performance in laboratory conditions (Losos et al. 2002, Irschick et al. 2005). For that reason, many trials on relatively fewer individuals may provide clearer insights into maximal ability; however, even these results should be interpreted with caution (Losos et al. 2002, Irschick et al. 2005). Due to logistical constraints, repeated trials were not possible for this study, and accordingly the high variation in performance obscured the trends predicted for the observed morphological differences between populations. Additionally, others have demonstrated that slow video frame rates are prone to errors in estimating acceleration of fast-moving animals (Walker 1998). A 50
Hz camera was the maximum speed available for this field study, and, although my calculated
values (Table 4) are commensurate with published values for closely related species
(Vanhooydonck et al. 2015), further work with high-speed cameras (exceeding 250 Hz) and
repeated trials will be necessary to show whether and how these observed morphological
differences translate to performance differences.

Few studies investigate relative lizard locomotion capacity over multiple experimental
substrates (Vanhooydonck et al. 2015). Studies that have, did not find that species racing on an
experimental substrate similar to their characteristic natural habitat necessarily performed better
(Tulli et al. 2012, Vanhooydonck et al. 2015). This study suggests one potential explanation: the
intraspecific differences observed here are commensurate with some published interspecific
comparisons (Tulli et al. 2012, Vanhooydonck et al. 2015), meaning that variation among source
populations could change the interpretation of interspecific comparisons. This study
demonstrates that locomotor behavior and performance is contingent on the structure and
ecology of source populations and not necessarily typological for a species.

Intraspecific context-dependence in locomotion morphometrics have been demonstrated
between physically isolated populations (e.g. island vs mainland; Van Damme et al. 1998), and
populations inhabiting dramatically different natural contexts (e.g. Des Roches et al. 2014).
Coordinated intraspecific changes in locomotion behavior, morphology, and performance are
strong indications that selection acts holistically on these traits across ecological contexts (Miles
et al. 2001, Calsbeek and Irschick 2007, Gifford et al. 2008). The differences related here in
lizard morphology and jumping behavior over small spatial scales are noteworthy, and
demonstrate the significant potential effect of anthropogenic microhabitat alteration on an
important whole-organism trait, locomotion.
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Figure 1: The island of Naxos in the Greek Cyclades and representative pictures of the sites with and without walls. I found significant differences in the body size (SVL) and hindlimb morphology of males (bold blue) and females (light red) from wall (top) and non-wall (bottom) sites. Total limb length was calculated from the sum of component parts, see Table 1 for segment-by-segment comparisons between the populations. Mean and standard error are presented for each measurement along with the p-value of the size-corrected LME model (see Table 1).

Figure 2: Lizards from wall sites had proportionally longer hindlimbs, relative to SVL (a). These longer hindlimbs corresponded to significantly faster accelerations among females over a rocky experimental substrate (b), and to significantly increased jumping propensity for both males and females (c). Shaded regions in (a) reflect 95% confidence intervals and standard error bars have been added for (b) and (c). All comparisons with (*) are significant p<0.05.
Figure 1:

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Figure 2: (a) Total log length (mm) of females and males as a function of SVL (mm). (b) Max acceleration over rock (m/s²) for non-wall and wall substrates for females and males. (c) Number of jumps for non-wall and wall substrates for females and males.
Table 1: Results of the linear mixed effects models comparing morphological measurements between wall and non-wall lizard populations. After SVL was shown to differ between sites, relative differences in morphology, that is, morphology standardized by SVL was tested. All morphometrics were Log10 transformed to meet assumptions of normality. A (*) denotes significance at the p<0.05 level.

| Morphometric: | Model: | ~ Wall | Site | ~ Wall + SVL | Site |
|---------------|--------|--------|------|-------------|------|
| SVL           | Males  |        |      | Females     |      |
| N             | X^2    | DF     | p    | N           | X^2  |
| 175           | 9.017  | 1      | 0.0027 * | 149         | 4.343 |
| Hip to knee   |        |        |      |             |      |
| N             | X^2    | DF     | p    |             |      |
| 175           | 0.473  | 1      | 0.4918 | 149         | 1.018 |
| Knee to ankle |        |        |      |             |      |
| N             | X^2    | DF     | p    |             |      |
| 175           | 0.066  | 1      | 0.7974 | 149         | 3.512 |
| Ankle to tip of toe | | | | | |
| N             | X^2    | DF     | p    |             |      |
| 175           | 5.226  | 1      | 0.0223 * | 149         | 9.016 |
| Longest toe   |        |        |      |             |      |
| N             | X^2    | DF     | p    |             |      |
| 175           | 5.774  | 1      | 0.0163 * | 149         | 19.701 |
| Total leg length |        |        |      |             |      |
| N             | X^2    | DF     | p    |             |      |
| 175           | 9.717  | 1      | 0.0018 * | 149         | 15.446 |

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Table 2: Linear mixed effects models comparing performance and behavior between wall and non-wall lizard populations. All performance and behavior metrics were Log10 transformed to meet assumptions of normality. A (*) denotes significance at the p<0.05 level.

| Performance metric     | ~ Wall + SVL | Site + SprintTemp | Males | Females |
|------------------------|--------------|-------------------|-------|---------|
| Max velocity rock      |              |                   |       |         |
| Max acceleration rock  |              |                   |       |         |
| Max velocity sand      |              |                   |       |         |
| Max acceleration sand  |              |                   |       |         |
| Jumps                  |              |                   |       |         |

|          | N  | X^2 | DF | p     | N  | X^2 | DF | p     |
|----------|----|-----|----|-------|----|-----|----|-------|
| Max velocity rock      | 171| 0.966  | 1  | 0.3256 | 143| 1.577 | 1  | 0.2092 |
| Max acceleration rock  | 170| 1.587  | 1  | 0.2078 | 143| 7.024 | 1  | 0.0080 *|
| Max velocity sand      | 166| 0.070  | 1  | 0.7915 | 142| 0.389 | 1  | 0.5329 |
| Max acceleration sand  | 165| 0.203  | 1  | 0.6526 | 141| 0.128 | 1  | 0.7202 |
| Jumps                 | 172| 3.810  | 1  | 0.0481 * | 145| 6.643 | 1  | 0.0099 *|
Table 3: Results of regressions between three morphological variables and the count of jumps across the rocky substrate. All variables were Log10 transformed to fit the assumption of normality. A (*) denotes significance at the p<0.05 level.

|                          | Males  | Females |
|--------------------------|--------|---------|
| SVL                      | 0.2573 | 0.1557  |
| $R^2$ Adj               | 0.0017 | 0.0073  |
| Length of longest toe    | 0.0181 | 0.0108 *|
| $R^2$ Adj               | 0.027  | 0.0389  |
| Total hindlimb length    | 0.1182 | 0.0031  |
| $R^2$ Adj               | 0.0085 | 0.0543  |
Table 4: Average and standard deviation of the performance of lizards from wall and non-wall sites.

|                  | Males                        | Females                      |
|------------------|------------------------------|------------------------------|
|                  | Wall | No Wall | Wall | No Wall |
| Velocity Rock (m/s) | 1.99 ± 0.45 | 1.91 ± 0.47 | 1.83 ± 0.44 | 1.76 ± 0.31 |
| Acceleration Rock (m/s/s) | 88.57 ± 29.87 | 79.84 ± 26.89 | 84.05 ± 28.67 | 73.32 ± 21.78 |
| Velocity Sand (m/s) | 1.98 ± 0.60 | 1.82 ± 0.42 | 1.73 ± 0.47 | 1.67 ± 0.34 |
| Acceleration Sand (m/s/s) | 87.88 ± 38.68 | 81.00 ± 30.60 | 77.82 ± 29.49 | 77.73 ± 35.55 |