

RESEARCH ARTICLE

Include the females: morphology–performance relationships vary between sexes in lizards

Alyssa Head^{1,2,*}, Princeton L. Vaughn³, Ethan H. Livingston¹, Cece Colwell¹, Martha M. Muñoz⁴ and Eric J. Gangloff¹

ABSTRACT

An animal's morphology influences its ability to perform essential tasks, such as locomoting to obtain prey or escape predators. While morphology–performance relationships are well-studied in lizards, most conclusions have been based only on male study subjects, leaving unanswered questions about females. Sex-specific differences are important to understand because females carry the bulk of the physiological demands of reproduction. Consequently, their health and survival can determine the fate of the population as a whole. To address this knowledge gap, we sampled introduced populations of common wall lizards (*Podarcis muralis*) in Ohio, USA. We measured a complete suite of limb and body dimensions of both males and females, and we measured sprint speeds while following straight and curved paths on different substrates. Using a multivariate statistical approach, we identified that body dimensions relative to snout-to-vent length in males were much larger compared with females and that body dimensions of *P. muralis* have changed over time in both sexes. We found that sprint speed along curved paths increased with relative limb size in both males and females. When following straight paths, male speed similarly increased as body dimensions increased; conversely, female speed decreased as body dimensions increased. Female sprint speed was also found to have less variation than that of males and was less affected by changes in body size and hindfoot length compared with males. This study thus provides insights into how selective pressures might shape males and females differently and the functional implications of sexual dimorphism.

KEY WORDS: Morphology, Multivariate analyses, *Podarcis muralis*, Sexual dimorphism, Sprint performance, Urbanization

INTRODUCTION

The morphology of an organism influences where it can live, how well it can navigate its surroundings, its ability to find and consume food and its reproductive success (Arnold, 1983; Irschick, 2002). The morphology–performance–fitness paradigm, as established by Arnold (1983), provides a framework for mapping variation in morphology to organismal performance which, in turn, affects an animal's fitness (Arnold, 1983; Irschick et al., 2008). This paradigm


was later expanded by Garland and Losos (1994) to include additional factors such as behavior, which acts as a link between performance and fitness; interspecific interactions, which affect behavior; and habitat structure which affects morphology, performance and behavior. The utility of this framework is evidenced by the fact that it persists in allowing researchers to evoke novel questions some 40 years after its inception. In particular, the application of Arnold's (1983) framework has provided a foundational understanding of morphology–performance relationships in squamate reptiles; however, the majority of this work has excluded females (e.g. Grizante et al., 2010; McElroy and Reilly, 2009; Vaughn et al., 2021, 2023; Brown et al., 1995b; Irschick and Jayne, 1999; Winchell et al., 2018; Battles et al., 2019; Losos, 1990b; Bergmann and Hare Drubka, 2015; McGlothlin et al., 2018). This lack of research on females has led to a substantial gap in our understanding of morphology–performance relationships, especially considering the large number of sexually dimorphic squamates (e.g. Butler et al., 2000; Cruz-Elizalde et al., 2020; Van Damme et al., 2008; Sacchi et al., 2015; Rubolini et al., 2006; Olsson et al., 2002; Olson and Madsen, 1995).

Studies addressing dimorphism between males and females indicate that investigating these differences in the context of the relationship between morphology and performance is essential for representing a complete scientific narrative (Lailvaux et al., 2019; Lowie et al., 2019; Sparkman et al., 2018; Simon et al., 2022; Butler, 2007). For instance, work with *Anolis carolinensis* demonstrates sex-specific ecological demands that shape morphology–performance relationships (Simon et al., 2022). In the same species, Lailvaux et al. (2019) found a negative correlation between sprint and bite performance in only females. Additionally, across 14 species of *Anolis*, variation in femur length was important in determining sprint speed for both males and females, while tibia length was important only for males (Lowie et al., 2019). Females are typically the limiting factor in reproduction and a population only grows if there are enough females capable of becoming gravid. Therefore, females are key to population establishment and persistence (Fargevieille et al., 2022; Roff, 1992). As a result, understanding how morphological traits affect female performance – and by extension fitness – is especially important (Vitt and Caldwell, 2013).

Previous research in lizards has shown that urban environments may result in altered limb dimensions (Winchell et al., 2018; Putman et al., 2019; Gómez-Benitez et al., 2021; Putman and Tippie, 2020) or changes in body length (Baxter-Gilbert et al., 2021; Putman and Tippie, 2020). A recent study of *Anolis cristatellus* demonstrated evidence of the genetic basis for morphological evolution that is beneficial in urban populations, but potentially deleterious in nonurban environments (Winchell et al., 2017). These urbanization-related morphological changes are likely to affect the performance capabilities of organisms *sensu* the

¹Department of Biological Sciences, Ohio Wesleyan University, Delaware, OH 43015, USA. ²Department of Evolutionary Biology, San Diego State University, San Diego, CA 92182, USA. ³Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. ⁴Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA.

*Author for correspondence (ahead5435@sdsu.edu)

 A.H., 0009-0007-1307-2483; P.L.V., 0000-0002-3744-4233; E.H.L., 0009-0008-1661-3086; M.M.M., 0000-0001-8297-2396; E.J.G., 0000-0002-9074-8009

morphology–performance–fitness paradigm (Arnold, 1983; Battles et al., 2019; Irschick, 2002; Winchell et al., 2018). For example, in an urban environment, female western fence lizards (*Sceloporus occidentalis*) had shorter femurs and slower sprint speeds compared with their counterparts in a nonurban environment, potentially because of decreased selective pressure from predation in the urban environment (Sparkman et al., 2018).

Introduced populations of the common wall lizard (*Podarcis muralis* Laurenti 1768) located in Ohio, USA are noteworthy because lizards have successfully established in urban environments and continue to expand despite being founded by a small number of individuals (Deichsel and Gist, 2001; Davis et al., 2021; Homan, 2013; N. Lescano, C. Homan and K. Petren, unpublished). Despite experiencing a genetic bottleneck owing to such a small founder population, wall lizards in Ohio possess sufficient genetic variation to maintain color polymorphisms (Amer et al., 2023). Research on males from these populations demonstrated that contemporary animals differ in body morphology compared with historical specimens collected several decades earlier, including smaller heads and some aspects of the limb being smaller (Vaughn et al., 2021); however, claw shape has not changed (Vaughn et al., 2023). Up to this point, there has not been an investigation into the sexually dimorphic trends in these introduced Ohio populations.

Podarcis muralis is a sexually dimorphic species (Sacchi et al., 2015; Žagar et al., 2012; Ljubisavljević et al., 2010; Rubolini et al., 2006). While many studies have concluded that males have bigger heads and limbs (Ljubisavljević et al., 2010; Žagar et al., 2017), results regarding overall body size, as quantified by snout–vent length (SVL), have been inconsistent, with males being the larger sex in some studies (Sacchi et al., 2023; Eroğlu et al., 2018) and females in others (Žagar et al., 2012). In an introduced population in Canada, there was no evidence of sexual dimorphism (Allan et al., 2006; Gullo et al., 2024). These studies were conducted using specimens from areas exhibiting diverse structural habitats (native range: islands along the Tuscan Archipelago, Slovenia, and Turkey; introduced populations: Vancouver Island, Canada, respectively), possibly contributing to the observed patterns of sexual dimorphism or lack thereof. Dimorphic shifts in limb and body size in newly established populations suggest that males and females may experience different selective pressures or evolutionary constraints in these new environments (Phillips et al., 2024).

In this study, we began our investigation by comparing morphology between male and female *P. muralis* to test for sexual dimorphism in introduced urban populations in Columbus and Cincinnati, Ohio, USA. Building on previous work done by Vaughn et al. (2021), we quantified body dimensions of females from both current populations and museum specimens. Furthermore, we tested whether morphology impacts sprinting performance similarly between sexes. With this study, we include both males and females to demonstrate the utility of testing whether morphology–performance relationships differ between sexes.

We hypothesized that females and males in current Ohio populations of *P. muralis* would differ in all relative body dimensions. We further hypothesized that there would be changes in morphology over time, and these changes would be similar in both males and females, as both sexes have faced similar selective pressures from this urban environment that may impact relative body dimensions. We predicted that females would be able to sprint just as fast as males, if sprint speed was selected for by predation pressure (Garland and Losos, 1994; Miles, 2004; Irschick et al., 2008). We also anticipated that females would have less variation in running speeds because of strong selection for absolute sprint speed

to compensate for the constraints on locomotion caused by egg-bearing and reproduction (Shine, 2003). Reduced sprint speed due to both mechanical constraints and energetic trade-offs inherent in reproduction make females even more vulnerable to predation (Schwarzkopf and Shine, 1992; Van Damme et al., 1989). Owing to an extended reproductive season, including multiple clutches, this period of impeded locomotion extends across much of the active season (Le Henaff et al., 2013). While males surely exhibit tradeoffs and behavioral compensation, the negative impact of gravidity on performance is unique to females. Additionally, while specific behaviors such as increased hiding may reduce the vulnerability of female lizards during this period of impeded performance, the ability to locomote is still necessary to navigate their surroundings, their ability to find and consume food, and their reproductive success. As such, a better understanding of how the differences between male and female morphology affect performance ability can contribute to a more complete vision of the morphology–performance–fitness paradigm as a whole and specifically provide insight into the success of introduced or urban populations (Sparkman et al., 2018; Lailvaux et al., 2019; Simon et al., 2022).

MATERIALS AND METHODS

Study species and field methods

Podarcis muralis is a small lacertid lizard and is considered a climbing specialist that lives in the cracks and interstices of stone walls, building remnants and around houses, allowing them to thrive in urban areas (Brown et al., 1995a,b). Originally distributed across much of southern Europe (Speybroeck et al., 2016), *P. muralis* has become a successful global invader with populations in England (Michaelides et al., 2015), Germany (Heym et al., 2013; Beninde et al., 2018), and multiple sites in North America including British Columbia, Canada and various areas in southern Ohio, USA (Engelstoft et al., 2020; Hedeon, 1984; Brown et al., 1995a,b). The species was introduced to Cincinnati in the 1950s, and it has since spread to much of the surrounding areas (Davis et al., 2021).

We caught adult lizards (SVL > 50 mm) from sites in Cincinnati and Columbus, Ohio, USA using the lasso method (Blomberg and Shine, 2006) or by hand (see Table S1 for specific locations and sampling dates). We measured morphology on lizards from Cincinnati populations in the field (see below) and then released them at the point of capture. Lizards from the Columbus population were transported back to the laboratory and we measured morphology within a day of arrival. In all populations, females were identified by their slimmer heads, thinner tail base, reduced femoral pores and absence of hemipenes. The Columbus population represents a recent range expansion in the state (approximately one generation difference), with founding individuals originating from Cincinnati populations and demonstrating no discernible genomic differentiation (E. R. Bode, H. L. Gibbs, K. Petren, E. J. Gangloff and A. J. Mason, unpublished data).

Animals were housed in small groups (2 to 5 animals) in plastic tubs (60 cm × 42 cm × 34 cm) with a wood shaving substrate, water dish, and two plastic structures that served as basking platforms and hides for the animals. Males and females were kept in separate tubs. Ambient light was provided for 14 h day⁻¹ and ultraviolet light for 12 h day⁻¹ (Reptisun 10.0 Fluorescent UVB Lamp, Zoo Med Laboratories, San Luis Obispo, California, USA). An incandescent heat bulb (DuraMax Indoor Flood R20, 45 W, Philips, Somerset, New Jersey, USA) provided a temperature gradient within tubs of approximately 20–45°C for 8 h day⁻¹ in 1–2 h intervals. Lizards were fed mealworms (*Tenebrio* spp. larvae) or crickets (*Acheta domesticus*) dusted with calcium and vitamin powder three times a

week. Enclosures were misted 3–4 times a week and water was provided in a small dish *ad libitum*. Husbandry conditions were identical to those used in Vaughn et al. (2021).

Before performance measurement tests, lizards were fasted for 48 h to ensure a post-absorptive state (Van Damme et al., 1991; Angilletta, 2001). We conducted performance measures once a week on individual animals. All research was conducted under Ohio Division of Wildlife Wild Animal Permit (23-014) and all procedures were approved by Ohio Wesleyan University Institutional Animal Care and Use Committee (2020-21-04).

Field performance

To quantify structural habitat use and performance on different substrates in the field, we performed opportunistic sampling of active adult lizards at six sites in Cincinnati, Ohio, USA from 7 June to 6 August 2021. After spotting a lizard, we approached the animal slowly while video recording (Sony DCR-SX40 at 29.97 frames s^{-1} or Panasonic AG-AC30 at 23.98 frames s^{-1}) until the animal fled to shelter. Using a tape measure, we then re-traced the route of the animal, recording the substrate and distance traveled for each distinct movement segment. We classified substrates into one of three categories: stone, including anthropogenic stone or asphalt structures; grass, including short natural vegetation and manicured lawns; and other, which included a variety of natural vegetation or anthropogenic debris (e.g. wooden planks, street signs). Because animals were recorded until they reached shelter, we did not capture lizards and are thus unable to include measurements of size or body temperature as covariates in analysis. All field observations were made during active hours during conditions favorable to lizard activity (air temperature range: 24.5–34.0°C). By moving to new locations in our sample area after each observation, we ensured that we did not observe the same animal more than once. Using Solomon Coder software (<https://solomoncoder.com>), we analyzed our video recordings to extract the time to traverse each segment and then calculated velocity.

Morphological measurements

We measured morphology on wild-caught animals ($N=38$ females, $N=16$ males; see Table S1 for sampling details) and we measured morphology on historically collected female specimens ($N=22$; see Table S2 for details) that were preserved in an aqueous solution of ethanol. Historical specimens, collected from 1981 to 2012 in the greater Cincinnati area, were provided by the Cincinnati Museum Center. Given the time to maturity of this species (Davis et al., 2021), this represents up to 20 generations between sample collection and the present day.

We performed all morphological measurements with a set of digital calipers (model CD-6, Mitutoyo, Japan) with precision to the nearest 0.01 mm. We measured snout–vent length (SVL) from the tip of the snout to the posterior end of the anal scale. Head length (HL) was measured from the tip of the snout to the posterior end of the parietal scales. The fourth toe (longest toe on each foot) was measured from the base of the toe to the tip of the claw. Metatarsus length was measured from the proximal end of the metatarsus at the wrist/ankle joint to the base of the fourth toe. The zeugopodium was measured from the elbow/knee joint to the distal end of the zeugopodium at the wrist/ankle joint. The stylopodium was measured from the axilla to the distal end of the stylopodium at the elbow/knee joint. Scapular girdle width (SG) was measured immediately posterior to the forelimb insertion on the dorsal side. Pelvic girdle width (PG) was measured immediately anterior to the hind limb insertion on the dorsal side. Morphology measures followed the same procedure as Vaughn et al. (2021) and were

conducted by the same researcher (E.J.G.). Each appendage measure was taken on both the left and right sides of the animal for each limb. We also included measures of tail length, defined as the distance from the cloaca to the tip of the tail, noting when tails were original growth or regenerated. We performed each measurement twice and re-measured if the coefficient of variation of the two measures was $>10\%$. We averaged the two measures for subsequent analyses. In the case of animals missing toes ($N=9$ historical specimens, $N=25$ wild-caught specimens), we used the toe on the opposite side as the average toe length value for that individual.

In addition to data on these individuals, we utilized previously published morphology data collected on male lizards ($N=53$ field-caught animals, $N=15$ historical specimens; Vaughn et al., 2021, 2023), excluding two individuals from the Vaughn et al. (2021) dataset because of insufficient SVL (<50 mm). We characterized the morphological phenotype with eight dimensions: four that were measured directly (shoulder girdle width, pelvic girdle width, head length and tail length) and four that were combined measurements (forelimb length, forefoot length, hindlimb length and hindfoot length). Forelimb and hindlimb lengths were calculated by taking the average of the right anterior/posterior limb (stylopodium length+zeugopodium length) and the left anterior/posterior limb. Forefoot and hindfoot lengths were calculated by taking the average of the right anterior/posterior foot (metatarsus length+fourth toe length) and the left anterior/posterior foot following the same calculations as used in Vaughn et al. (2021). To scale these measures to body size, we created a \log_{10} – \log_{10} regression of each measure on SVL and utilized the residual value for downstream analyses (Kaliontzopoulou et al., 2007; Muñoz and Losos, 2018; Vaughn et al., 2021).

Sprint performance

We quantified the sprint performance of adult female lizards from a single population ($N=14$) following identical protocols to Vaughn et al. (2021) (excluding trials on inclines). Lizards were considered eligible for performance experimentation if they possessed an original tail or a regrown tail of a similar length to that of an original tail. Female lizards were in captivity for 113–184 days before sprinting trials (performed 9 September to 12 October 2022), ensuring that sprinting was performed outside the reproductive season, as previous studies have shown a reduction of sprint speed in gravid lizards (Shine, 2003; Bauwens et al., 1995; Garland Jr, 1985; Seigel et al., 1987). An hour before testing began, lizards were placed in an incubator set to 36°C, which approximates the optimal temperature for sprint performance (Telemeco et al., 2022; Vaughn et al., 2021).

Our racetrack design – specifically the choice of substrate and the use of obstacles – is intended to provide a standardized laboratory proxy for variation in structural habitat utilized by lizards (Battles et al., 2019; Winchell et al., 2018; Tulli et al., 2012). Such environmental variation is theorized to influence morphology, performance and behavior in the expanded morphology–performance–fitness paradigm *sensu* Garland and Losos (1994). Lizards were raced on three substrates that mimic ecologically relevant surfaces (cork, sandpaper and turf) on a 2 m racetrack outfitted with photocells (Trackmate Racing, Surrey, British Columbia, Canada) 2 cm above the track at intervals of 25 cm along the track, as in Vaughn et al. (2021). Specifically, lizards are most often found on stone or artificial asphalt substrates, for which sandpaper acts as a proxy. Lizards also move through grass and short vegetation, for which turf is a proxy. Furthermore, we have

observed lizards moving on fallen logs and woody debris, for which cork acts as a proxy. Lizards were raced on each substrate both with and without obstacles (a total of six trials per individual), as the results of previous studies on sprinting performance have revealed that the inclusion of obstacles causes dramatic shifts in performance capability (Wynn et al., 2015; Parker and Mcbrayer, 2016; Higham et al., 2001; Adams and Gifford, 2020). The obstacles were eight polyvinyl chloride pipes (10.2 cm diameter) with cardboard attachments to prevent the animals from going over or behind them. They were placed along the racetrack at intervals of 25 cm. The obstacles forced the lizards to move in a sinuous (curved) path, approximating how they move in the wild, whereas without obstacles, the lizards ran in a straight path. The sprinting conditions for each lizard (i.e. substrate and straight or curved path), as well as the order in which animals were sprinted, were randomly selected daily.

Each individual ran three times per trial in rapid succession (generally in <60 s) to ensure maximum locomotor performance was achieved. While lizards under these conditions do decrease in body temperature (lizards in separate trials decreased on average 2.00°C, Table S5), repeated sprinting trials ensure that maximum performance is obtained: in our trials, 30% (25 of 84) maximum burst speeds were recorded in the third run. All performance measures were carried out during active daylight hours (09:30 h–14:30 h). We then extracted the fastest speed over an interval of 25 cm, which is within the natural range of *P. muralis* observed field movements (Braña, 2003; Monasterio et al., 2009), including in our study populations. Near the end of our experiment, the health of two individuals quickly degraded. Sprint data collected from those two individuals were removed from analysis. Our analysis also includes male sprinting data originally presented in Vaughn et al. (2021), which were collected on the same track under identical conditions. We re-analyzed the raw data from this experiment, extracting the fastest 25 cm interval of sprint speed for each individual under each condition (the original study utilized the fastest 50 cm interval for analysis), again excluding two individuals with SVL<50 mm. We would like to note the caveat that logistical constraints necessitated sprinting males and females in different seasons. To our knowledge seasonal variation in sprint speed in lizards has not been documented. To confirm that time in captivity did not affect sprint performance, we re-ran a subset of females ($N=6$) in May 2023 under two of our test conditions (straight and curved paths on turf). Sprint speed did not differ between the two time periods (paired t -test: $t_{11}=0.97$, $P=0.35$; Table S5).

Statistical methods

We processed data and conducted all statistical analyses in the R Programming Language (R version 4.2.1; <https://cran.r-project.org/bin/windows/base/old/4.2.1/>). With our field observations, we tested for variation in structural habitat use with a chi-square test and for the effect of substrate on sprint speed with a linear mixed model, including \log_{10} -transformed sprint speed as the dependent variable, a single categorical predictor of substrate type, and the random effect of individual to account for measurements made on the same individual as it traversed the different segments of its run. The model met the assumption of normal distribution of residuals and we assessed the significance of substrate type using an F -test, with denominator degrees of freedom corrected with the Kenward–Roger method (Kenward and Roger, 1997).

We described the morphology of lizards using eight measured characters (see above). We used a nonparametric multivariate analysis of variance (NP-MANOVA) with residual randomization

in a permutation procedure (RRPP), a statistical framework which allows a simultaneous decomposition of morphological variation into orthogonal axes of variation and comparison among groups (Collyer and Adams, 2018; Collyer et al., 2015). The RRPP approach performs well when there is a high ratio of measured traits to sample size and further provides a unified framework to simultaneously describe patterns of within-individual correlation of traits (via PC analysis) and test hypotheses of differences among groups (Collyer et al., 2015; Telemeco and Gangloff, 2020). To include six female historical specimens with either missing or partially regenerated tails in our morphological analyses, we used multiple linear regression to impute the missing tail length values (as described in Telemeco and Gangloff, 2020). We standardized each dependent variable in the PC analysis (here, size-scaled morphological measurements) to mean of 0 and standard deviation of 1 for analysis.

We first tested for differences between male and female morphology using only the individuals for which we had sprint data and then for all contemporary animals. These models included only the two-level factor of sex as a fixed effect. We then conducted an analysis including all historical and contemporary males and females for which we measured morphology. We tested for differences among four groups (contemporary females, historically collected females, contemporary males, and historically collected males) using a model that included a single four-level factor. For all models, we implemented 999 iterations of the residual randomization procedure, assessed differences among groups with F -tests, and implemented pairwise comparisons of least-squares means. We then extracted the fitted values in PC space for each individual and estimated least-squares means and 95% confidence intervals for predicted values for each trait for each group.

We then tested for differences in burst sprint speed due to sprint conditions (six substrate and path combinations, see above), sex and morphology. We included data from females that were sprinted as part of this experiment as described above ($N=14$) and re-analyzed raw data from previously measured males [$N=24$ from Vaughn et al. (2021)] to extract the fastest sprint speed over a 25 cm interval, so that our sprinting data are comparable to other lizard studies (e.g. Lailvaux et al., 2022). We then used the fitted PC values for each individual from the RRPP model that included only contemporary animals for which we had sprint data (see above). These values describe morphological differences between females and males. In this analysis, data are rotated such that PC1 maximally separates the two groups in multivariate space. These values thus describe a morphological continuum on a scale of ‘female–male’ and best serve as a continuous explanatory variable in the model of sprint speed to test our hypothesis of interest (see below).

We implemented mixed linear models with the lme4 package (<https://github.com/lme4/lme4/>; Bates et al., 2015) to test for the influences of sprint conditions, morphology and sex on sprint speed. Our dependent variable was the maximum sprint speed measured for each individual on each of the six substrate–path combinations ($N=228$ observations on $N=42$ lizards). We first created a model with only the fixed effect of sex and a random effect for individual to test for differences between the sexes overall. We then created more complex models including categorical fixed effects of substrate type (cork/sandpaper/turf) and path type (curved/straight), as well as the linear predictors of SVL and the PC1 score describing morphology for each individual lizard (see above). The initial model included the four-way interaction term and all lower-ordered interactions among four predictors. We did not

include the factor of sex in the model because PC1 and sex are directly confounded: as sex provides a categorical distinction between females and males, and PC1 describes an individual's morphology on a scale of female-typical to male-typical with no overlap between males and females in PC1 score (Fig. S1). Given the possibility of multiple factors interacting, we think this approach is the most appropriate in identifying factors influencing sprint speed.

We then utilized a backward-selection procedure and sequentially removed unimportant interactions from the model (all $P > 0.09$), beginning with the highest-order interactions one at a time and re-running the model. The only interaction term retained in the final model was that between PC1 for morphology and the path type. We included a random intercept for individual to account for covariation of repeated measures made on the same individual. Sprint speed was \log_{10} -transformed before analysis to meet the assumption of normally distributed model residuals, which we assessed by viewing a histogram of residuals and performing a Shapiro–Wilks normality test ($P = 0.42$ in final model). The importance of fixed effects was assessed using type III sums of squares, correcting denominator degrees of freedom for F -tests (Kenward and Roger, 1997).

To further explore how variation in sprint speed might be related to variation in morphology, and how this relationship may vary between females and males, we used F -tests to assess differences in variance between sexes in sprint speed, SVL and the eight body dimensions. The variation among hindfoot lengths (defined as length of metatarsus+fourth toe, as above) was significantly different between sexes, along with the variation in shoulder girdle width and pelvic girdle width. However, hindfoot length was the only character of those significantly different measurements where females exhibited less variation than males, following the same pattern of variation as sprint speed. Because of this and the recognized importance of relative foot and toe length in lizard locomotion (Fieler and Jayne, 1998; Irschick and Jayne, 1999; Braña, 2003; Higham and Jayne, 2004; Sparkman et al., 2018; Putman et al., 2019; Donihue, 2016), we further assessed the importance of hindfoot length on sprint performance (\log_{10} -transformed) with a linear mixed model. This model was structured similarly to the above model, including the fixed effects of substrate type, path type, sex and SVL, in addition to hindfoot length. The initial model included the five-way interaction of these terms, and we employed a backward selection process as above to reduce the model to include only important interactions. We included individual as a random effect, assessed the importance of fixed effects with F -tests, and tested model residuals as above (Shapiro–Wilks normality test $P = 0.81$ in final model). We ran similar linear mixed models including the fixed effect of each of the collected measurements, and hindfoot length was the only measurement that both significantly influenced sprint speed and significantly differed in variance between sexes. We created all data figures with *ggplot2* (Wickham, 2016) and *persp3D* (<https://rdr.io/cran/plot3D/man/persp3D.html>) packages.

RESULTS

In the field, we observed 42 movement segments from 36 individual animals. Lizards traveled a median distance of 0.47 m to shelter (mean±s.d.: 1.30±2.19 m). They utilized stone substrate in 81.0% of observed movement segments, more than grass (7.1%) and other substrates (11.9%; $\chi^2 = 43$, $P < 0.0001$). Median speed per segment was 0.48 m s⁻¹ (mean±s.d.: 1.07±1.38 m s⁻¹) and did not vary among substrates ($F_{2, 12.7} = 0.732$, $P = 0.500$).

Of the sprinted lizards, the females tended to be slightly larger than males (mean female SVL 3.2 mm larger; $t_{34.8} = 2.00$, $P = 0.053$). Our multivariate analysis demonstrates a clear distinction in body morphology between the sexes when including just sprinted lizards ($F_{1,36} = 45.7$, $P = 0.001$) and all contemporary lizards ($F_{1,105} = 108.6$, $P = 0.001$), with males exhibiting larger size relative to SVL in all dimensions except tail length (Fig. 1, Fig. S1). The first axis of variation between sexes explains >99% of variation in both analyses (Table S3). The positive loadings for all measured body parts (except for tail length) signify that as the PC1 value increases, there is an increase in the relative size of all body parts (PC scores associated with data shown in Fig. 1 and Fig. S1 can be found in Table S3), with the strongest loading being that of head length. Because males are described by larger PC1 values, all measurements included in this PC analysis excluding tail length are larger in male individuals.

Using data from all individuals, including historical specimens, there was no difference in SVL between sexes ($t_{106.9} = -0.60$, $P = 0.55$). The results of our multivariate models demonstrate clear differences in morphology among male and female historical and contemporary specimens ($F_{3,136} = 54.8$, $P = 0.001$), with significant differences in all pairwise comparisons between groups (all $P < 0.01$; Table 1).

In our analysis of all individuals, the first two axes of variation describe differences among groups and account for over 95% of variation (PC1: 89.17%, PC2: 6.70%; Table S4). As in the PC analysis of contemporary lizards, PC1 loads positively for all body dimensions except tail length, creating a clear separation of male and female lizards (Fig. 2A). Contemporary and historical specimens are partitioned on PC2, such that historical specimens have higher scores. On PC2, loadings for pelvic girdle width, hindfoot length and forefoot length were positive indicating that they have decreased in size over time in both males and females. Tail length, hindlimb length and forelimb length loaded negatively on PC2, indicating that those traits have increased over time in both males and females (Table S4).

Without accounting for other factors, females sprint on average 26% faster than males (comparison of least-squares means: 1.25 versus 0.93 m s⁻¹; $F_{1,36} = 4.24$, $P = 0.047$; Fig. 3). More complex models demonstrate that lizards sprinted fastest on the cork substrate and were slowest on sandpaper. Furthermore, lizards were slower sprinting in a curved path than in a straight path (Table 2, Fig. 4). When there are obstacles present causing lizards to run in curved paths, there is a positive relationship between body dimensions ('Morphology PC1' loadings are described in Table S3) and sprint speed, indicating that for both females and males, individuals with longer limbs and wider girdles run faster. When running following straight paths, males follow this same trend, but females follow the inverse: individuals with smaller body dimensions (lower scores on Morphology PC1) run faster (Fig. 5).

Maximum sprint speed is more variable in males than in females (Table 3). Of the measurements with significant differences in variance between sexes, females exhibit more variation in their pelvic girdle width and shoulder girdle width, while males exhibit more variation in their hindfoot length.

When lizards are sprinting on straight paths, body size (SVL) positively impacted performance in males more strongly than in females (Table 4, Fig. 6). SVL has a minimal effect on sprint speed of the females with the smallest hindfoot lengths. As hindfoot length increases in size, the more impact SVL has on the maximum speed. When sprinting on curved paths, the slowest individuals of both sexes had the largest hindfoot lengths and small SVLs.

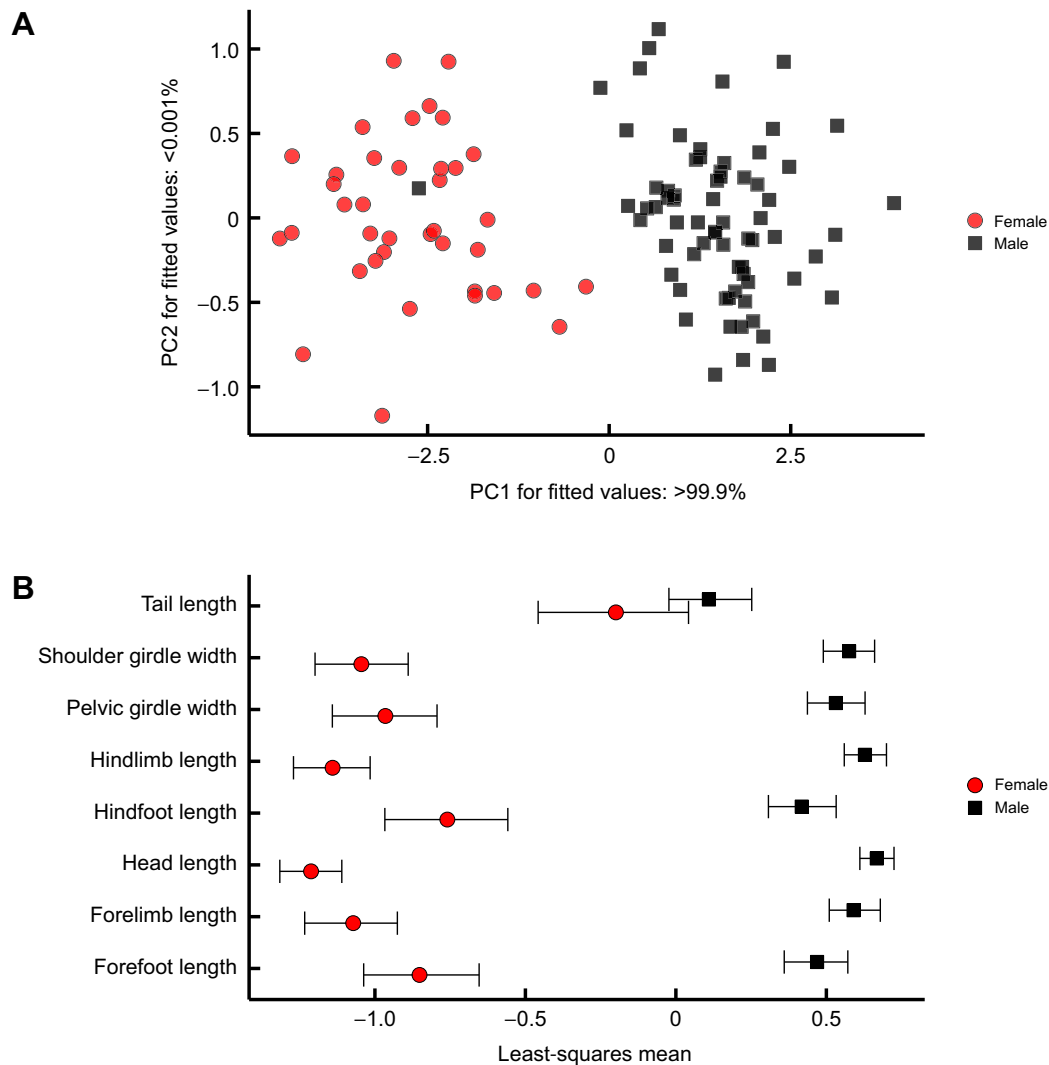


Fig. 1. Morphological traits related to sex in common wall lizards (*Podarcis muralis*) from established populations in Ohio, USA. (A) Principal component (PC) scores displaying the morphological phenotype of contemporary male and contemporary female lizards. See main text for statistical details. (B) Least-squares means and 95% confidence intervals of predicted values for body size-scaled and standardized morphological traits. Values were generated using a non-parametric multivariate analysis of variance (NP-MANOVA) with randomized residuals in a permutation procedure (see main text for statistical details). $N=38$ females, $N=69$ males.

Because males have the largest hindfoot lengths, this combination (clownfeet: large hindfoot, small SVL) is present exclusively in males (Fig. 6B).

DISCUSSION

In this study, we characterized patterns of sexual dimorphism in introduced populations of the common wall lizard (*P. muralis*) in Ohio, USA. We observed that absolute size (SVL) did not differ

between sexes, but, relative to body size, males had larger limbs, feet, pelvic and shoulder girdles, and heads compared with females, as demonstrated by a clear separation of these groups on the first axis of variation in the PCA analysis (Fig. 1, Fig. S1, Table 3). We further tracked how these traits have shifted over time in both sexes by comparing preserved museum specimens to contemporary individuals. Patterns of sexual dimorphism persisted since their original introduction to Ohio, even as

Table 1. Pairwise comparisons of estimated least-squares means among sex and time combinations of common wall lizards (*Podarcis muralis*) from established populations in Ohio, USA

Comparison	d	95% Upper confidence limit	Z	$Pr>d$
Contemporary females: contemporary males	3.99	0.95	5.33	0.001**
Contemporary females: historical females	1.72	1.32	2.38	0.010**
Contemporary females: historical males	5.18	1.40	5.22	0.001**
Contemporary males: historical females	3.64	1.23	4.47	0.001**
Contemporary males: historical males	1.93	1.34	2.63	0.003**
Museum females: historical males	4.67	1.62	4.75	0.001**

d , distance between means in multivariate space (effect size of difference). Significant differences are shown in bold (** $P\leq 0.01$).

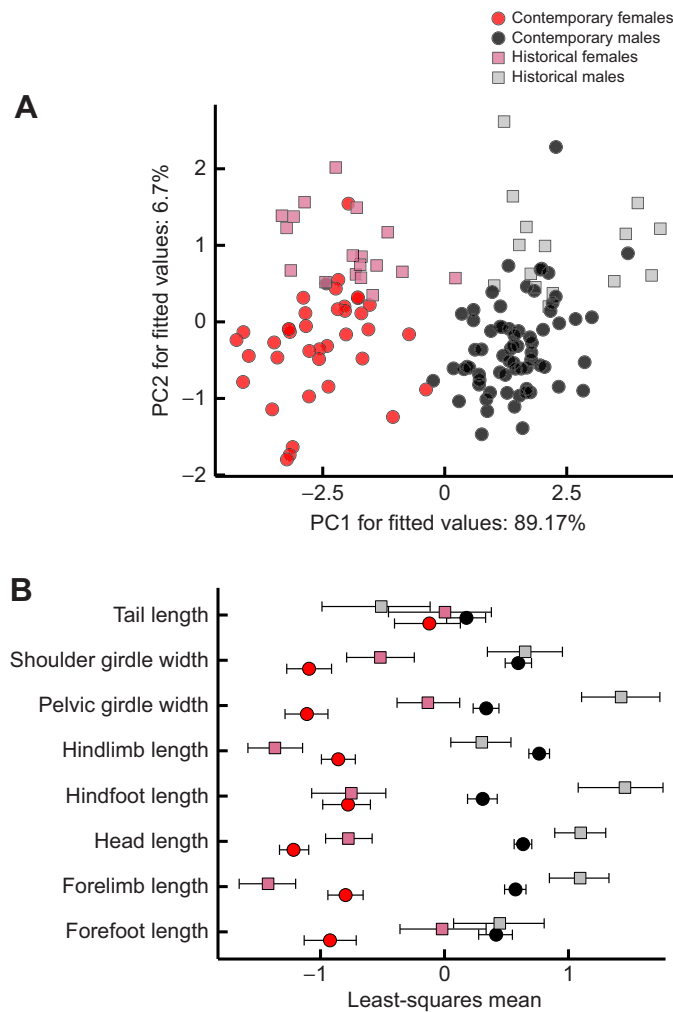


Fig. 2. Morphological traits in contemporary and historical populations of common wall lizards. (A) Principal component (PC) scores displaying the morphological phenotype of historical female, historical male, contemporary female and contemporary male lizards. See main text for statistical details. (B) Least-squares means and 95% confidence intervals for predicted values of body size-scaled and standardized morphological traits. $N=18$ historical females, $N=38$ contemporary females, $N=69$ contemporary males, $N=15$ historical males.

certain traits have shifted over the last approximately 20 generations (lizards now have smaller pelvic girdles and hindfeet, but larger hind- and forelimbs). Our results reveal opposing patterns in the influence of the size of body dimensions on sprinting speed between sexes. When following straight paths, males with larger body dimensions run faster, whereas females with smaller body dimensions are faster. We also found that sprint speed is more affected by changes in SVL and hindfoot length in males as compared with females. These findings highlight the importance of including females in studies relating morphology to performance as causal relationships established in male lizards may not be true for females. For instance, the often-assumed idea that longer limbs provide faster sprinting has been shown in males in a variety of studies (Bauwens et al., 1995; Goodman et al., 2008; Winchell et al., 2018), but this trend was not followed in the females we studied. The few other studies which have included females also found differences in how morphology predicts performance (Lowie et al., 2019).

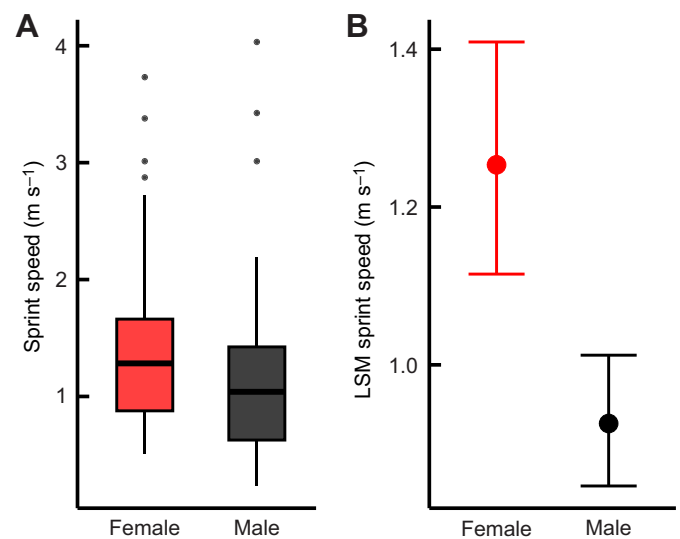


Fig. 3. Relationship between sprint speed and sex in common wall lizards. (A) Boxplot detailing the relationship between maximum sprint speed and sex. Tukey boxplots show median, interquartile range, and the limits of $1.5\times$ interquartile range. Without accounting for other factors, females sprint on average 26% faster than males. (B) Plot of the least-squares means (\pm s.e.) of sprint speed by sex (comparison of least-squares means: 1.25 versus 0.93 m s^{-1} ; $F_{1,36}=4.24$, $P=0.047$). $N=14$ females, $N=24$ males.

We confirmed that male *P. muralis* in established populations have larger head lengths and longer limbs compared with females, consistent with *P. muralis* in their native range (Ljubisavljević et al., 2010; Žagar et al., 2017). Results regarding sexual dimorphism in overall body size, as measured by SVL, have been inconsistent among studies (Sacchi et al., 2023; Žagar et al., 2012). Our study showed that while SVL and tail length do not differ between males and females, males were larger in all other body dimensions relative to body size. This could be due to trunk length (distance between limb joints) being longer in females than in males. While we did not measure trunk length for the individuals used in this study, we have collected these data from animals in the same populations and confirmed that females do have longer relative trunk length (mean trunk length females: 33.2 mm, mean trunk length males: 31.9 mm; $t_{159,6}=2.47$, $P=0.014$; our unpublished data). This difference in body proportions (males with larger heads, females with longer trunks) explains the similarities in overall body size despite the increased length in head size in males.

It is important to note that our analysis of sexual dimorphism includes a few outliers (Figs 1, 2A). Some individuals that were identified as males, owing to the presence of hemipenes, did not have the other male-typical morphological characteristics; in terms of limb length, shoulder girdle width and pelvic girdle width: they were similar to females. Many factors can lead to limb length variation, both during embryonic development and after; therefore, variation in limb length can be influenced by many different pathways, not just those contributing to sex differences (Cordero et al., 2021). We think that it would be counter-productive to dismiss these points as mere outliers and they could well carry biological significance. As scientific understanding of the limits of the binary sex framework expands, it is relevant to note that although secondary sex characteristics, such as these trends in body dimensions, are expected to be sexually dimorphic, there are many exceptions (McLaughlin et al., 2023). For example, in side-blotched

Table 2. Results of linear mixed model analysis of the effects of substrate, path type, snout–vent length and morphology PC1 on sprint speed

Source of variation	Estimate±s.e.	Test statistic [<i>F</i> (d.f. _n ,d.f. _d)]	<i>P</i> -value
Substrate		6.83 (2,186)	0.001**
Sandpaper	−0.0745±0.0203		
Turf	−0.0309±0.0203		
Path type (curved path)	−0.129±0.0165	60.8 (1,186)	<0.0001**
Snout–vent length (SVL)	0.0223±0.00488	21.0 (1,35)	<0.001**
Morphology PC1	−0.0177±0.0120	0.660 (1,35)	0.422
Obstacle×morphology PC1	0.0168±0.00728	5.29 (1,186)	0.0226*

Significant differences are shown in bold (**P*<0.05; ***P*<0.01). See text for model details (*N*=14 females; *N*=24 males). d.f._n, numerator degrees of freedom; d.f._d, denominator degrees of freedom.

lizards (*Uta stansburiana*), males with female-typical morphology utilize a ‘sneaker’ strategy where they impersonate females in order to avoid male–male competition and increase mating opportunities (Sinervo and Lively, 1996). It is possible that the female-like morphology in individuals with otherwise male-typical anatomy use a similar strategy in our study populations.

Previous work in these populations have noted that contemporary male lizards have wider shoulder girdles, and historical male lizards had wider pelvic girdles and a longer head, hindfoot length and forelimb length (Vaughn et al., 2021). Our current results identify similar, but not identical, shifts in morphology over time and demonstrate that female morphology has also changed over time. We found that contemporary specimens exhibit larger hind- and forelimb lengths, as well as smaller pelvic girdle width and hind- and forefoot length, compared with historical specimens (Table S4). The comparable progression of either shortening or lengthening of these body dimensions in both males and females over generations could be a result of similar directional selection on these traits in both sexes. This would mean that a longer hindlimb length has been more advantageous for both male and female survival in their new environment. As described by Lowie et al. (2019), in many male and female *Anolis* lizards, overall limb length has been shown to drive variation in sprint speed, with femur length, specifically, being a principal driver of maximal speed. Our results show that in other aspects of morphology, traits have shifted in different trajectories between sexes.

When running in curved paths, both males and females with larger relative body dimensions (as encapsulated in PC1 for

morphology) ran faster (Fig. 5). In contrast, when there were no obstacles present, allowing lizards to run in a straight path, females followed an inverse trend (individuals with larger body dimensions being slower) while males continued to run faster when they had larger relative body dimensions. Previous studies have concluded that in a variety of *Anolis* lizards, longer limbs consistently translate into faster sprint speed, but notably, these studies only used male lizards in their experiments (Losos and Sinervo, 1989; Losos, 1990a,b; Winchell et al., 2018). The fact that females follow a different morphology–performance trend than males could show that selective pressures have favored compensatory sexually dimorphic kinematic strategies. In other words, males and females differ in how body size and shape contribute to performance, suggesting they utilize their bodies differently to achieve similar maximum sprinting performance.

Importantly, when accounting for overall differences in body dimensions between sexes, we found no direct interaction between substrate and the type of path (Table 2), indicating that running a circuitous route had a similar effect on absolute sprint speed regardless of habitat selection. However, in our analysis focusing on the importance of hindfoot length, the clearly sexually dimorphic measure of hindfoot length, substrate and path type all interacted to impact sprint speed (Table 4). This suggests a potential role for selection in shaping limb morphology depending on habitat occupied, as previously demonstrated for variation in claw shape (Vaughn et al., 2023). Our field observations demonstrate that adult lizards extensively use stone and asphalt human-made structures. While sprint speeds measured in the field were generally

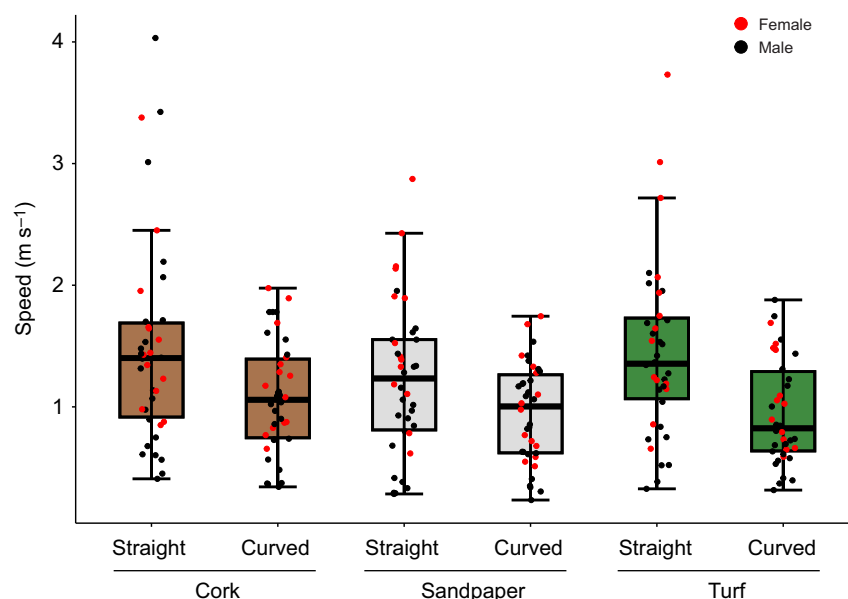
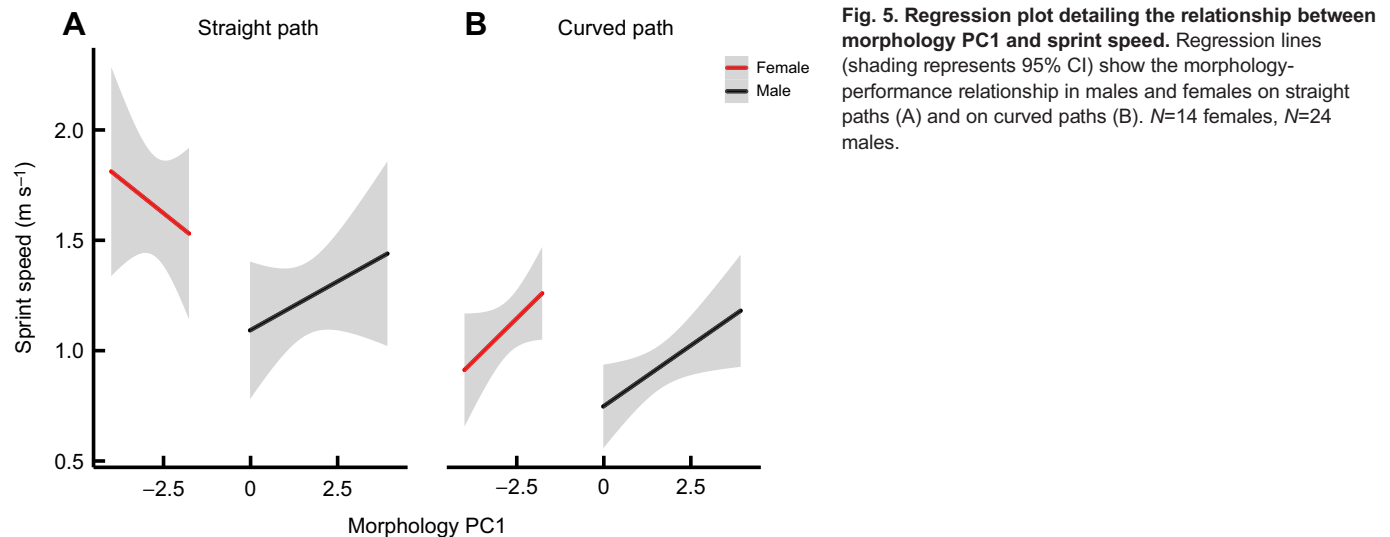


Fig. 4. Boxplots and raw values of sprint speed across all conditions in adult female and male common wall lizards. Tukey boxplots show median, interquartile range and 1.5× interquartile range of raw data values. *N*=14 females, *N*=24 males.



commensurate with those measured in the controlled experiments, lizards exhibited great variance in distance traveled and speed. We attribute this variation to the variety of extrinsic factors (e.g. habitat structure, temperature) and intrinsic factors (e.g. motivation, physiological status) that can affect sprint performance (Wilson et al., 2015; Husak, 2006; Schulte et al., 2004). We further note that juveniles are often found in grass and areas of short vegetation (our pers. obs.), thus suggesting an important avenue for future research examining shifts in habitat selection and performance across ontogeny.

Morphology affects performance because of how the morphology of the body is engaged by the organism to produce motion, understood through the study of kinematics. For example, a lizard with shorter limbs but a longer trunk, as we observe in female *P. muralis* in our study populations, might curve their bodies while running (i.e. increase lateral undulations of the vertebral column) to increase their stride length. Furthermore, morphology-performance relationships and the effectiveness of kinematic strategies are impacted by the organism's behavior and the environment in which it lives, as described in Garland and Losos's (1994) expanded morphology-performance-fitness paradigm. Therefore, a change in environment might necessitate a corresponding alteration in kinematic strategies used and, eventually, a change in morphology. It could be possible that the changes in morphology in both males and females that happened over time in these populations could be a result of selection due to urban environments in Cincinnati where there is a prevalence of human-made asphalt and stone structures. This change in morphology over time could also be

due to the loss of alleles in the population as a result of drift following a genetic bottleneck that occurred in their establishment. Furthermore, these changes in morphology over time could have resulted in differing kinematic strategies between native populations in Italy and this introduced population in Cincinnati. A useful next step would be to test the hypothesis that shifts in kinematic strategies, such as in stride lengths or body curvature, accompany shifts in morphology across environmental gradients and differ between sexes.

At the outset of this research project, we assumed that male and female morphology-performance relationships would be similar, if not the same, based upon a preconceived framework built using data from only male organisms to draw broad conclusions (Arnold, 1983; Ah-King, 2022). However, because females are gravid throughout much of the active season (Le Henanff et al., 2013; Kwiat and Gist, 1987), and given the unique physical changes that females undergo while gravid, it would make sense to assume that the major impediment that gravidity poses on female sprinting performance (Shine, 2003) would cause different selective pressures to act upon them compared with males. This could lead to changes in performance and kinematic strategies between sexes to compensate. If the morphology-performance-fitness paradigm is accepted, and morphology affects performance, then it would follow that sexually dimorphic traits would lead to unique movement strategies between sexes to achieve similar performance abilities (Arnold, 1983; Garland and Losos, 1994; Irschick et al., 2008). We think it is important to restate the question originally posed by Butler (2007): 'Why have so many researchers assumed

Table 3. F-test comparison of variance between measurements of male and female common wall lizards

Sex variance comparison	F	d.f. _n	d.f. _d	P-value	Male variance	Female variance
Max. sprint speed	0.587	83	143	0.009**	0.0624	0.0366
Snout-vent length	1.31	55	83	0.263	25.638	33.592
Tail length	1.144	55	83	0.572	0.011	0.0125
Shoulder girdle width	1.716	55	83	0.0256*	0.0011	0.0019
Pelvic girdle width	1.711	55	83	0.0264*	0.0012	0.0021
Head length	0.937	55	83	0.807	0.000266	0.000249
Hindlimb length	1.062	55	83	0.793	0.000388	0.000413
Hindfoot length	0.276	55	83	<0.00001***	0.0021	0.00059
Forelimb length	0.763	55	83	0.287	0.000494	0.000377
Forefoot length	1.423	55	83	0.145	0.00065	0.000921

Significant differences are shown in bold with one ($P<0.05$), two ($P<0.01$), or three ($P<0.001$) asterisks. $N=14$ females; $N=24$ males.

Table 4. Results of linear mixed model analysis investigating the interaction between substrate type, path type, sex, SVL and hindfoot measurement of common wall lizards

Source of variation	Estimate±s.e.	Test statistic [<i>F</i> (d.f. _n ,d.f. _d)]	<i>P</i> -value
Substrate		7.27 (2,176)	0.0009***
Sandpaper	−0.0898±0.0278		
Turf	−0.00861±0.0278		
Sex (male)	0.3879±1.139	0.513 (1,32)	0.479
Path type (curved path)	1.46±0.528	1.33 (1,176)	0.250
Snout–vent length (SVL)	0.0235±0.0132	7.65 (1,32)	0.009**
Hindfoot length	−1.080±0.784	0.357 (1,32)	0.554
Substrate×path type		1.851 (2,176)	0.160
Sandpaper×curved path	0.0306±0.0393		
Turf×curved path	−0.0445±0.0393		
Substrate×hindfoot length		0.4856 (2,176)	0.616
Sandpaper×hindfoot:	−0.0415±0.0281		
Turf×hindfoot	−0.0240±0.0281		
Path type×hindfoot length	1.28±0.474	7.30 (1,176)	0.00758**
Path type×SVL	−0.0243±0.00797	2.688 (1,176)	0.103
SVL×hindfoot length	0.0159±0.0117	0.341 (1,32)	0.563
Path type×sex	−2.33±0.688	11.485 (1,176)	0.0009***
SVL×sex	−0.00673±0.0173	0.462 (1,32)	0.502
Path type×SVL×hindfoot length	−0.0188±0.00707	7.05 (1,176)	0.00866**
Substrate×path type×hindfoot length		3.29 (2,176)	0.0396*
Sandpaper×curved path×hindfoot	0.0458±0.0398		
Turf×curved path×hindfoot	−0.0561±0.0398		
Path type×SVL×sex	0.0359±0.0104	11.818 (1,176)	0.000732***

Hindfoot measurements were scaled to a mean of 0 and unit variance. Significant differences are shown in bold (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). $N = 14$ females; $N = 24$ males.

that the performance and kinematic strategies utilized by sexually dimorphic species are the same?.

In addition, females were more consistent than males in sprint speed across different substrates and path shapes. This agrees with Kaliontzopoulou et al. (2013), who found that changes in path conditions affected *Podarcis bocagei* males alone. Lailvaux et al. (2019) suggest that within-session variability in male performance, or lack thereof in females, could be a function of larger variation in the size of males relative to females. In contrast to this study, which found that female *A. carolinensis* exhibited more variance in SVL than males (Lailvaux et al., 2019), female *P. muralis* in our study did not exhibit this greater variance in SVL. Females had less variance in

head length, tail length and shoulder girdle width when scaled to body size, while males had more variance in hindfoot length when scaled to body size (Table 3). This implies, following the suggestion of Lailvaux et al. (2019), that the larger variance in hindfoot length in males could cause their inconsistent running speeds across varying terrains and conditions. In other words, the larger variance in hindfoot length causes the larger variation in sprint speed. The hindfoot in climbing-specialized species, such as *P. muralis*, tends to have larger lateral displacement (i.e. their posture is more sprawled) when running on level surfaces as compared with running specialists such as Bosc's fringe-toed lizard, *Acanthodactylus boskianus* (Druelle et al., 2019). The larger lateral displacement of the hindfoot that

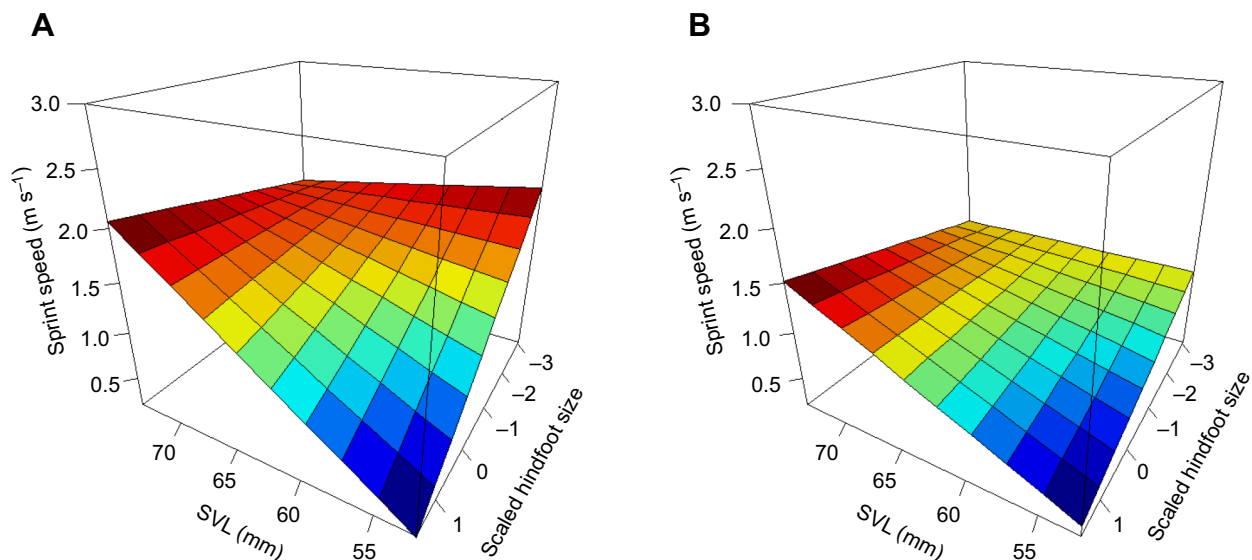


Fig. 6. Relationship among snout–vent length (SVL), hindfoot length and sprint speed. 3D surface plot detailing the relationship among SVL, hindfoot length and sprint speed when sprinting on a straight path (A) and on a curved path (B). $N = 14$ females, $N = 24$ males.

occurs when running on level surfaces could explain the larger impact that hindfoot size has on sprinting velocity overall.

The results of our study led us to believe that sexually dimorphic kinematics might play an essential role in explaining the similarities in sprint performance despite the morphological variation that exists between sexes. A fruitful research avenue would be to perform a more in-depth kinematic analysis that compares differences in the mechanics of motion between sexes. Currently, many kinematic analyses in reptiles that are focused on sprinting do not address potential differences between sexes (Russell and Bels, 2001; Fieler and Jayne, 1998; Higham and Jayne, 2004; Clemente et al., 2012; Reilly and Delancey, 1997; Foster and Higham, 2014). Some work has been done identifying movement differences between sexes in birds, providing insight into sexually dimorphic kinematic strategies. For example, Rose et al. (2015) found differences in gait utilization between males and females in leghorn chickens (*Gallus gallus domesticus*). We are directing future work to test these hypotheses in wall lizards.

This study confirmed the presence of sexually dimorphic body size and shape in introduced populations of *P. muralis* in Ohio, USA. Furthermore, we observed morphological changes over several decades of establishment in a new environment in female *P. muralis*, similar to that in males (Vaughn et al., 2021). In the context of invasion biology, females exhibited less variation in their sprinting speed, suggesting that this trait is under selective pressure, more so in females than in males. By selection acting on females during periods when they are gravid, and thus slower and more likely to be predated, selection may have shaped their morphology to provide residual positive effects on performance and thus fitness during non-gravid periods. Our analysis of morphology–performance relationships shows that male and female performance is dictated by different morphological characteristics. We encourage more researchers to include female specimens in their studies to obtain a more complete scientific narrative regarding morphology–performance relationships.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.A.H., P.L.V., E.J.G.; Methodology: A.A.H., P.L.V., M.M.M., E.J.G.; Formal analysis: A.A.H., E.J.G.; Investigation: A.A.H., P.L.V., E.H.L., C.C., M.M.M., E.J.G.; Data curation: A.A.H.; Writing - original draft: A.A.H.; Writing - review & editing: A.A.H., P.L.V., E.H.L., C.C., M.M.M., E.J.G.; Visualization: A.A.H., E.J.G.; Supervision: E.J.G.; Project administration: E.J.G.; Funding acquisition: E.J.G.

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Data availability

Data and analysis code from this paper are available from the Dryad digital repository (Head et al., 2024): <https://doi.org/10.5061/dryad.xgxd254r7>

ECR Spotlight

This article has an associated ECR Spotlight interview with Alyssa Head.

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