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SYMPOSIUM

Sex-specific Morphological Shifts Across Space and Time in Replicate Urban Wall Lizard Introductions

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Synopsis As species move into new environments through founder events, their phenotypes may diverge from native populations. Identifying the drivers underlying such variation, and the constraints on the adaptive potential of this variation, is essential for understanding how organisms respond to new or rapidly changing habitats. Such phenotypic divergence may be especially evident in populations introduced to new environments via human-assisted transport or populations in dramatically altered environments such as cities. Sexually dimorphic species beg the additional questions of how these new environments may influence sexes differently and how dimorphism may shape the range of potential responses. The repeated translocation, establishment, and spread of wall lizards (*Podarcis* spp.) from native European populations to new locations in North America provide an excellent natural experiment to explore how phenotypes may differ after establishment in a new environment. Here, we quantify body shape and the multivariate morphological phenotype (incorporating limb dimensions and head length) of common wall lizards (*P. muralis*) and Italian wall lizards (*P. siculus*) in replicated North American introductions. In both species, males are larger and have larger head length and limb dimensions than females across all sampled groups. Sexual dimorphism in the multivariate morphological phenotype was of similar magnitude when comparing native and introduced populations for both species, though the trajectory angles in multivariate trait space differed in *P. siculus*. When comparing introduced lizards from contemporary and historically collected museum specimens, we identified differences of similar magnitude but in different trajectories between sexes in *P. siculus*, and differences in both magnitude and direction of sexual dimorphism in *P. muralis*. These idiosyncratic patterns in phenotypic trajectories provide insight to the potential array of processes generating phenotypic variation within species at the intersection of invasion biology and urban evolution.

Introduction

A fundamental question in biology is how the phenotype of an organism relates to its environment (Lande and Arnold 1983). Correlations between trait values and axes of environmental variation suggest adaptive evolution (Endler 1986; Schluter 2000; Merilä and Hendry 2014). Biological invasions present opportunities for organisms to respond to a dramatically new environment on a short time scale (Herrel et al. 2008; Stern and Lee 2020; Sherpa et al. 2023; Sabolić et al. 2024). Moreover, human activity, especially transportation networks, may facilitate the introduction of species to new locations outside their original range (Hufbauer et al. 2012). Urban environments may represent a unique

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stage for such introductions, given that homogenization of urban environments may facilitate the repeated establishment of urban-adapted organisms into new cities (McKinney 2006; Groffman et al. 2014). As such, species with a proclivity for establishing in both urban environments and environments beyond their original range offer useful systems to assess the mechanisms of phenotypic responses, covariation among traits involved in a response, and patterns of trait trajectories across both space and time (Borden and Flory 2021). For example, urban-associated changes in habitat structure can exert directional selection on morphological traits important for locomotion (Winchell et al. 2020), producing clear patterns of morphological trait variation both within (Donihue 2016; Winchell et al. 2018; Putman et al. 2019; Winchell et al. 2023a) and across species (Falvey et al. 2020).

Replicated introductions of ecologically similar species can be leveraged as useful unintentional natural experiments for studying phenotypic evolution. Species that can establish in myriad environments may possess inherent flexibility (or generalizability), and by studying these species, we can gain insight into which species may succeed or fail as their environments rapidly shift. Many lizards are prolific urban dwellers and are some of the most widely introduced vertebrates globally via trade and human-aided transportation to major cities (Rödder et al. 2008; Capinha et al. 2017; French et al. 2018). Wall lizards in the genus *Podarcis* have established in a wide range of urban and human-altered habitats (Donihue 2016; Beninde et al. 2018; Gherghel and Tedrow 2019; Vaughn et al. 2021; Haro et al. 2023). Consisting of approximately 27 species, this clade of lacertids is found across southern Europe, south into Africa, and east into Asia, with species exhibiting complex distributions that result from individual movement, landscape changes over geological times (Yang et al. 2022), hybridization (Beninde et al. 2018; Yang et al. 2021), and human-mediated transport (Michaelides et al. 2013; Santos et al. 2019; Kowalik et al. 2024). Many wall lizard species have occupied a landscape that has been transformed by humans for millennia, from ancient stone walls and buildings to large modern urban centers (Podnar et al. 2005; Salvi et al. 2013; Yang et al. 2022). This affinity for human-altered landscapes has likely facilitated the establishment of new populations outside the original range, including northern and eastern Europe (e.g., Schulte et al. 2012; While et al. 2015; Kolenda et al. 2020; Oskyrko et al. 2020; Kowalik et al. 2024) and in North America (Deichsel et al. 2010; Mendyk and Adragna 2014; Hollingsworth and Thomson 2016; Engelstoft et al. 2020; Davis et al. 2021; Friestad et al. 2023). These repeated introductions, sometimes with known source populations and propagule size, offer rich opportunities for replicate studies of trait shifts between source and established populations.

Importantly, responses to new or changing environments are not uniform within a species. For example, sexual dimorphism may be the cause or consequence of selection for different types of performance between the sexes. The fitness consequences of morphological variation are well-established under the ecomorphological paradigm and its extensions (Arnold 1983; Garland and Losos 1994), and such morphology-performance relationships can differ between sexes (e.g., Simon et al. 2022). For example, male wall lizards generally have larger heads and accompanying jaw musculature compared to females (Ljubisavljević et al. 2010; Kaliontzopoulou et al. 2012; Donihue et al. 2016), which is important for intrasexual competition and mate acquisition (Braña 1996; Scharf and Meiri 2013). Females typically exhibit larger relative trunk sizes to accommodate embryo development (Braña 1996; Kaliontzopoulou et al. 2008). While such cases offer relatively intuitive explanations of trait differences, morphological traits may differ between the sexes despite performance outcomes being important for fitness in both sexes (Kaliontzopoulou et al. 2012). For example, females and males can achieve similar locomotor performance—important for predator avoidance and food acquisition—through different morphological pathways (Van Damme et al. 2008; Simon et al. 2022; Head et al. 2024). Notably, the patterns of sexual dimorphism in *Podarcis* differ among species and contexts. For example, in some populations of the common wall lizard (*P. muralis*), females are larger in body size (Žagar et al. 2012), in others males are larger (Sacchi et al. 2023), and in others there is no difference between the sexes (Gullo et al. 2024; Head et al. 2024). Further, females and males may exhibit different morphological trends associated with gradients of environmental variation (Perry et al. 2024). Variation in these patterns across space suggests that morphological lability, including between sexes, may contribute to the success of *Podarcis* spp. in novel habitats. As such, comparisons of phenotypic trajectories between female and male animals can inform sex-specific predictions about the underlying pathways that produce potential adaptive phenotypic variation.

In this study, we examine the multivariate morphological trajectories of growing and expanding introduced populations of two species of wall lizards in North America, the common wall lizard (*P. muralis*) and the Italian wall lizard (*P. siculus*). We assess how these trajectories between females and males differ to understand how sexual dimorphism shapes responses to new environments. We measure morphological traits and assess sexual dimorphism in two comparisons: first, in lizards from contemporary North American (introduced) and European (native) populations, and second, in lizards from contemporary introduced populations with historically collected specimens from these same populations (approximately 20 generations in *P. muralis* and 5 generations in *P. siculus*). In each species, we test for shifts in both absolute body size and in relative limb and head size, morphological traits important for habitat navigation (e.g., sprinting, climbing, clinging). Further, we test for shifts in the magnitude and direction of sexual dimorphism in multivariate trait space among these groups. Changes in both absolute body size or the multivariate phenotype might be expected in the introduced environment for several reasons, including rapid selection on traits advantageous in the urban environments (as demonstrated in other traits, e.g., Isaksson 2015; While et al. 2015), developmental disruption due to the challenges of living in cities (e.g., Lazić et al. 2015, 2017), changes in food availability or diet (Giery et al. 2025), or the result of non-random individuals forming the initial propagule. Such tests of parallelism in sexually dimorphic trait trajectories provide a foundation for understanding how evolutionary processes may shape females and males differently, leading to intraspecific variation in morphology as populations move into new environments.

Methods

Species accounts: natural history and introduction history

Podarcis muralis and *P. siculus* are active diurnal lizards (adult maximum size 75 and 90 mm, respectively) that are often conspicuous on a variety of anthropogenic structures in towns, villages, and cities (Brown et al. 1995; Speybroeck et al. 2016; Gherghel and Tedrow 2019; Davis et al. 2021; Meek et al. 2024). Furthermore, both species have well-established populations outside their native range, including for *P. muralis* in the UK (While et al. 2015), Germany (Beninde et al. 2018), Eastern Europe (Oskyrko et al. 2020), and North America (Deichsel and Gist 2001; Engelstoft et al. 2020; Davis et al. 2021) and for *P. siculus* in the Iberian Peninsula (Ribeiro and Sá-Sousa 2018), UK (Silva-Rocha et al. 2014), Eastern Europe (Silva-Rocha et al. 2014; Oskyrko et al. 2022), and North America (Mendyk and Adragna 2014; Haro et al. 2023). Populations of *P. muralis* in Ohio, USA, are the result of a single introduction of 10 individuals from northern Italy in the early 1950s, as described by the person responsible (Hedeen 1984; Davis et al. 2021) and corroborated with genomic analyses (Bode 2025). *Podarcis siculus* were introduced to San Pedro, California, USA, as the result of a single introduction of seven adult individuals (three males, four females) from Taormina, Sicily, Italy, in 1994, which has been confirmed by the person responsible (Deichsel et al. 2010) and is supported by genetic analysis (Oskyrko et al. 2022).

Lizard collection

For both species, we sampled individuals from three different combinations of location and timepoints, which we refer to as sample groups: contemporary individuals from populations in the native (European) range, contemporary individuals from populations in the introduced (North American) range, and historically collected museum specimens from introduced populations. Included in our *P. muralis* dataset are morphological measures from three previously published studies (Vaughn et al. 2021, 2023; Head et al. 2024) as well as new samples from both native and introduced populations. Contemporary populations were sampled between 2020 and 2023. Historical specimens were from the collection of the Cincinnati Museum Center, mostly collected in the 1980s (date range 1981–2012; see details in Vaughn et al. 2021; Head et al. 2024). All work in France was conducted under permit from the Direction régionale de l'environnement, de l'aménagement et du logement (DREAL) Midi-Pyrénées and Pyrénées Atlantique (Arrêté INTERDÉPARTEMENTAL n° DREAL-OCC-2023-s-11), under current ethical committee approval (APAFIS DAP #35,080), and in accordance with Directive 2010/63/EU on protection of animals used for scientific purposes. In Ohio, work was conducted under Ohio Division of Natural Resources permit (SC220002) and approved by Ohio Wesleyan University IACUC (protocols 02–2024-03_1 and 02–2024-04).

All morphological data for *P. siculus* were collected for this study and have not been published elsewhere. Historical (2013 and 2014) and contemporary (2022) data for *P. siculus* from San Pedro were measured from preserved specimens deposited in the Natural History Museum of Los Angeles County. Work with live animals in California was conducted under permission from the University of California, Berkeley IACUC (Protocol AUP-2021-08-14567) and the California Department of Fish and Wildlife (SC-4307). All work in Italy was conducted with permission from the Italian Ministry of the Environment (Protocol N.0032985/2022–2024).

All contemporary animals were caught by hand or with a looped filament attached to an extendable fishing pole. See Table 1 for sample sizes and Table S1 for complete details of sampling locations for both species. Only adult animals (snout-vent length [SVL] >50 mm) are included in analyses. We differentiated sex based on overall body shape, relative head shape, presence

Table 1 Sample sizes and snout-vent length (SVL) for adult female and male wall lizards (*Podarcis muralis* and *P. siculus*) from contemporary native (European), contemporary introduced (North American), and historical introduced (North American) specimens.

Species	Continent	Time	Location	N female	Female SVL (mm) mean ± SD	N male	Male SVL (mm) mean ± SD
P. muralis	North America (Introduced)	Contemporary	Cincinnati and Columbus, Ohio, USA	65	61.94 ± 5.36	107	63.87 ± 5.28
		Historical	Museum specimens from Cincinnati, Ohio, USA	19	58.87 ± 4.64	18	60.36 ± 4.47
	Europe (Native)	Contemporary	Ariège and Hautes-Pyrénées, France	30	59.57 ± 4.57	38	63.01 ± 3.76
P. siculus	North America (Introduced)	Contemporary	San Pedro, California, USA	24	65.91 ± 6.12	24	70.03 ± 8.13
		Historical	Museum specimens from San Pedro, California, USA	25	64.94 ± 6.12	25	71.75 ± 6.54
	Europe (Native)	Contemporary	Taormina, Sicily, Italy	32	62.05 ± 4.01	30	71.60 ± 5.43

Please see Table S1 for additional sampling details.

of eggs, prevalence of femoral pores, or eversion of hemipenes. For some specimens, sex was confirmed through examination of the gonads.

Morphology measurements

We collected new morphological data in both species following the methodology of previous studies (Vaughn et al. 2021, 2023; Head et al. 2024) using digital calipers (model CD-6, Mitutoyo, Japan) with precision to the nearest 0.01 mm. Details of the seven body dimensions measured are presented in Fig. 1. We measured each body dimension twice; if the coefficient of variation was >10%, we re-measured. Averages of the two measures were used for subsequent analyses. We used only measurements from the right side for body parts that are found on both the left and right sides of the body. We often encountered individuals missing toes; in these cases, we used the measurements from the left toe ($N = 25$ *P. muralis* individuals).

Statistical analyses

All data processing and analyses were conducted using R version 4.4.2 (R Core Team 2024). We made all data figures with the package ggplot2 (Wickham 2016). We analyzed each species in separate but identical analyses as described below. Statistical significance was assessed at an alpha level of 0.05 for all tests.

Univariate analyses: body size

To test for the presence of sexual dimorphism in total body size, we constructed a linear model with SVL as the dependent variable and sample group (factor with three levels: native contemporary, introduced contemporary, and introduced historical), sex (factor with two levels: female and male), and their interaction as predictors. We visually inspected residual histograms for normality and assessed the significance of predictors using *F*-tests with type III sums of squares. To test for differences among sample groups in *P. muralis,* where the interactive effect was significant (Table 2), we estimated marginal means using the *emmeans* package (Lenth 2016, 2023) and used linear contrasts, correcting for multiple comparisons with the Šidák method.

Multivariate analyses: body dimensions

Similar to our tests of sexual dimorphism in body size, we tested for dimorphism and shifts in the multivariate body shape phenotype of lizards comparing native contemporary, introduced contemporary, and introduced historical groups. We first scaled each of the seven body dimensions (see Fig. 1) to overall body size by creating a $\log_{10}$–$\log_{10}$ regression of each measure on SVL and utilizing the residual value for downstream analyses (Kaliontzopoulou et al. 2007; Muñoz and Losos 2018). We then simultaneously described patterns of within-individual correlation of traits (via principal component [PC] analysis) and tested hypotheses of differences among groups using a nonparametric multivariate analysis of variance (NP-MANOVA) with residual randomization in a permutation procedure (RRPP) in the *RRPP* package (Collyer et al. 2015; Collyer and Adams 2018). As in the univariate analyses, models included the fixed effects of sample group, sex, and their interaction. For all models, we implemented 999 iterations of the residual randomization procedure with the *lm.rrpp* function and assessed differences among groups using *F*-tests with type III sums of squares with the *anova* function. From the models, we estimated least-squares means and

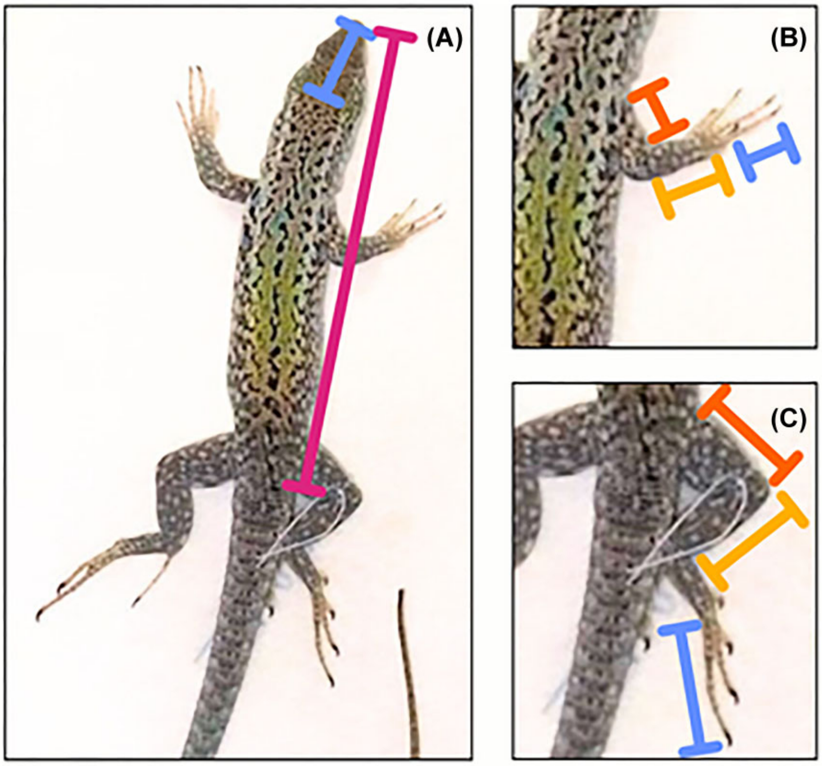

Fig. 1 (A) Lines showing head length and snout-vent length (SVL). (B) Right anterior fourth digit, right anterior zeugopodium, and right anterior stylopodium. (C) Right posterior fourth digit, right posterior zeugopodium, and right posterior stylopodium.

Table 2 Results of linear model testing the effect of sample group (native contemporary, introduced contemporary, introduced historical) and sex on body size in adult wall lizards (*Podarcis muralis* and *P. siculus*).

		Sample group (Reference: Native contemporary)	**Sex (Reference: Female)**	**Sample group × Sex (Reference: Female native contemporary)**
P. muralis	**Estimate ± SE**	Introduced contemporary: 2.36 ± 1.09 Introduced historical: −0.71 ± 1.45	Male: 3.43 ± 1.21	Male native contemporary: −1.50 ± 1.44 Male introduced historical: −1.94 ± 2.03
	F (df_n, df_d)	8.87 (2, 271)	13.68 (1, 271)	0.67 (2, 271)
	***P*-value**	**0.0002**	**0.0003**	0.51
P. siculus	**Estimate ± SE**	Introduced contemporary: 3.86 ± 1.64 Introduced historical: 2.90 ± 1.62	Male: 9.56 ± 1.54	Male native contemporary: −5.44 ± 2.33 Male introduced historical: −2.74 ± 2.31
	F (df_n, df_d)	1.19 (2, 154)	54.29 (1, 154)	2.74 (2, 154)
	***P*-value**	0.31	$<$ **0.0001**	0.068

Significant effects ($P < 0.05$) are indicated by *P*-values in bold. Please see text for statistical details.

95% confidence intervals for predicted values for each trait for each group (using the *predict* function) and extracted the fitted values (model predictions based on input data) in PC space for each individual. We further performed phenotypic change vector analyses (using the *trajectory.analysis* function) within each species by comparing trajectory magnitude and direction in multivariate phenotype between sexes in two comparisons: (1) contemporary native and contemporary introduced populations and (2) contemporary and historical specimens within introduced populations (Adams and Collyer 2007, 2009; Bolnick et al. 2018; Collyer and Adams 2018). Dependent variables in the multivariate analyses (i.e., size-scaled morphological measure-

Table 3 Proportion of variance explained and variable loadings of fitted principal component (PC) values for first two axes of variation describing the morphology of adult female and male wall lizards (*Podarcis muralis* and *P. siculus*) from contemporary native populations, contemporary introduced populations, and historically collected specimens from introduced populations.

	Podarcis muralis		***Podarcis siculus***	
	PC1	**PC2**	**PC1**	**PC2**
Proportion of variation	87.2%	6.9%	70.2%	26.5%
Head length	0.50	−0.23	0.27	−0.64
Anterior stylopodium	0.34	−0.65	0.37	−0.04
Anterior zeugopodium	0.35	0.43	0.21	−0.48
Anterior toe	0.31	−0.02	0.24	−0.21
Posterior stylopodium	0.37	−0.16	0.48	0.46
Posterior zeugopodium	0.43	0.56	0.50	0.31
Posterior toe	0.29	0.02	0.45	−0.07

Predicted 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.

ments) were standardized to mean of 0 and standard deviation of 1 before analysis.

Results

Univariate analyses: body size

Body size varied among sample groups in *P. muralis* only; post-hoc comparison using linear contrasts demonstrates that contemporary introduced (North American) specimens are larger than historically collected specimens (difference in least-squares mean ± SE: 6.57 ± 1.81 mm, $P = 0.001$). Contemporary native (European) lizards did not differ in body size from either contemporary or historically collected introduced lizards ($P > 0.07$). Male wall lizards were larger than females in both species (Table 2, Fig. 2). Sample group (i.e., a three-level factor of native contemporary, introduced contemporary, and introduced historical) did not interact significantly with sex in either species, indicating that sexual dimorphism in body size was consistent in each group (Table 2).

Multivariate analyses: body dimensions

In both multivariate analyses, the vast majority (> 94%) of variation in morphological phenotypes among groups is described by the first two principal component axes (Table 3). The first axis alone described the majority of variation for both species, with all relative body size measurements loading positively. As such, this first axis of variation describes a continuum of animals with larger relative limb size and head length. The second axis described less variation (up to 26.5%) and loaded differentially across characters between the species. In *P. muralis*, the second axis of variation describes a continuum of lizards with generally smaller head length and anterior stylopodia, but larger anterior and posterior zeugopodia, to lizards with the opposite combination of traits. In *P. siculus*, the second axis of variation describes a continuum of lizards with shorter heads and smaller anterior zeugopodia and toes, but larger posterior stylopodia and zeugopodia, to lizards with the opposite combination of traits (Table 3).

In *P. muralis*, males scored higher on PC1 indicating larger body dimensions in all traits measured (Table 3, Fig. 3A, Fig. S1A), though the magnitude of this difference varied across sample groups (as indicated by the significant interaction of sample group and sex). Sexual dimorphism was consistent in magnitude and direction when comparing contemporary native and introduced lizards, but differed in both magnitude and direction when comparing introduced contemporary and historical lizards (Table 4). Additionally, the multivariate morphological phenotype differed between native and introduced samples, such that introduced lizards had higher scores on PC1, indicating larger relative limb and head size, in both males and females (Table 3, Fig. 3A, Fig. S1A). When comparing contemporary and historical lizards from introduced populations, sexual dimorphism differed in both magnitude and direction, whereby contemporary males have higher PC2 scores relative to historical males. Morphological phenotypes of female lizards were similar between contemporary and historical introduced specimens (Table 4, Fig. 3A, Fig. S1A).

Similar to *P. muralis*, *P. siculus* males had larger body dimensions in all traits compared to females (Table 4, Fig. 3B, Fig. S1B). The multivariate morphological phenotype differed among the sample groups (contemporary native, contemporary introduced, historical introduced; Table 4). Morphology differed similarly between female and male lizards in each sample group, as indicated by a significant effect of sex but not the interaction between sex and sample group (Table 4). While the magnitude of sexual dimorphism in the morphological phenotype did not differ across sample groups in *P. siculus*, the direction of dimorphism differed between contemporary native and contemporary introduced lizards (Table 4, Fig. 3B, Fig. S1B).

Discussion

Our study design allowed us to compare absolute body size and the multivariate morphological phenotype, as well as sexual dimorphism in these traits, in two lizard species that have established populations in urban envi-

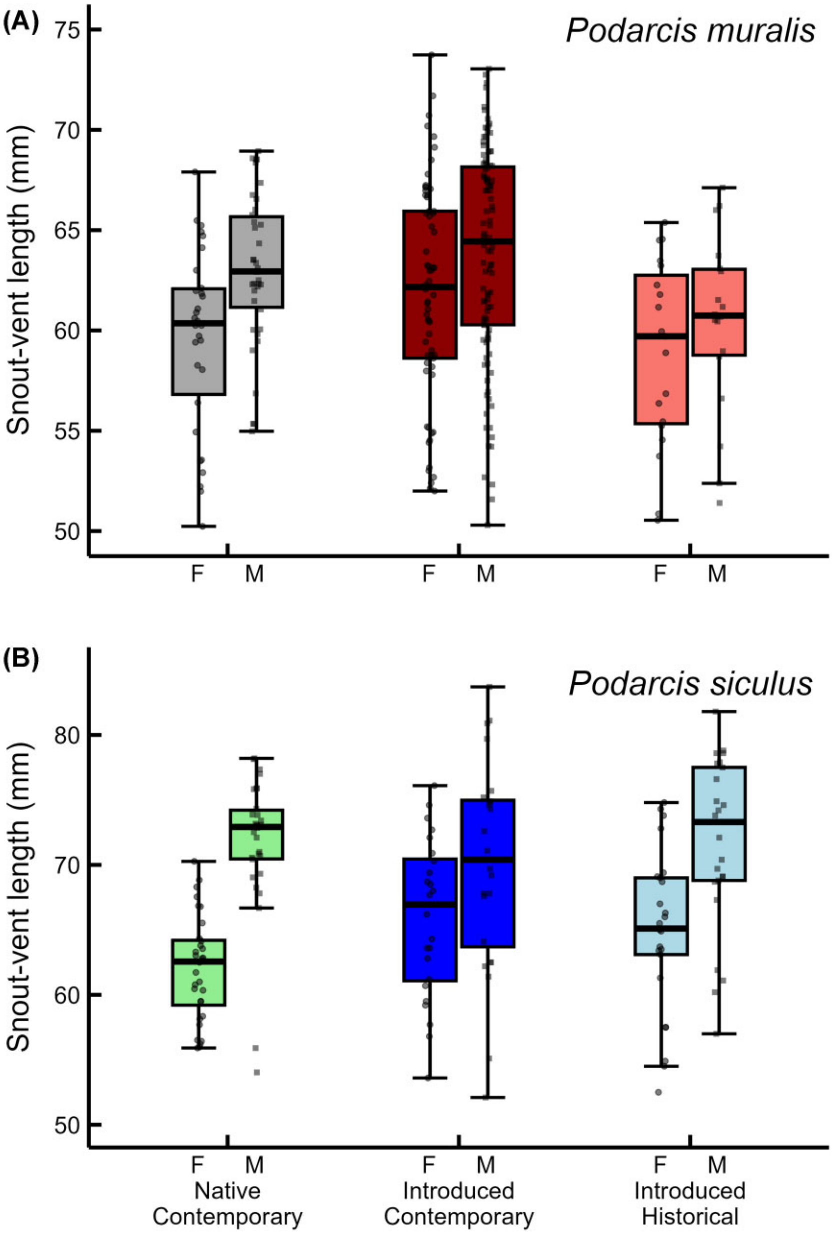

Fig. 2 Body size (snout-vent length) in adult female and male common wall lizards (*Podarcis muralis*; panel A) and Italian wall lizards (*Podarcis siculus*; panel B) from contemporary native populations, contemporary introduced populations, and historically collected specimens from introduced populations. Plots show raw data and Tukey box plots (including median, interquartile range, and 1.5 × interquartile range).

ronments around the world. Both *Podarcis muralis* and *P. siculus*, two closely related lizard species with similar transcontinental introduction histories, demonstrated pronounced shifts in morphology between native and introduced populations (Fig. 3, Table 4). For *P. muralis*, this included similar increases in relative head and limb sizes for females and males. For *P. siculus*, head and limb sizes were different in introduced populations compared to native populations and the trajectory of sexual dimorphism between males and females was not parallel (Table 4). Shifts in morphological space from native to introduced populations and from historical to contemporary introduced populations across short temporal scales (< 50 years) suggest that trait flexibility due to plasticity or response to selection may facilitate the successful establishment and rapid population growth following introduction (Isaksson 2015; While et al. 2015; Sacchi et al. 2023). However, within introduced populations, the species differed in patterns of trait shifts between historical and contemporary lizards. *Podarcis muralis* increased body size over time (Fig. 2, Table 1), while male and female morphological traits diverged in opposing directions in multivariate space (Fig. 3, Table 4). Introduced populations of *P. siculus* did not

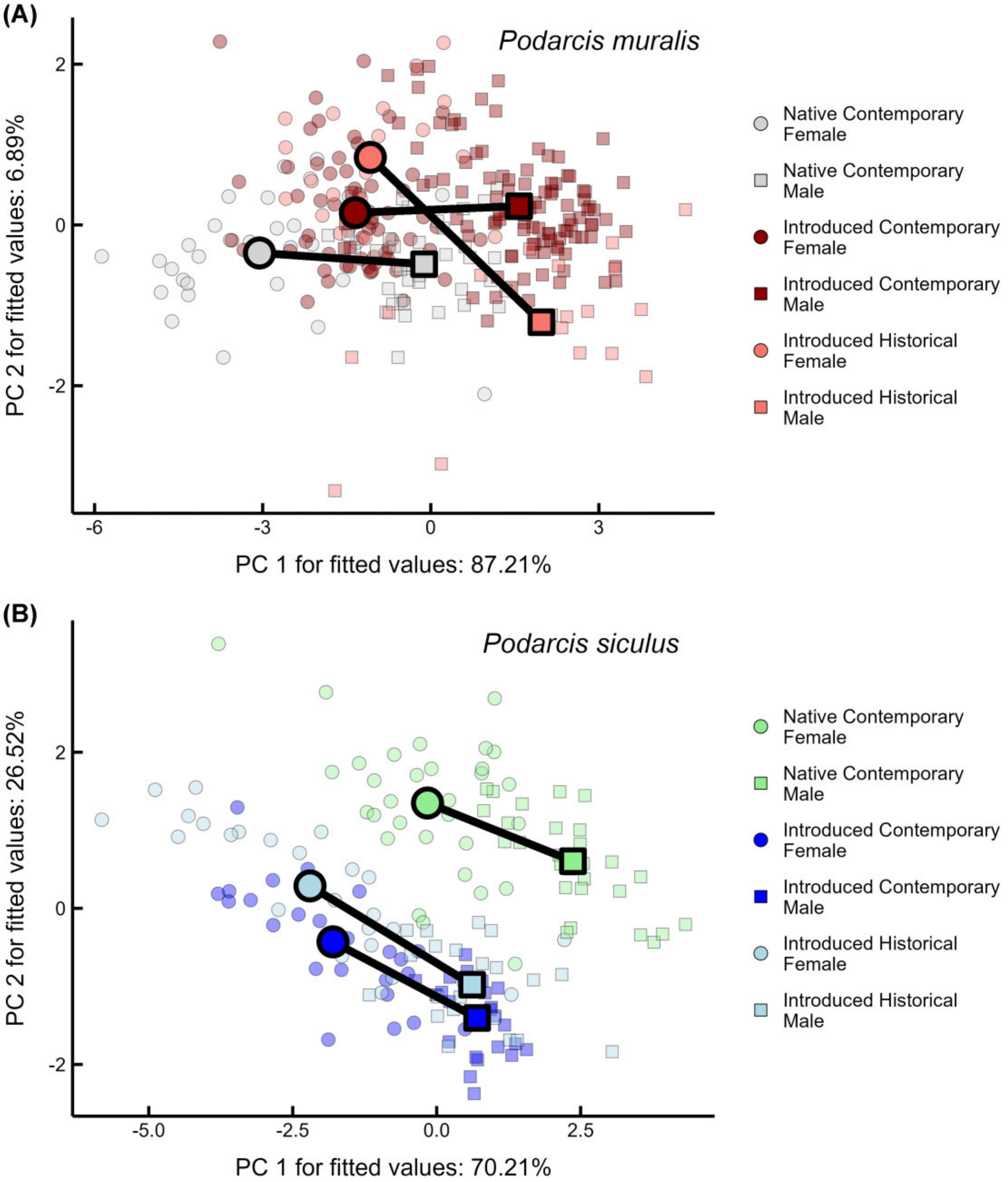

Fig. 3 Comparisons of body dimensions in adult female and male common wall lizards (*Podarcis muralis*; panel A) and Italian wall lizards (*Podarcis siculus*; panel B) from contemporary native populations, contemporary introduced populations, and historically collected specimens from introduced populations. Plots show fitted principal component (PC) scores describing the morphological phenotype and trajectories showing differences between sexes in mean phenotype within each sample group. Values were generated using a non-parametric multivariate analysis of variance (NP-MANOVA) with randomized residuals in a permutation procedure. Note that species were analyzed separately, so PC axes represent different patterns of morphological variation. Please see Table 1 for sample sizes, Table 3 for explanation of PC axes, and main text for statistical details.

exhibit such shifts in overall body size or the multivariate morphological phenotype over time. These patterns suggest differential impact of the founder event or the subsequent exposure to a novel urban environment between these two species. As such, we are limited in drawing broad conclusions about the pathway for species to successfully establish in novel urban environments.

Across both species, males were larger than females in mean body size (Table 2), with the magnitude of dimorphism differing among sample groups in *P. muralis* (Table 2, Fig. 2). In both species, sexual dimorphism in the multivariate phenotype was of similar magnitude (trajectory length) in contemporary native (European) populations and contemporary introduced (North American) populations. The direction (trajec-

Table 4 Results of the nonparametric multivariate analysis of variance (NP-MANOVA) with residual randomization in a permutation procedure (RRPP).

		Model results				Difference in trajectory length	Difference in trajectory angle
		Sample group	Sex	Sample group × Sex			
P. muralis	$F(\mathrm{df}_n, \mathrm{df}_d)$ *P*-value	14.1(2, 271) **0.001**	37.3(1, 271) **0.001**	5.3(2, 271) **0.001**	**Across space (Native—Introduced)**	d = 0.01 95% UCL: 0.64 $Z = -1.90$ *P*-value = 0.96	Angle (°) = 5.62 95% UCL: 14.40 $Z = -1.26$ *P*-value = 0.89
					Across time (Historical—Contemporary)	d = 0.78 95% UCL: 0.76 $Z = 1.62$ *P*-value = **0.045**	angle (°) = 37.57 95% UCL: 17.32 $Z = 5.33$ *P*-value = **0.001**
P. siculus	$F(\mathrm{df}_n, \mathrm{df}_d)$ *P*-value	16.4(2, 154) **0.001**	31.3(1,154) **0.001**	1.86(2, 154) 0.08	**Across space (Native—Introduced)**	*d* = 0.02 95% UCL: 0.90 $Z = -1.91$ *P*-value = 0.97	angle (°) = 21.73 95% UCL: 18.03 $Z = 2.40$ ***P*-value = 0.007**
					Across time (Historical—Contemporary)	*d* = 0.40 95% UCL: 1.00 $Z = 0.21$ *P*-value = 0.43	angle (°) = 14.32 95% UCL: 18.58 $Z = 0.81$ *P*-value = 0.208

Shown are ANOVA statistics from non-parametric linear model testing for differences among sample groups (native contemporary, introduced contemporary, and introduced historical) on the multivariate morphological phenotype of adult female and male wall lizards (*Podarcis muralis* and *P. siculus*). Also shown are results of the trajectory analysis, which tests for differences in the magnitude of change in morphological phenotype between sexes and for differences in the angle of change in morphological phenotype between sexes. 95% UCL: 95% upper confidence limit. Significant effects ($P < 0.05$) are indicated by *P*-values in bold. Please see Table 1 for sample sizes and main text for statistical details.

tory angles) of sexual dimorphism comparing native and introduced populations was parallel in *P. muralis*, but in slightly, but significantly, different directions in *P. siculus* (Table 4, Fig. 3). In the introduced populations over time, however, the species exhibited different patterns of sexual dimorphism. Male and female *P. siculus* morphology shifted minimally from historical to contemporary timepoints in the introduced population, and dimorphism did not change over time in magnitude or direction (Table 4, Fig. 3B). In contrast, in *P. muralis* sexual dimorphism in the multivariate phenotype shifted in both magnitude and direction in the introduced population. Over the approximately 40 years between when our samples were collected in these urban environments in the introduced range, female *P. muralis* decreased scores on PC2, indicating increases in head and anterior stylopodium length and decreases in both anterior and posterior zuegopodia lengths, while contemporary males in the introduced range exhibited the opposite trends (Table 3). Females and males in introduced contemporary populations still differ in their morphological phenotype, but not in the same way as several decades previously. These sex-specific shifts suggest that the environment may be imposing differential selective pressures on females and males (Hudson et al. 2016; Morooka et al. 2025). The identification of such patterns of morphological variation and dimorphism provides an informed basis to test specific hypotheses of the functional implications of this variation and the ultimate (selective) causes of the observed trajectories. For example, a detailed study of sexual differences in structural habitat use combined with measures of performance differentials in different conditions (substrate, distance, movement patterns) could reveal how the importance of morphological characters for performance differs between sexes (e.g., Butler 2007; Simon et al. 2022).

Differences in overall body size and aspects of the multivariate morphological phenotype may differ among populations within a species due to responses to local environments (including plasticity and adaptation), different age class structures of populations, or stochastic processes such as genetic drift (Yuan et al. 2023). Given the small size of founding populations of both *P. muralis* in Ohio (Davis et al. 2021) and *P. siculus* in California (Deichsel et al. 2010; Oskyrko et al. 2022), it is likely that both evolutionary and stochastic processes are important in differentiating the phenotypes of these lizards from those in the native European range. Sexual dimorphism, on the other hand, can be driven by intrasexual competition, sexual selection, and differential selection on performance traits between the sexes. Importantly, these processes are not exclusive and likely interact to shape morphological trait trajectories over space and time, which can explain variation in dimorphism from different populations, similar to previous work in *P. siculus* (Muraro et al. 2022). In our study, males were larger than females in both *P. mu-*

ralis and *P. siculus*, though sexual dimorphism in *P. siculus* is much more exaggerated than in *P. muralis* (mean SVL difference between sexes in native contemporary populations of 9.55 vs. 3.44 mm). Future work could be directed toward testing the potential selective pressures driving body size variation in both sexes; for example, in females selection due to increased fecundity is correlated with larger body size (Kaliontzopoulou et al. 2007; Le Henanff et al. 2013; Kouyoumdjian et al. 2019). The high density of many wall lizard populations, especially in urban environments, provides much opportunity for shared habitat and social interactions between the sexes (Steward 1965; Brown et al. 1995; Meek et al. 2024). Both female and male lizards need to navigate complex structural habitat, often including anthropogenic structures (Donihue 2016; Gomes et al. 2016; Head et al. 2024). In both species, the magnitude of sexual dimorphism between contemporary native and introduced lizards was the same length (Table 4, Fig. 3A, B), providing support that novel selection pressures in a new environment, in this case urban, affect the sexes equally. In *P. muralis*, males and females exhibited parallel shifts when comparing native and introduced contemporary populations, supporting the conclusion that shared environmental variation drives differences between populations, whereas differences between sexes in the relative importance of performance measures (e.g., bite force and reproductive capacity) drives sexual dimorphism. However, the pattern of parallelism in shifts of sexual dimorphism was not maintained when comparing native and introduced contemporary populations of *P. siculus*, though the magnitude of differences in dimorphism was small (Table 4, Fig. S1A).

Previous studies in other lizard species have identified patterns in morphological variation linked to performance in urban habitats. For example, western fence lizards (*Sceloporus occidentalis*) inhabiting human-built environments exhibit consistent patterns of reduced limb length associated with changes in structural habitat (Sparkman et al. 2018; Putman et al. 2019). In contrast, urban-dwelling Puerto Rican crested anoles (*Anolis cristatellus*) exhibit longer limbs compared with those inhabiting forests, which is advantageous for this species to locomote in city habitats (Winchell et al. 2016, 2018). Our previous work in introduced populations of *P. muralis* did not provide evidence that shifts in morphology were linked to living in urban habitats; while both female and male *P. muralis* body dimensions differed over a time scale of approximately 40 years, the shifts were idiosyncratic across body parts and did not impact sprint performance (Vaughn et al. 2021; Head et al. 2024). Our current analysis shows that these shifts in morphology over time in introduced populations are of a much greater magnitude and in a different direction in males compared to females in *P. muralis*. This suggests that limb dimensions may be important for a different aspect of performance in North American cities or that this species experienced intersexual niche partitioning at some time since the introduction (Morooka et al. 2025). One clear pattern that emerged from the analysis of body dimensions in *P. siculus* is that both females and males from native populations have longer rear limbs (posterior stylopodia and zeugopodia) compared to introduced populations (Table 3, Fig. S1). Longer hind limbs are associated with a more sit-and-wait predator strategy, as observed in wall-dwelling populations of the Aegean wall lizard (*P. erhardii*; Donihue 2016). The clear reduction in posterior limb length in both sexes suggests a shift in foraging strategy in introduced populations, potentially due to structural habitat or prey availability differences. Our understanding of the observed patterns of trait shifts will benefit from future experimental work testing the impact of the observed morphological variation on locomotion and performance traits in the context of habitat differences between native (European) and introduced (North American) populations.

Given that the introduced populations of *P. siculus* and *P. muralis* that we studied are the result of single introductions, the contemporary lizards share common recent ancestors with historical specimens, though the contemporary specimens may not be their direct descendants. Employing genetic approaches to identify relatedness across time would allow more direct quantification of how selection or other processes may be acting on these aspects of morphology. Further, in both species it would be most beneficial to measure traits on animals collected closer to the time of introduction (1951 for *P. muralis*, 1994 for *P. siculus*). If the founder population experienced strong selection on morphological traits, we might expect that morphology would have shifted rapidly in the first years following introduction. Unfortunately, to the best of our knowledge such museum specimens do not exist. We also note the caveat that the process of preserving museum specimens can lead to body shape distortion (generally shrinkage), though change in character size is expected to be minimal (<1.5%; Maayan et al. 2022). Given that the clear differences among groups do not match the expectation of such trait changes due to preservation (and the opposite directions of trait change in male and female introduced *P. muralis*), we think that the preservation process may introduce noise, but not systemic bias, into our comparisons of living and historically collected lizards.

The contemporary native and introduced *P. siculus* populations surveyed here are likely closely related, as the population on Taormina, Sicily is the source of the San Pedro introduction (Deichsel et al. 2010; Oskyrko et al. 2022). As such, we can interpret differences between these groups as shifts in traits since their divergence (founder event) approximately 30 years ago. Our ability to draw interpretations of differences in the contemporary *P. muralis* populations is less clear, however. The native populations studied here were caught in southern France. While these populations are squarely within the native European range of the species, they are likely from a different lineage than those from northern Italy that founded the introduced population (Salvi et al. 2013; While et al. 2015). Within the native range, these lineages differ in body and head size, which can influence our interpretation of morphological trajectories: females from the Italian *P. muralis* lineage (*sensu* While et al. 2015; the source of North American lizards) are smaller than females from the Western Europe lineage (which we measured here), and males from the Italian lineage have larger heads than males from the Western Europe lineage (While et al. 2015). Notably, however, both males and females from introduced North American populations had significantly larger overall body size and head size relative to either European lineage. While we are limited in our ability to make specific claims about phenotypic shifts within a given lineage, our data present suggestive evidence that introduced lizards have diverged significantly from those in the native range in the time since introduction. This finding is consistent with the idea that species with traits permitting success in new—and especially urban—environments may be capable of further dispersal and establishment (Borden and Flory 2021). From a conservation perspective, this elicits the concern that species such as wall lizards that are now thriving in urban environments may move into more natural habitats, potentially presenting a threat to ecosystems and competing with native species (Friestad et al. 2023).

At the intersection of urban evolution and invasion biology, wall lizards in North America offer a novel and useful system for exploring the ecological implications of sexual dimorphism and how patterns of dimorphism may shift across contexts. We view the current study as a step toward a broader understanding of the drivers of phenotypic variation across space and time in urban environments and specifically the role of sexual dimorphism in processes important to establishment in urban environments. This work can inform future experiments to assess the functional implications of such shifts. For example, both *P. muralis* and *P. siculus* exhibit larger relative head length in introduced populations compared to native populations. Assessments of diet and intensity of intraspecific competition can inform the underlying mechanisms and functional implications of this head enlargement (Herrel et al. 2008; Sabolić et al. 2024). Such work would be greatly informed by measurements of historical specimens collected from the original source populations, something to which we are currently directing efforts. Future research examining morphological, dietary, and evolutionary shifts in introduced populations will be dependent upon available museum specimens, and we advise that researchers put more effort into collecting representative samples of introduced populations early and repeatedly. New advancements in predictive technologies (e.g., machine learning, Lailvaux et al. 2022) can be utilized to infer how shifts in morphology over time would alter performance measures. Additionally, the question of the relative influences of plasticity, additive genetic variation, and development on morphological traits still lingers. This could be addressed by quantifying ontogenetic trait trajectories in lizards from different populations and assessing patterns of habitat association and sexual dimorphism as individuals mature (e.g., Hassell et al. 2012). Measurements across early development are especially informative in this clade, which exhibits habitat-associated variation in limb morphology that generally develops post-hatching (Cordero et al. 2020). Finally, close examination of morphological differences between female and male individuals, and how patterns in dimorphism relate to differences in habitat, can inform our growing understanding of sex as a multivariate phenotype (McLaughlin et al. 2023; Smiley et al. 2024). Future work would benefit immensely from quantifying myriad traits associated with different reproductive roles to provide a mechanistic basis for associated trait variation, to better inform our understanding of how traits change over time along different axes of the phenotype (e.g., hormonal, morphological, behavioral), and to identify the functional implications for differences in these traits. We are directing future work toward disentangling the non-exclusive roles of plasticity, adaptive evolution, drift, and exaptation in facilitating the ongoing spread of these species across the globe (Winchell et al. 2022; 2023b).

Author contributions

Eric J. Gangloff: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing—Original Draft, Writing—Review & Editing, Visualization, Supervision, Project administration, Funding acquisition. Anusha P. Bishop: Investigation, Data curation, Writing—Review & Editing, Funding acquisition. Alyssa Head: Conceptualization, Methodology, Investigation, Data curation, Writing—Review & Editing, Funding acquisition. Gregory B. Pauly: Methodology, Validation, Investigation, Resources, Data curation, Writing—Review & Editing, Supervision, Project administration, Funding acquisition. Constant Perry: Investigation, Data curation, Writing—Review & Editing. Princeton L. Vaughn: Conceptualization, Methodology, Investigation, Data curation, Writing—Review & Editing, Funding acquisition. Kristin M. Winchell: Conceptualization, Writing—Review & Editing. Kinsey M. Brock: Conceptualization, Methodology, Validation, Investigation, Resources, Data curation, Writing—Review & Editing, Supervision, Project administration, Funding acquisition.

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Supplementary data

Supplementary materials available at *ICB* online.

Conflict of interest

The authors declare no conflict of interest.

Data availability

Data and analysis code are available in the Dryad data repository: https://datadryad.org/dataset/doi:10.5061/dryad.q573n5tvf

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