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Geographic variation in lizard hind-limb morphology in relation to predation: no evidence for an evolutionary basis

Patrick A. Bula, Laura K. Wright and Peter A. Zani*

Department of Biology, University of Wisconsin-Stevens Point, Stevens Point, Wisconsin, USA

ABSTRACT

Question: Do populations of side-blotched lizards (*Uta stansburiana*) have longer hind limbs when exposed to greater potential predation? If so, is the pattern due to evolved responses among populations?

Methods: We measured hind-limb lengths of male side-blotched lizards as well as abundance and composition of several predator types (other lizards, snakes, and birds) from 22 wild populations in Oregon, Nevada, and Washington states.

Findings: Variation in the length of the distal limb elements (pes and fourth toe) is associated with the abundance and diversity (number) of predatory lizard species in the environment. Specifically, the hind limbs of side-blotched lizards in the wild are longer at sites with more predatory lizards. However, lizards reared in a common laboratory environment do not exhibit these patterns in limb variation.

Conclusions: The association between limb dimensions and predation in the wild does not appear to be due to evolved differences among populations.

Keywords: ecomorphology, morphometrics, phenotypic plasticity, predator type, *Uta stansburiana*.

INTRODUCTION

Since the introduction of the ecomorphological paradigm linking variation in morphology to organismal performance and ultimately to fitness (Arnold, 1983), numerous studies of functional morphology have demonstrated links between organismal form and function in traits ranging from locomotion (e.g. Emlet, 1994; Garland and Losos, 1994; Ghalambor *et al.*, 2003) to feeding (e.g. McBrayer, 2004; Herrel *et al.*, 2005) and clinging [the ability to hold on to a surface (e.g. Emerson, 1991; Zani, 2000; Irschick *et al.*, 2006)]. As such, functional relationships have been established between limb dimensions or limb musculature and performance traits such as sprinting (e.g. Bonine and Garland, 1999; Vanhooydonck *et al.*, 2006), jumping (e.g. Harris and Steudel, 2002; Toro *et al.*, 2004), clambering [moving over an uneven surface (Vanhooydonck and Van Damme, 2001)], and climbing ability (Sinervo and Losos, 1991; Vanhooydonck and Van Damme, 2001). Thus, owing to the expected relationship between

Correspondence: P.A. Zani, Department of Biology, University of Wisconsin-Stevens Point, Stevens Point, WI 54481, USA. e-mail: pzani@uwsp.edu

performance traits and fitness-related traits, such as survival (Warner and Andrews, 2002; Miles, 2004; Husak, 2006) and reproductive success (Husak *et al.*, 2006a; see also Chappell and Odell, 2004; Blumstein *et al.*, 2010), relative limb dimensions have the potential to serve as a morphological predictor of both locomotor performance and potential fitness.

Despite the functional links between morphology and performance, the connection between performance and fitness, let alone between morphology and fitness, has been more difficult to establish. Consistent with the predictions of the ecomorphology paradigm, a growing body of evidence has revealed correlations between performance capabilities and fitness (e.g. Snell *et al.*, 1988; Calsbeek and Irschick, 2007; Irschick *et al.*, 2008), and between morphology and fitness (Irschick *et al.*, 2008). For example, faster start times in mosquitofish (*Gambusia hubbsi*) are correlated with increased survivorship (Langerhans, 2009). Additionally, male collared lizards (*Crotaphytus collaris*) with faster sprint speeds sire more offspring (Husak *et al.*, 2006a). However, studies have also indicated the absence of a relationship between performance and fitness (Brodie, 1992; Clobert *et al.*, 2000) or reported mixed results (Jayne and Bennett, 1990). For example, Brodie (1992) reported a lack of differential survival related to the speed of hatchling garter snakes (*Thamnophis ordinoides*), although he did show correlational selection between performance and colour pattern. Nevertheless, the evolutionary response of limb morphology should be related to variation in performance capacity, provided that the morphological elements facilitating performance capacity are heritable.

One indirect technique for studying survival and reproduction related to performance capacities is to examine the consequences of predator–prey interactions in nature. Studies of such consequences have indicated that differences in predator composition between populations can result in selection for morphological changes of prey (Endler, 1995; Smith and Van Buskirk, 1995; Vervust *et al.*, 2007). For instance, in response to the introduction of piscivorous pike (*Esox lucius*), Crucian carp (*Carassius carassius*) evolved an increased body depth, which decreased vulnerability to the gape-limited pike (Brönmark and Miner, 1992). Similarly, the introduction of predatory curly-tailed lizards (*Leiocephalus carinatus*) onto replicate Bahamian islands caused longer legged brown anoles (*Anolis sagrei*) to be favoured initially (Losos *et al.*, 2006). Thus, natural selection has the potential to act on morphology by means of differential survival and reproduction, which is then correlated to an individual's performance capacity (Arnold, 1983).

Studies of predator–prey interactions (e.g. Losos *et al.*, 2004, 2006; Calsbeek and Irschick, 2007; Calsbeek and Cox, 2010) have often used isolated populations, such as those on separate islands, to replicate conditions as well as to ensure that barriers to gene flow exist between populations. Such study systems also allow for control of predator composition acting on prey populations, and the results of these studies have been instrumental for advancing our understanding of ecomorphological evolution. In a classic study comparing lizard communities on numerous islands in the Gulf of California, Case (1975) reported that the densities of side-blotched lizards (*Uta stansburiana*) were negatively correlated with the number of other lizard species present (i.e. predator diversity) and in particular to the densities of heterospecific predatory lizards. These findings suggest that a predator assemblage can impact prey populations and that certain components of the predator community (e.g. foraging behaviour of predators, predator abundance, or specific predator types) may be more influential on prey populations than other factors. Different predator communities may therefore be considered as distinct predation environments where the presence or absence as well as the abundance and type of specific predators contribute to the predation pressure exerted on populations. Although the effects of multiple predators have been studied as they relate to prey behaviour

(Templeton and Shriner, 2004; Amo *et al.*, 2005; Blumstein, 2006), previous studies of ecomorphological evolution have typically focused on only a single predator or a comparison of two distinct (i.e. categorical) predation environments such as predators being present versus absent (e.g. Van Buskirk and McCollum, 1999; Losos *et al.*, 2004). Thus, these previous studies had only a limited ability to distinguish among the effects of specific components of the selective environment imposed by the predator community.

In this study, we explored how differences in predation environment are related to differences in limb morphology of side-blotched lizards across a wide range of genetically similar populations of this species. We relied on the documented relationship between maximal sprint speed and stride length in phrynosomatid lizards (Bonine and Garland, 1999) and the fact that hind limbs provide the primary propulsive force for most lizards (Losos, 1990) to predict the existence of ecomorphological relationships among populations in this study system. Specifically, we hypothesized that because selection would favour faster individuals, populations of side-blotched lizards experiencing greater potential predation will possess longer hind-limb lengths than those experiencing less potential predation. Because differences in microhabitat, intraspecific interactions, and prey availability between sites may relate to differences in hind-limb morphology between populations, we attempt to minimize the effects of these factors by studying numerous populations representative of each type of predation environment (i.e. replicate populations with similar predator assemblages), but that otherwise occupy similar macrohabitats (shrub-steppe). However, because any relationships observed in the field cannot rule out phenotypic plasticity in limb morphology (e.g. Losos *et al.*, 2000; Hall *et al.*, 2013; Langford *et al.*, 2014), we also performed an experiment in which we reared the offspring of wild-caught animals in a common-garden laboratory environment. We predict that a greater abundance and diversity of predators will correlate with elongated limbs and that this elongation will be retained when animals are reared in the absence of environmental differences between populations, which would be consistent with genetic, not plastic, causes of the pattern.

MATERIALS AND METHODS

Study organism

We studied northern side-blotched lizards (*Uta stansburiana stansburiana*). Northern side-blotched lizards are small (individuals hatch at about 22 mm body size, mature at 40 mm, and grow up to 55 mm), largely insectivorous lizards that occur in western North America from the mid-latitudes of Nevada north into Oregon, Washington, and Idaho states (Fig. 1). Community types in the range of northern side-blotched lizards are predominantly shrub-steppe habitat and can be divided into the Great Basin shrub-steppe [dominated by sagebrush, *Artemesia* and shadescale, *Atriplex* (Nowak *et al.*, 1994)] and the Snake-Columbia shrub-steppe [dominated by sagebrush and bunchgrasses (Franklin and Dyrness, 1988)]. In some areas, the shrub-steppe habitat grades into juniper woodlands, although *Uta* are restricted to more open areas in this habitat. In the northern portions of its range, the side-blotched lizard is a ground-dwelling species that inhabits rocky areas and regularly basks on elevated perches, such as boulders. In many cases, study sites were located by using Google Earth to identify ancient lake shores that had exposed sufficient rock through erosion to provide suitable rocky habitat.

Side-blotched lizards are known to be depredated by numerous predators (Case, 1975; Wilson, 1991), including multiple other lizard species, snakes, and birds. Many potential predators

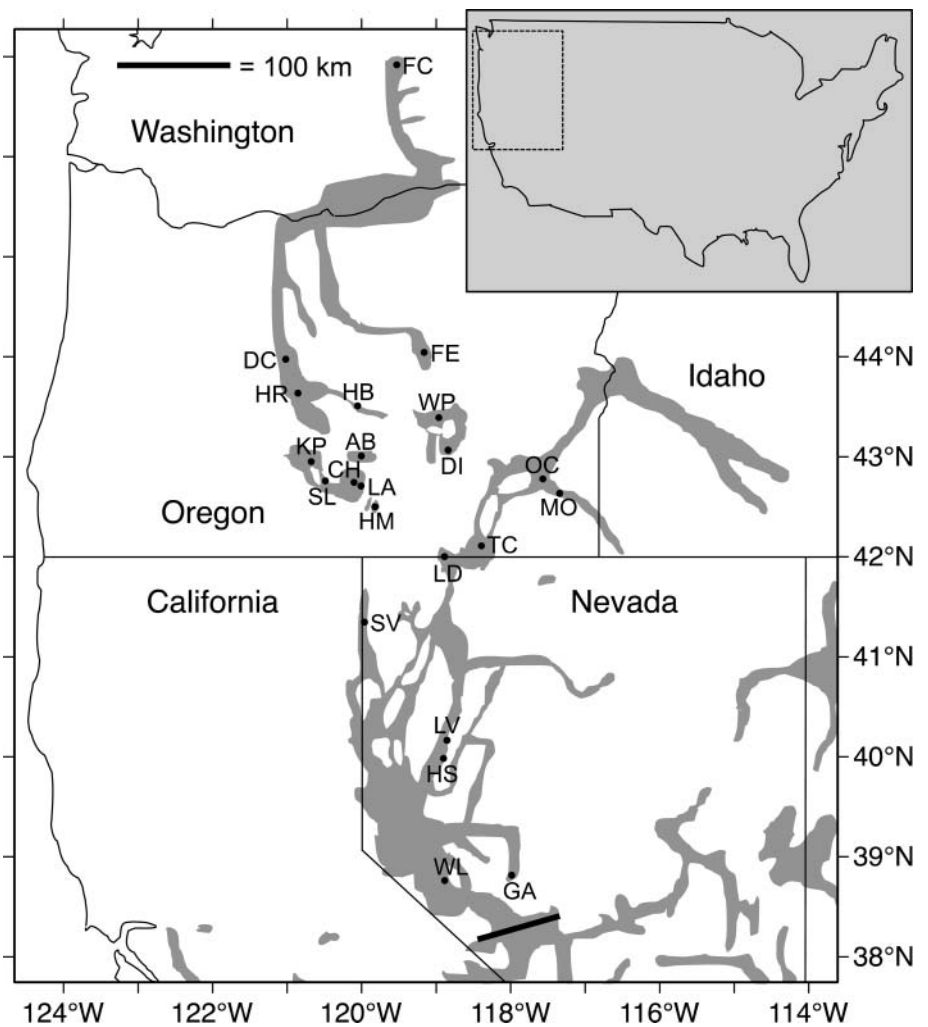

Fig. 1. Map of western United States showing the distribution of side-blotched lizards (shaded areas) based on museum records (herpnet.org) and field observations. Black bar indicates southern extent of *U. s. stansburiana* (McKinney, 1971). See Table 1 for site descriptions. Inset shows map of United States with study area indicated by dashed box.

occur throughout most or all of the geographic range of northern side-blotched lizards (Nussbaum *et al.*, 1983; Wilson, 1991). Although other lizard species are considered important predators of *Uta* where they co-occur (see Case, 1975), these other predatory lizards do not occur throughout the range of northern side-blotched lizards. For example, predators such as Great Basin collared lizards (*Crotophytus bicinctores*), long-nosed leopard lizards (*Gambelia wislizenii*), and tiger whiptail lizards (*Aspidoscelis tigris*) are range limited in northern Nevada and southern Oregon (Nussbaum *et al.*, 1983). Other predatory lizards, such as desert spiny lizards (*Sceloporus magister*) and zebra-tailed lizards (*Callisaurus draconoides*), are even more range restricted and do not occur north of the mid-latitudes of Nevada. Thus, there are numerous northern populations of *Uta* that experience potential differences

in predator composition depending on the species present, with the most obvious difference in predation environment being a decrease in the number of other predatory lizards at progressively higher latitudes (Fig. 1).

While we do not know for certain the cause behind the above change in predation environment across latitude, likely causes include: (1) a recent range expansion of *Uta* with insufficient time for predators to expand their range into suitable habitat; (2) the presence of abiotic limiting factors such as cold temperatures or short growing seasons; or (3) range reduction of formerly widespread predators. Support for this latter idea can be noted because there appear to be discontinuous distributions of certain reptiles in the northern Great Basin. For example, in Oregon and Idaho there are disjunct populations of certain lizards (notably *Gambelia* and *Aspidoscelis*) and snakes (notably long-nosed snakes, *Rhinocheilus lecontei* and western groundsnakes, *Sonora semiannulata*) north of the Great Basin Desert (Nussbaum *et al.*, 1983). Palaeoclimatological studies of the northern Great Basin have suggested that it was warmer and drier about 6000 years ago (Mehringer, 1985). Thus, many species that may have expanded their range under those conditions could have been forced to contract their range more recently. However, low levels of genetic variation among widely dispersed populations of *Uta* in Nevada, Oregon, and Washington states (Corl *et al.*, 2009) suggest that the range expansion of this northern subspecies was so recent as to preclude the time for molecular evolution. Yet, whether populations of side-blotched lizards that currently lack certain predators have done so for only a few generations or for thousands of years is unknown.

Predator–prey distributions provide an opportunity to study the effects of differences in selection on the morphological evolution of prey in a continental (non-island) system. However, we acknowledge that gene flow among study populations is non-zero and that populations may have only recently come to experience their current predation environment. Yet, we note that the effects of these potentially confounding factors make it less, not more, likely to find a statistical relationship and that any detectable pattern is likely robust in the face of these factors.

We chose to limit this study to male side-blotched lizards because, unlike females, males are brightly coloured and regularly conduct territorial displays (e.g. Zani *et al.*, 2013). Furthermore, many of the potential predators are visually oriented and movements by prey can elicit an attack from such predators (Herzog and Burghardt, 1974; Gluesing, 1983). Consequently, we concluded that males are more likely to experience natural selection on morphological (i.e. limb) phenotypes via predator–prey interactions mediated by locomotor performance and thus more likely to show an evolutionary response.

Study sites

Collection of animals took place between mid May and early July each year. Each study site was north of the zone of intergradation identified by McKinney (1971) between the northern side-blotched lizards (*U. s. stansburiana*) and western side-blotched lizards (*U. s. elegans*) (see also Fig. 1). Thus our study was performed within a single, closely related clade of side-blotched lizards (Corl *et al.*, 2009). Study sites were chosen for their abundance of *Uta* (30–50 adults per hectare), predator community, and general proximity to one another.

In an attempt to limit bias towards factors besides predation that may influence hind-limb morphology (e.g. resource availability, macrohabitat), we targeted study populations that allowed us to replicate predation environments experienced by side-blotched lizards (see Table 1). However, we acknowledge that due to possible gene flow between populations,

Table 1. Description of study sites shown in Fig. 1

Alkali Buttes (AB)	Mixed sagebrush-salt scrub habitat located in south-central Oregon; characterized by ancient eroded rocky lake shore overlooking dry lake bed (43.01°N, 120.03°W, elevation 1350 m).
Coleman Hills (CH)	Mixed sagebrush-salt scrub north of Lake Abert in Chewaucan Basin of south-central Oregon; characterized by ancient eroded rocky lake shore overlooking drying lake bed (42.75°N, 120.15°W, elevation 1330 m).
Deschutes Canyon (DC)	Mixed sagebrush-juniper habitat along Deschutes River of central Oregon; characterized by igneous rim and flows interspersed with numerous juniper overlooking river (44.38°N, 121.29°W, elevation 780 m).
Diamond Craters (DI)	Sagebrush-steppe habitat in southern Malheur Basin of eastern Oregon; characterized by volcanic splatter cone and igneous rock with occasional brush overlooking Malheur Wetlands (43.08°N, 118.76°W, elevation 1295 m).
Frenchman Coulee (FC)	Sagebrush-steppe habitat along Columbia River in Washington state; characterized by scablands atop lava exposed by floods from Ancient Lake Missoula overlooking a large canyon (47.04°N, 119.96°W, elevation 375 m).
Foree (FE)	Sagebrush-steppe habitat along John Day River of north-central Oregon; characterized by lava flows atop volcanic-ash deposits overlooking river (44.65°N, 119.64°W, elevation 685 m).
Gabbs (GA)	Sagebrush-steppe habitat at base of Gabbs Valley Range of central Nevada; characterized by rocky dry wash and adjacent cinder cone (38.80°N, 117.96°W, elevation 1470 m).
Hampton Buttes (HB)	Mixed sagebrush-juniper habitat in central Oregon; characterized by igneous rim interspersed with pumice and sand deposits overlooking sagebrush flats (43.78°N, 120.39°W, elevation 1455 m).
Hart Mountain (HM)	Sagebrush-steppe habitat at base of Hart Mountain in southeastern Oregon; characterized by boulder field along outwash of DeGarmo Canyon overlooking Warner Wetlands (42.48°N, 119.79°W, elevation 1450 m).
Horse Ridge (HR)	Mixed sagebrush-juniper habitat in Great Sandy Desert of central Oregon; characterized by mounds of exposed lava separated by large expanses of sand (43.86°N, 121.07°W, elevation 1175 m).
Humboldt Sink (HS)	Salt scrub habitat adjacent to Ancient Lake Lahontan in north-central Nevada; characterized by ancient eroded rocky lake shore overlooking dry lake bed (39.95°N, 118.74°W, elevation 1245 m).
Klippel Point (KP)	Mixed sagebrush-salt scrub north of Summer Lake in Chewaucan Basin of south-central Oregon; characterized by ancient eroded rocky lake shore overlooking drying lake bed (43.02°N, 120.71°W, elevation 1350 m).
Lake Abert (LA)	Mixed sagebrush-salt scrub north of Lake Abert in Chewaucan Basin of south-central Oregon; characterized by ancient eroded rocky lake shore overlooking drying lake bed (42.72°N, 120.12°W, elevation 1315 m).
Long Draw (LD)	Sagebrush-steppe habitat at base of lava flow in Alvord-Continental Basin of northern Nevada; characterized by a rocky plateau overlooking a dry wash (41.99°N, 118.87°W, elevation 1390 m).

Lovelock (LV)	Salt scrub habitat adjacent to Ancient Lake Lahontan in north-central Nevada; characterized by rocky lake shore made of tufa formations overlooking dry lake bed (40.22°N, 118.54°W, elevation 1255 m).
Middle Owyhee (MO)	Mixed sagebrush-salt scrub habitat along Owyhee River of southeastern Oregon; characterized by igneous rim overlooking river (42.69°N, 117.27°W, elevation 1415 m).
Owyhee Canyon (OC)	Mixed sagebrush-salt scrub habitat along Owyhee River of southeastern Oregon; characterized by igneous rim overlooking river (42.83°N, 117.61°W, elevation 1135 m).
Summer Lake (SL)	Mixed sagebrush-salt scrub habitat east of Summer Lake in Chewaucan Basin of south-central Oregon; characterized by ancient eroded rocky lake shore overlooking drying lake bed (42.78°N, 120.55°W, elevation 1360 m).
Surprise Valley (SV)	Mixed sagebrush-salt scrub habitat of northwestern Nevada at base of Hays Canyon Range; characterized by ancient eroded rocky lake shore overlooking dry lake bed (41.38°N, 119.99°W, elevation 1420 m).
Trout Creek (TC)	Sagebrush-steppe habitat in Alvord Basin of southeastern Oregon; characterized by rocky slopes of Trout Creek Mountains overlooking a small creek (42.16°N, 118.44°W, elevation 1455 m).
Walker Lake (WL)	Salt scrub habitat adjacent to Walker Lake in north-central Nevada; characterized by granitic boulder field at base of Wassuk Range along a dry wash overlooking a lake (38.75°N, 118.77°W, elevation 1290 m).
Wrights Point (WP)	Sagebrush-steppe habitat in Malheur Basin of southeastern Oregon; characterized by igneous rim projecting into and overlooking Malheur Wetlands (43.44°N, 118.93°W, elevation 1320 m).

this has the potential to lead to pseudo-replication of certain meta-populations. To minimize this, we selected populations in distinct basins or sub-basins within the Great Basin Desert. In the high-latitude portions of its range, *Uta* does not occur above ~1800 m (6000 feet) (see McKinney, 1971; Nussbaum *et al.*, 1983). Thus, the elevational barriers separating distinct basins are probably the strongest barriers to gene flow in this species.

Next, we attempted to choose populations separated by other historical barriers (such as dried Pleistocene lakes) as a means of increasing isolation by distance within a basin. However, we observed that predators are sometimes discontinuously distributed within a basin. For instance, tiger whiptail lizards in Oregon occur at isolated sites in the Malheur and Chewaucan Basins, while at other sites in those basins they are absent. Thus, in a few instances we included sites within the same basin and even within close proximity, but with no clear barrier to gene flow because of the differences in predation environment between sites. For example, two of our sites at the north end of Lake Abert in the Chewaucan Basin are only separated by 5 km. However, long-nosed leopard lizards are fairly abundant at one site, but have never been observed at the other site possibly due to slight differences in soil characteristics, aspect, or a nearby highway bisecting the site. Both sites were included precisely because they differed measurably in their predation environment even if gene flow was highly likely. We justify this because, if anything, it would make detecting a difference related to predation more, not less, difficult (decrease Type-I error).

Predation environment

Previously, researchers have attempted to quantify predation pressure (often with mixed success) by measuring tail-loss frequency (Bateman and Fleming, 2009), clay-model-attack frequency (Husak *et al.*, 2006b; Vervust *et al.*, 2007), or recapture probability (Wilson, 1991; Reznick and Bryant, 2007). However, each of these methods was deemed inappropriate for the purposes of the present study. First, tail-loss frequency may be biased by predator efficiency (Schoener and Schoener, 1980; Jaksić and Greene, 1984; Bateman and Fleming, 2009) or attack behaviour (Vervust *et al.*, 2011). Preliminary data on tail-loss frequency (P.A. Zani, unpublished data) indicated that populations with low predator densities had among the highest tail-loss frequency. Second, preliminary attempts of measuring predation using clay-model-attack frequency indicated that birds and mammals attacked the models, but that predatory lizards and snakes did so at disproportionally low frequencies (P.A. Zani, unpublished data). Third, mark-recapture studies are labour-intensive and require multiple visits during the active season to determine the survival due to predation (Wilson, 1991). Furthermore, estimates of survival during activity seasons can be confounded by substantial winter mortality (Wilson and Cooke, 2004). Because our goal was to include as many replicate populations as possible, conducting a mark-recapture study of animals at each site was not logistically feasible. Therefore, we chose to estimate predation environment using two alternative methods from those described above.

Our first estimate of predation environment used a method similar to Pianka (1970) in which we recorded the observed abundances of each species of potential predator as we walked transects through the habitat. To identify potential predators, we primarily relied on the list of species presented by Wilson (1991). However, because mammals were almost never observed in the field and were less likely to prey upon active lizards (thus were considered less likely to select for locomotor performance/limb dimensions), we excluded mammals as a category of potential predators. To estimate other predator abundance (other lizards, snakes, and birds), we recorded the occurrence of predators while conducting daily lizard surveys during field seasons from 2011 to 2015. These surveys were conducted when conditions were favourable for lizard activity (i.e. not during early spring or the post-breeding season, not prior to daily lizard activity or during the midday inactive period, and not during inclement weather). Survey methods were standardized in order to make data among sites and among years comparable. In short, observers (usually one to three in number) were spaced 5 m apart and walked parallel systematic transects through appropriate habitat while attempting to identify and count each lizard, snake, and bird.

For each predator species, including other side-blotched lizards (Wilson, 1990), we recorded every individual observed during an observation period. We took care not to overlap transects, not to collect data from the same area multiple times per day (though we did use the same areas on separate days), and to work as a team so as to avoid counting individual predators more than once. We then divided the number of predators detected by the number of observers and the distance walked during each survey (recorded using handheld GPS) to determine the number of predators observed per person per kilometre (hereafter referred to as 'predator abundance').

Measurement of predation environment for many of our study sites occurred between 2011 and 2015. Although we did not visit each site each year, we included all data available to us in our attempt to quantify predation environment. The minimum time allowed for estimating predation environment included at least two years at each site and at least three total days of data collection.

Since the body sizes and energetic requirements of ectotherms and endotherms differ greatly (e.g. Pough, 1980), we attempted to scale our estimations of the predation environment by incorporating data on mass and metabolic rates of each species. To do this we used previously published size and resting metabolic rate data for the lizards (Andrews and Pough, 1985; Karasov and Anderson, 1998), snakes (Andrews and Pough, 1985; Stinner, 1987; Secor and Nagy, 1994), and birds (Bennett and Harvey, 1987) included in this study. In the few instances where metabolic rates were not available (e.g. *Sceloporus magister*), we substituted data from a congener for that species. Since energetic data are typically reported per unit mass and per unit time (e.g. mL $O_2 \cdot g^{-1} \cdot h^{-1}$), we multiplied the metabolic rate of each species by the reported mass for that species and standardized by time. Next, we multiplied the metabolic rates by the abundance data from each site. Finally, we summed these metabolism-corrected estimates of abundance for each of the three predator types (lizards, snakes, birds) as well as separately for side-blotched lizards. In this way, we were able to create metabolism- and abundance-scaled estimates of the predation environment that were population specific.

Our second estimate of predation environment used a method similar to Case (1975) and Schoener and Schoener (1978) in which we recorded the number of predator species present in an environment. Because an observable difference among study populations was the number of predatory species present at each site, we counted the number of predatory species present, which we term 'predator diversity'. In a sense, predator diversity represents our attempt to simplify the quantification of predation environment.

Limb morphology in the wild

Specific elements of the hind limb may be as important in determining stride length, a major determinant of sprint speed, as the overall leg length (e.g. Braña, 2003). However, total hind-limb length (HLL) is positively correlated with locomotor performance in lizards (Bonine and Garland, 1999). Without clear justification for focusing on one aspect of limb morphology or the other, we chose to include both aspects (limb elements and HLL) in order to determine if a response to predation is occurring in individual aspects of the limb or in the entire limb.

To measure limb morphology, freshly caught lizards were chilled in hard-sided plastic containers in an ice-filled cooler (often overnight) until they were sufficiently immobilized. We then placed chilled lizards on a glass platform with two mirrors behind the subject mounted such that the dorsal or ventral view was visible in one of the mirrors when viewed from the side. This device was placed inside a cardboard box painted white with a translucent light diffuser placed in the lid of the box to provide ample illumination. A camera was then mounted at a set height and distance from the subject to provide a lateral view. For scale, we used 10-mm cubes marked on all sides with 1-mm reference marks. We placed a scale cube at the cranial and caudal ends of the subject in the plane of the anterior-posterior axis and oriented each cube perpendicularly to the camera lens to minimize parallax. We then took digital photographs of each individual, imported these photographs into ImageJ v.1.46r (http://imagej.nih.gov/ij), and used the best photo – determined by our ability to see relevant landmarks on subjects (Fig. 2) – for measurements. For measurements, we recorded the pixel lengths of both 10-mm scale bars in the ventral view as well as the pixels corresponding to the snout–vent length (SVL) (from tip of nose to posterior-most portion of the vent) and each limb element. Using the known distance averaged from the two scale bars, we calculated limb dimensions for each lizard from pixel measurements using Microsoft Excel.

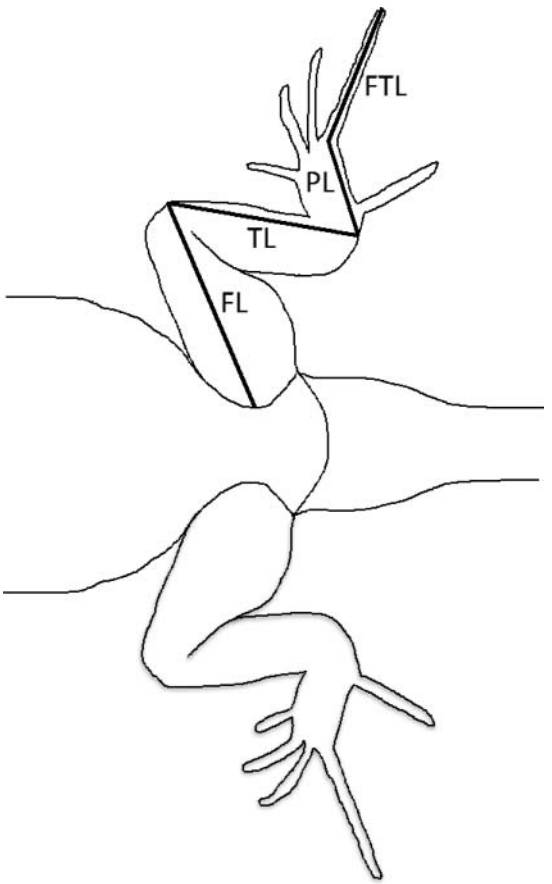

Fig. 2. Drawing of ventral view of the hind limbs of a side-blotched lizard showing relevant landmarks used to measure limb elements: FL = femur length, TL = tibia length, PL = pes length, FTL = fourth-toe length. Total hind-limb length (HLL) was the sum of these elements.

Limb elements were measured as the animal sat in a natural (anatomical) position (Fig. 2) and included: (1) femur length (FL) = parallel to the femur from the medial-most point of insertion of the upper leg into the body wall (as indicated by the difference in scalation between limb and venter) to the junction between the patella and the foreleg (as indicated by the distal bend in the knee); (2) tibia length (TL) = from the distal bend in the knee parallel to the tibia to the distal bend of the ankle just proximal to the insertion point of the fifth toe; (3) pes length (PL) = parallel to the line between the fourth and fifth toes from the bend in the ankle to a point equal to the proximal-most anterior junction between the third and fourth toes but along the midline of the fourth toe; and (4) fourth-toe length (FTL) = along the midline of the fourth toe from the junction between the third and fourth toes to the distal-most extent of the claw on the fourth toe. Although these measurements may not perfectly match the internal elements, we chose these landmarks because of their repeatability and distinguishing features in this species. The sum of the individual elements provided total hind-limb length (HLL) for each individual.

Limb morphology in the lab

To test for phenotypic plasticity in limb morphology, we reared animals from 12 populations in a common-garden environment from hatching. Test subjects for this experiment were acquired by first collecting adult side-blotched lizards [9–17 dams (mean ± 1 SEM per site = 14.1 ± 0.64) and 2–4 sires (3.8 ± 0.18)] early in the 2013 breeding season; all animals were collected between late March and early May. These animals were shipped overnight to the University of Wisconsin-Stevens Point and maintained in an animal care facility.

Lizard cages were constructed of aluminium flashing and measured ~85 × 75 cm with walls ~31 cm tall. Each cage contained 2–4 cm of dry sand substrate and 17 small (15 × 5 × 1 cm) concrete blocks arranged in four small piles to provide basking sites as well as retreats in both warm and cool portions of the cage. A thermogradient was established in the cage using a 100-W incandescent light bulb (Zoo Med PowerSun UV mercury vapour lamp) suspended 28–30 cm above the sand substrate, but directly above a wall dividing two cages. A basking site was positioned on either side of the dividing wall 20–22 cm directly below the light. In this way, the single bulb heated and illuminated two cages as well as created a thermal gradient in the cages. In addition, each pair of cages had two 32-W fluorescent bulbs suspended ~25 cm above the cage substrate. Incandescent and fluorescent lights were maintained on separate timers. The incandescent lights provided a thermoperiod and were set to turn on/off ~2 hours after/before the fluorescent lights, respectively. The fluorescent lights provided a photoperiod that mimicked natural changes in lighting. Light periods were increased or decreased 15–20 min per week to simulate spring (starting at 12/12 hours light/dark), summer (as much as 18/6 hours light/dark), and fall (as little as 11/13 hours light/dark) conditions as needed. Using this setup, cages averaged (±1 SEM) daily high and low temperatures of 30.7 ± 1.19°C (range: 25.5–32.0°C) and 21.9 ± 0.37°C (range: 21.5–23.0°C), respectively.

Lizards for this lab-rearing experiment originated from 12 of the 22 field sites (WP, DI, AB, OC, SL, CH, HM, LD, SV, HS, GA, and WL of Fig. 1). These sites were chosen specifically because they represented replicate sites with distinct predation environments, especially predatory lizards: three sites (WP, AB, HM) lacked predatory lizards, three sites (SL, CH, DI) had one predatory lizard species present, three sites (OC, LD, SV) had three predatory lizard species present, and three sites (HS, GA, WL) had five predatory lizard species present.

Depending on the site and time of collection, females entering the lab ranged from having unenlarged (early vitellogenic) follicles to shelled eggs. Females were housed 4–5 per cage (all from one site) with one male [three cages per site randomly (assigned using Microsoft Excel) spread throughout the animal room]. Males were rotated among the cages for that site weekly to increase the possibility of female choice and to stimulate mating (side-blotched lizards frequently mate immediately after the introduction of a new male). All lizards were fed crickets, mealworms, wax worms, and fruit flies daily or twice daily *ad libitum*.

When females began shelling eggs (determined by weekly abdominal palpation), they were placed into isolation to oviposit. Cages for oviposition consisted of 15-cm diameter × 30-cm tall aluminium flashing cylinders. These cylinders were placed into 8-cm deep moistened sand-peat moss mix (roughly 50:50) held within a 10-cm deep clear plastic dish. A small (8 × 6 × 1 cm) tray of aluminium flashing filled with dry sand provided a basking surface or cover object for females while the moist substrate allowed them to dig burrows for

oviposition. Females typically burrow to the bottom of the substrate to lay eggs; clear dishes containing substrate made checking for oviposition from below fairly unobtrusive. Within ~6 hours of oviposition, females were removed and weighed. Substrate was then sifted through 3-mm × 3-mm hardware cloth to separate eggs. These eggs were then individually weighed, labelled, and placed on 60 mL of 9:1 (by volume) vermiculite : water substrate in a 75-mL Nalgene beaker. Beakers were covered with plastic wrap held in place by a rubber band and placed inside a 6.7-litre Rubbermaid snap case (30 eggs per case). Eggs for each clutch were spatially spread among at least two snap cases (no more than two eggs per case) to minimize incubation effects. Snap cases were placed in stacks of three inside a Styrofoam-lined plastic case with a small fan and thermostat set to 28°C. Stacks of eggs were rotated daily among the positions within the incubator to minimize incubation effects.

At hatching, lizards were immediately measured and permanently marked using unique toe clips (removing a combination of toes). Hatchlings of both sexes were housed in the same types of cages as adults at densities of 10–12 per cage irrespective of population of origin (i.e. cohorts were based on age rather than source population to ensure equal access to food of similar-sized individuals). Depending on when they hatched, the 181 lab-reared males used for this study were allowed 67–109 days to grow (mean ± SD: 88.9 ± 8.32 days) and weighed every 15–25 days to monitor condition/growth. At the end of the growing season (as indicated by the photoperiod reaching 11/13 hours light/dark), we measured body size (SVL) and took photos of all surviving male lizards from which we measured limbs (using the same protocol as described above). Thus test subjects (males only) for this experiment were reared under common conditions since embryogenesis (including all incubation and pre-adult growth) prior to determination of limb dimensions.

Differential reproduction and survival of eggs and juveniles meant that some dams did not produce offspring included for morphometric measurement. Of the 172 initial females used to create the lab generation, only 97 contributed surviving males to the lab population. Because siblings cannot be considered statistically independent, we averaged the body size and limb dimensions of all surviving offspring to create 97 family averages. These mid-offspring (family) averages were used to calculate statistical residuals as well as for subsequent statistical analyses.

Statistical analyses

Since each population had a single type of predation environment, we deemed it inappropriate to analyse the data using each individual as the unit of variance because this would have vastly overestimated the degrees of freedom. Rather, we considered the population of origin as a more appropriate unit of variance for analyses despite it being a much more conservative analysis. Thus we calculated the average trait value for each population to be used in analyses.

Owing to the large number of variables included in this study, we used principal components analysis to reduce the number of traits used in statistical tests. We used a varimax rotation to ensure the statistical independence of the resulting principal components. Furthermore, we included only those principal components that explained one or more trait's worth of variation (i.e. eigenvalues ≥ 1.0). In this way, we were able to reduce the metabolism-scaled predation environment to three factors and limb dimensions to two factors. However, hind-limb length (HLL) was retained as a separate variable since it was calculated as the sum of each of the limb elements.

As the goal of this study was to compare the limb dimensions of populations, we calculated statistical residuals from a least-squares regression of each limb dimension plotted against SVL prior to principal components analysis. We felt this was justified because limb dimensions are highly correlated with body size and this allowed us to take body-size differences among individuals into account. Thus the dependent variables used to test our hypothesis were the two principal components created using the body-size-corrected (residual) population averages as well as the residual HLLs for each population.

Statistical testing of our hypothesis used multiple regression analyses in which the three principal components of metabolism-scaled predator environment were used to explain limb dimensions. Individual effect tests allowed us to determine which factor (and by extension which variables loading heavily on that factor) could explain variation in limb morphology. We repeated the same analyses described above separately for the datasets from wild-caught and lab-reared lizards using the same predation principal components. All data were analysed using the program JMP v.10.0.0 (SAS, Cary, NC, 2012) for Macintosh.

RESULTS

Predation environment

We collected predator abundance data during 291 time periods from 2011 to 2015 from 22 different populations in Nevada, Oregon, and Washington states (Fig. 1, Table 1, Table 2; mean sample size ± SD: 13.2 ± 17.93 periods per site; range: 3–80 periods). Potential predators were classified as one of four categories: predatory (heterospecific) lizards (0.58 ± 0.660 observed per person per kilometre), snakes (0.10 ± 0.117 observed per person per kilometre), predatory birds (0.64 ± 0.749 observed per person per kilometre), and other (conspecific) side-blotched lizards (2.27 ± 0.951 observed per person per kilometre).

In an attempt to determine how many observation periods were necessary to estimate predation environment, we calculated the running average of each predation-environment estimate using two sites (OC and WP) for which we had substantial observation periods (48 and 80, respectively). We then performed a least-squares regression comparing these running averages with the observation-period sequence (sample number). Results indicate that for both sites, sample number affected the running averages of some but not all classes of predators. Namely, we found variation related to sample number in snakes (OC: $F_{1,46} = 37.79$, $P = 0.001$; WP: $F_{1,78} = 43.85$, $P < 0.001$), birds (OC: $F_{1,46} = 80.84$, $P < 0.001$; WP: $F_{1,78} = 77.07$, $P < 0.001$), and other *Uta* (OC: $F_{1,46} = 44.22$, $P < 0.001$; WP: $F_{1,78} = 9.41$, $P = 0.003$), but not in other predatory lizards (OC: $F_{1,46} = 0.91$, $P = 0.346$; WP: n/a) or all predators combined (OC: $F_{1,46} = 1.48$, $P = 0.230$; WP: $F_{1,78} = 1.72$, $P = 0.193$). This suggests that the actual predation environment experienced by side-blotched lizards is not stable, but is continually changing as activity conditions and populations of predators change. However, visual inspection of the data also suggests that 5–10 observation periods are sufficient to arrive at an accurate estimate of predation environment.

We also attempted to detect annual differences in predation environment by performing a one-factor analysis of variance (ANOVA) on observed predators with year as the factor at two sites (OC and WP) for which we had sufficient data (48 and 80 observations, respectively). Similar to sample number, we found significant inter-annual variation in some but not all estimates of predation environment. Namely, we found inter-annual variation

Table 2. Estimates of predation environment of different types of predators of side-blotched lizards observed at each of 22 study sites listed in order from north to south (see Fig. 1)

Site	Observation periods	Observed (non-*Uta*) lizards	Observed snakes	Observed birds	Observed *Uta*
FC	3	0	0.06 ± 0.030 (0.00–0.10)	0.27 ± 0.113 (0.16–0.50)	2.89 ± 1.075 (1.49–5.00)
FE	3	0.53 ± 0.083 (0.38–0.67)	0.16 ± 0.049 (0.06–0.22)	0.39 ± 0.073 (0.24–0.48)	0.86 ± 0.249 (0.38–1.21)
DC	5	0	0.13 ± 0.111 (0.00–0.57)	1.23 ± 0.368 (0.33–2.13)	5.05 ± 1.253 (1.33–9.14)
HR	4	0	0	0.14 ± 0.089 (0.00–0.40)	3.62 ± 0.850 (1.20–5.10)
HB	13	0	0	1.50 ± 0.363 (0.19–4.57)	5.09 ± 1.235 (1.07–16.00)
WP	80	0	0.55 ± 0.084 (0.00–3.60)	2.54 ± 0.257 (0.57–11.58)	2.93 ± 0.235 (0.41–10.75)
DI	6	0.28 ± 0.096 (0.01–0.52)	0.11 ± 0.082 (0.00–0.50)	0.66 ± 0.388 (0.00–2.50)	3.70 ± 1.054 (0.20–7.14)
KP	5	0.30 ± 0.215 (0.01–1.14)	0	0.97 ± 0.458 (0.19–2.67)	2.91 ± 1.001 (0.50–6.00)
AB	6	0	0.07 ± 0.047 (0.00–0.25)	0.64 ± 0.252 (0.00–1.33)	3.15 ± 0.679 (1.90–5.56)
OC	48	1.49 ± 0.305 (0.02–6.00)	0.16 ± 0.053 (0.19–1.37)	3.00 ± 0.290 (0.00–10.53)	1.84 ± 0.600 (0.05–5.72)
SL	12	0.57 ± 0.097 (0.01–1.15)	0.08 ± 0.043 (0.00–0.44)	0.34 ± 0.125 (0.00–1.33)	2.07 ± 0.373 (0.10–4.00)
CH	15	0.39 ± 0.159 (0.02–2.40)	0.03 ± 0.013 (0.00–0.17)	0.23 ± 0.044 (0.00–0.44)	1.74 ± 0.257 (0.44–4.00)
LA	4	0	0.02 ± 0.021 (0.00–0.08)	0.50 ± 0.390 (0.00–1.67)	1.70 ± 0.795 (0.09–3.75)
MO	5	0	0.38 ± 0.086 (0.16–0.67)	2.17 ± 0.616 (0.67–3.56)	0.84 ± 0.226 (0.33–1.42)
HM	4	0	0.22 ± 0.087 (0.00–0.40)	0.36 ± 0.325 (0.00–1.33)	5.07 ± 2.421 (1.18–12.00)
TC	10	1.35 ± 0.220 (0.94–3.07)	0.10 ± 0.020 (0.00–0.18)	1.01 ± 0.197 (0.40–1.96)	1.44 ± 0.156 (0.68–2.38)
LD	10	1.17 ± 0.419 (0.02–3.60)	0.12 ± 0.027 (0.00–0.29)	0.60 ± 0.085 (0.33–1.20)	2.50 ± 0.582 (0.75–6.00)
SV	7	0.68 ± 0.214 (0.08–1.50)	0.06 ± 0.057 (0.00–0.40)	0.15 ± 0.112 (0.00–0.80)	1.04 ± 0.316 (0.38–2.80)
LV	20	1.79 ± 0.367 (0.00–6.67)	0.01 ± 0.004 (0.00–0.61)	0.47 ± 0.101 (0.00–1.50)	1.64 ± 0.271 (0.11–4.50)
HS	21	1.31 ± 0.269 (0.05–3.75)	0.02 ± 0.009 (0.00–0.17)	0.18 ± 0.055 (0.00–1.00)	2.78 ± 0.455 (0.13–7.33)
GA	3	1.30 ± 0.890 (0.00–3.00)	0.02 ± 0.022 (0.00–0.07)	0	2.83 ± 0.572 (1.93–3.89)
WL	7	3.66 ± 1.942 (0.19–9.00)	0.10 ± 0.070 (0.00–0.50)	0.15 ± 0.110 (0.00–0.77)	4.65 ± 1.347 (2.12–12.50)

Note: Data presented are mean ± SEM (min–max) predators observed per person per kilometre for each predator of that type. Although metabolism-scaled abundance estimates were used in subsequent analyses, data presented here are un-scaled abundance estimates for clarity.

in other predatory lizards (OC: $F_{1,46} = 4.22$, $P = 0.046$; WP: n/a), snakes (OC: $F_{1,46} = 40.75$, $P = 0.001$; WP: $F_{1,78} = 56.15$, $P < 0.001$), and birds (OC: $F_{1,46} = 0.16$, $P = 0.695$; WP: $F_{1,78} = 79.74$, $P < 0.001$), but not in other *Uta* (OC: $F_{1,46} = 3.60$, $P = 0.064$; WP: $F_{1,78} = 0.08$, $P = 0.778$) or all predators combined (OC: $F_{1,46} = 0.067$, $P = 0.797$; WP: $F_{1,78} = 1.69$, $P = 0.198$). These results support the idea that the predation environment experienced by side-blotched lizards has been changing through time.

Finally, we performed an analysis of variance relating the average predation environment of all 22 populations to latitude. We found that latitude was related to predatory lizards ($F_{1,20} = 27.27$, $P < 0.001$; Fig. 3A) such that the observed predatory lizards decreased with latitude. However, there was no relationship between latitude and the other classes of predators: snakes ($F_{1,20} = 0.89$, $P = 0.357$; Fig. 3B), birds ($F_{1,20} = 0.92$, $P = 0.350$; Fig. 3C), or other *Uta* ($F_{1,20} = 0.20$, $P = 0.656$; Fig. 3D). In addition, there was no relationship between latitude and all predators combined ($F_{1,20} = 0.71$, $P = 0.411$). These results suggest that while predation environments may vary between populations and across time, only predatory lizards experience latitude-related limitations to their populations across the range of side-blotched lizard populations studied.

Using principal components analysis, we reduced the seven predation-environment traits to three orthogonal factors explaining 63.8% of the total variation (Table 4). PC1 loaded primarily with the abundance and diversity of predatory lizards. PC2 loaded primarily with the abundance and diversity of predatory birds. PC3 loaded primarily with the abundance and diversity of predatory snakes as well as the inverse of side-blotched lizard abundance.

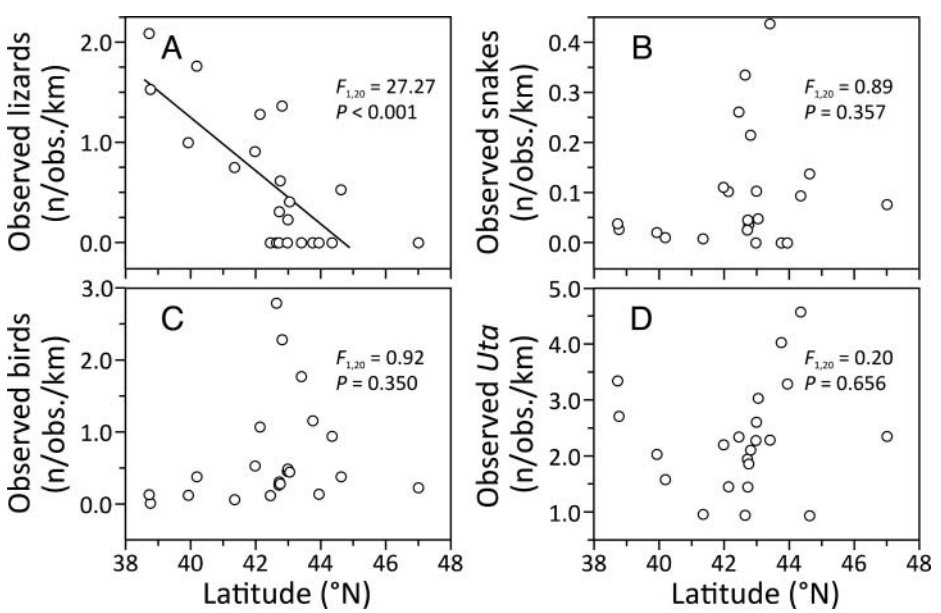

Fig. 3. Relationship between latitude and un-scaled estimates of predation environment showing that only (A) other predatory lizards, but not (B) snakes, (C) birds, or (D) *Uta* are related to latitude. Although metabolism-scaled abundance estimates were used in subsequent analyses, the data presented here are un-scaled abundance estimates for clarity.

Table 3. Body size and hind-limb elements of male side-blotched lizards for each of 22 study sites listed in order from north to south (see Fig. 1)

Site	*n*	Snout–vent length (mm)	Femur length (mm)	Tibia length (mm)	Pes length (mm)	Fourth-toe length (mm)	Total hind-limb length (mm)
FC	49	46.7 ± 0.48 (33.5–52.5)	11.05 ± 0.098 (10.96–11.15)	10.76 ± 0.098 (10.66–10.86)	5.57 ± 0.058 (5.51–5.63)	8.99 ± 0.073 (8.92–9.06)	36.38 ± 0.263 (36.12–36.64)
FE	19	46.0 ± 0.47 (42.9–50.5)	11.57 ± 0.146 (11.42–11.71)	10.98 ± 0.117 (10.87–11.10)	5.53 ± 0.070 (5.46–5.60)	9.64 ± 0.114 (9.52–9.75)	37.71 ± 0.348 (37.36–38.06)
DC	28	46.2 ± 0.39 (42.9–49.4)	11.51 ± 0.108 (11.40–11.62)	11.04 ± 0.083 (10.95–11.12)	5.55 ± 0.037 (5.52–5.59)	9.52 ± 0.095 (9.42–9.61)	37.61 ± 0.220 (37.39–37.83)
HR	44	44.8 ± 0.51 (38.2–49.3)	10.90 ± 0.123 (10.78–11.03)	10.51 ± 0.116 (10.39–10.62)	5.28 ± 0.054 (5.22–5.33)	8.65 ± 0.058 (8.59–8.71)	35.33 ± 0.284 (35.05–35.62)
HB	36	51.0 ± 0.32 (44.1–54.7)	12.29 ± 0.081 (12.21–12.37)	11.57 ± 0.074 (11.49–11.64)	5.83 ± 0.052 (5.78–5.88)	9.52 ± 0.089 (9.43–9.61)	39.21 ± 0.219 (38.99–39.42)
WP	47	50.3 ± 0.46 (44.3–55.1)	12.04 ± 0.117 (11.92–12.16)	11.34 ± 0.114 (11.23–11.46)	5.82 ± 0.061 (5.76–5.88)	9.48 ± 0.099 (9.38–9.58)	38.68 ± 0.324 (38.36–39.01)
DI	28	46.3 ± 0.54 (39.2–50.3)	11.48 ± 0.152 (11.32–11.63)	10.98 ± 0.125 (10.85–11.11)	5.41 ± 0.054 (5.35–5.46)	8.91 ± 0.086 (8.82–9.00)	36.77 ± 0.362 (36.41–37.13)
KP	27	49.9 ± 0.43 (44.5–52.8)	12.22 ± 0.125 (12.10–12.35)	11.59 ± 0.107 (11.48–11.70)	5.69 ± 0.040 (5.65–5.73)	9.68 ± 0.144 (9.54–9.83)	39.19 ± 0.297 (38.89–39.48)
AB	33	47.2 ± 0.44 (42.0–51.7)	11.51 ± 0.134 (11.38–11.64)	10.90 ± 0.095 (10.81–11.00)	5.47 ± 0.043 (5.43–5.52)	9.33 ± 0.069 (9.26–9.40)	37.22 ± 0.265 (36.95–37.48)
OC	39	49.5 ± 0.36 (44.3–54.4)	12.10 ± 0.098 (12.01–12.20)	11.69 ± 0.087 (11.61–11.78)	5.69 ± 0.054 (5.63–5.74)	9.67 ± 0.070 (9.60–9.73)	39.15 ± 0.252 (38.90–39.40)
SL	49	47.2 ± 0.50 (40.9–52.7)	11.51 ± 0.136 (11.38–11.65)	10.97 ± 0.135 (10.83–11.11)	5.62 ± 0.057 (5.56–5.67)	9.16 ± 0.077 (9.08–9.23)	37.26 ± 0.348 (36.91–37.60)
CH	31	46.7 ± 0.43 (43.3–51.5)	11.27 ± 0.123 (11.14–11.39)	10.73 ± 0.116 (10.62–10.85)	5.40 ± 0.053 (5.35–5.46)	8.96 ± 0.066 (8.90–9.03)	36.36 ± 0.274 (36.09–36.64)
LA	32	46.6 ± 0.42 (43.1–50.6)	11.31 ± 0.107 (11.20–11.41)	10.62 ± 0.109 (10.51–10.73)	5.37 ± 0.056 (5.32–5.43)	9.15 ± 0.110 (9.04–9.26)	36.45 ± 0.247 (36.20–36.70)
MO	11	51.0 ± 0.84 (46.5–56.4)	12.71 ± 0.266 (12.45–12.98)	12.00 ± 0.189 (11.82–12.19)	5.98 ± 0.100 (5.88–6.08)	10.27 ± 0.177 (10.09–10.45)	40.97 ± 0.630 (40.34–41.60)
HM	42	47.2 ± 0.34 (42.7–52.4)	11.39 ± 0.087 (11.30–11.48)	10.91 ± 0.074 (10.84–10.99)	5.30 ± 0.046 (5.25–5.34)	9.00 ± 0.079 (8.92–9.08)	36.60 ± 0.201 (36.40–36.80)
TC	27	49.9 ± 0.37 (46.0–53.7)	12.60 ± 0.095 (12.50–12.69)	11.73 ± 0.085 (11.64–11.81)	6.01 ± 0.047 (5.96–6.05)	9.77 ± 0.104 (9.67–9.88)	40.10 ± 0.261 (39.84–40.36)
LD	40	47.8 ± 0.48 (42.3–54.9)	11.60 ± 0.137 (11.46–11.74)	11.10 ± 0.116 (10.99–11.22)	5.55 ± 0.058 (5.49–5.61)	9.56 ± 0.089 (9.47–9.65)	37.81 ± 0.315 (37.49–38.12)
SV	32	46.7 ± 0.42 (41.5–51.4)	11.39 ± 0.108 (11.28–11.49)	10.92 ± 0.103 (10.82–11.02)	5.50 ± 0.046 (5.46–5.55)	9.48 ± 0.100 (9.38–9.58)	37.30 ± 0.315 (36.98–37.61)
LV	54	46.1 ± 0.36 (39.8–52.8)	11.00 ± 0.103 (10.90–11.10)	10.53 ± 0.086 (10.44–10.62)	5.55 ± 0.065 (5.48–5.61)	9.17 ± 0.079 (9.09–9.25)	36.25 ± 0.280 (35.97–36.53)
HS	32	46.9 ± 0.50 (41.3–51.0)	11.69 ± 0.113 (11.58–11.80)	11.14 ± 0.100 (11.04–11.24)	5.73 ± 0.050 (5.68–5.78)	9.50 ± 0.069 (9.44–9.57)	38.06 ± 0.262 (37.80–38.32)
GA	36	48.3 ± 0.67 (43.9–53.8)	12.19 ± 0.092 (12.09–12.28)	11.45 ± 0.083 (11.37–11.53)	5.94 ± 0.055 (5.89–6.00)	9.82 ± 0.094 (9.72–9.91)	39.40 ± 0.266 (39.13–39.66)
WL	38	51.6 ± 0.20 (49.0–54.8)	12.82 ± 0.076 (12.74–12.90)	12.26 ± 0.072 (12.19–12.33)	6.23 ± 0.038 (6.20–6.27)	10.56 ± 0.083 (10.48–10.64)	41.87 ± 0.189 (41.68–42.06)

Note: Data presented are sample size (*n*) and mean ± SEM (min–max). Although size-scaled limb measurements were used in subsequent analyses, data presented here are un-scaled limb dimensions for clarity.

Limb morphology in the wild

We collected limb morphology data from 774 male side-blotched lizards from 2011 to 2013 (Table 3; mean sample size ± SD: 35.2 ± 10.20 individuals per site; range: 11–54 individuals). Using PCA we reduced the four limb-dimension traits to two orthogonal factors explaining 74.7% of the total variation (Table 4). PC1 loaded primarily with the proximal limb elements (femur and tibia lengths). PC2 loaded primarily with the distal limb elements (pes and fourth-toe lengths).

Table 4. Orthogonal PCA loadings of predation environment and limb dimensions for 22 populations of wild side-blotched lizards

	Factor loadings		
Variable	PC1	PC2	PC3
Predation environment			
Scaled *Uta* abundance	–0.127	0.114	**–0.411**
Scaled lizard abundance	**0.942**	–0.047	0.214
Scaled snake abundance	–0.223	0.176	**0.489**
Scaled bird abundance	–0.316	**0.814**	0.032
Lizard diversity	**0.940**	–0.156	–0.021
Snake diversity	0.176	0.196	**0.720**
Bird diversity	0.056	**0.850**	0.115
Eigenvalue	1.972	1.494	1.002
% Variation explained	28.2	21.3	14.3
Limb dimensions			
Residual femur length	**0.780**	0.468	—
Residual tibia length	**0.796**	0.438	—
Residual pes length	0.352	**0.682**	—
Residual fourth-toe length	0.499	**0.705**	—
Eigenvalue	1.615	1.374	—
% Variation explained	40.4	34.3	—

Note: Primary factor loadings are indicated in **bold**.

Table 5. Results of multiple regressions on wild side-blotched lizards between predation factors and limb factors as well as residual hind-limb length

Predation factor	Limb factor 1 (+FL, +TL)	Limb factor 2 (+PL, +FTL)	Residual HLL
Predation factor 1 (+predatory lizards)	0.716^{NS}	**11.320****	**5.728***
Predation factor 2 (+predatory birds)	1.705^{NS}	0.245^{NS}	0.264^{NS}
Predation factor 3 (+predatory snakes, –*Uta*)	0.189^{NS}	1.048^{NS}	0.725^{NS}

Note: In all cases, the degrees of freedom = 3, 18. Data presented are *F*-values. Primary loadings on each factor are provided in parentheses. Significant relationships are presented in **bold**. FL = femur length; TL = tibia length; PL = pes length; FTL = fourth-toe length; HLL = hind-limb length.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant ($P > 0.05$).

Multiple regression analyses relating metabolism-scaled estimates of predation environment to size-adjusted side-blotched lizard limb dimensions revealed that predation environment could explain variation in limb PC2 ($F_{3,18} = 4.382$, $P = 0.018$, $R^2 = 0.422$) as well as HLL ($F_{3,18} = 3.345$, $P = 0.042$, $R^2 = 0.381$). However, predation environment could not explain limb PC1 ($F_{3,18} = 0.883$, $P = 0.469$, $R^2 = 0.128$). Examination of the individual predictor variables indicates that the factor explaining the abundance and diversity of predatory lizards (predation PC1) was the only significant predictor of limb dimensions (Table 5). That is, the abundance and diversity of predatory lizards is positively related to the elongation of the distal (but not proximal) elements of the hind limb of *Uta* and this is sufficient to explain the elongation in total HLL as well.

Limb morphology in the lab

We collected lab morphometric data from 181 male side-blotched lizards representing 97 families from 12 different populations (Table 6; mean family sample size ± SD: 1.9 ± 0.93 offspring per dam; range: 1–5 individuals from each family; mean family number per site:

Table 6. Body size and hind-limb elements of male side-blotched lizards for each of 12 study sites listed in order from north to south (see Fig. 1)

Site	*n*	Snout–vent length (mm)	Femur length (mm)	Tibia length (mm)	Pes length (mm)	Fourth-toe length (mm)	Total hind-limb length (mm)
WP	6	35.0 ± 0.70 (31.6–39.2)	8.62 ± 0.161 (7.99–9.60)	8.86 ± 0.178 (8.09–9.75)	4.48 ± 0.007 (4.07–4.79)	7.99 ± 0.100 (7.61–8.60)	29.95 ± 0.478 (28.04–32.74)
DI	10	34.9 ± 0.86 (32.1–40.8)	8.84 ± 0.221 (7.93–9.99)	8.80 ± 0.225 (7.74–10.11)	4.57 ± 0.137 (4.15–5.42)	7.82 ± 0.155 (6.61–9.41)	30.04 ± 0.667 (26.81–34.05)
AB	10	34.8 ± 0.74 (33.0–37.6)	8.47 ± 0.182 (8.04–9.20)	8.69 ± 0.149 (8.28–9.29)	4.39 ± 0.044 (4.21–4.50)	7.80 ± 0.177 (7.47–8.55)	29.36 ± 0.521 (29.99–31.46)
OC	16	34.9 ± 0.48 (33.0–36.4)	8.80 ± 0.150 (8.10–9.16)	8.92 ± 0.220 (7.90–9.63)	4.70 ± 0.139 (4.20–5.04)	7.94 ± 0.149 (7.17–8.30)	30.35 ± 0.587 (27.79–31.87)
SL	14	36.4 ± 0.51 (33.4–37.8)	9.07 ± 0.136 (8.42–9.60)	9.21 ± 0.141 (8.53–9.69)	4.61 ± 0.087 (4.34–4.99)	8.32 ± 0.183 (7.78–9.45)	31.2 ± 0.483 (29.14–33.63)
CH	18	35.5 ± 0.60 (32.1–37.9)	8.76 ± 0.168 (7.78–9.68)	8.83 ± 0.14 (7.93–9.32)	4.51 ± 0.111 (4.08–5.33)	7.78 ± 0.155 (6.90–8.65)	29.89 ± 0.524 (26.70–32.81)
HM	12	35.0 ± 0.83 (32.3–40.0)	8.55 ± 0.214 (7.85–9.92)	8.76 ± 0.196 (7.84–10.00)	4.36 ± 0.143 (3.73–4.90)	7.47 ± 0.219 (6.97–9.06)	29.14 ± 0.723 (26.46–33.83)
LD	16	35.8 ± 0.85 (30.0–38.9)	8.85 ± 0.173 (7.93–9.79)	9.09 ± 0.181 (8.00–9.89)	4.56 ± 0.132 (4.04–5.15)	7.99 ± 0.240 (6.53–8.83)	30.49 ± 0.669 (26.51–33.64)
SV	2	36.9 ± 1.50 (35.4–38.4)	8.91 ± 0.220 (8.69–9.13)	9.39 ± 0.143 (9.25–9.53)	4.80 ± 0.364 (4.43–5.16)	8.01 ± 0.135 (7.88–8.15)	31.12 ± 0.592 (30.52–31.71)
HS	22	36.0 ± 0.41 (34.1–37.8)	8.78 ± 0.130 (8.23–9.56)	8.97 ± 0.196 (8.24–9.47)	4.71 ± 0.120 (4.04–5.25)	8.08 ± 0.141 (7.42–8.64)	30.53 ± 0.431 (29.21–32.84)
GA	23	39.3 ± 0.51 (37.2–40.9)	9.65 ± 0.095 (9.32–10.01)	9.86 ± 0.121 (9.51–10.42)	5.22 ± 0.087 (4.84–5.56)	8.87 ± 0.147 (8.12–9.41)	33.61 ± 0.382 (32.19–35.12)

Note: Data presented are family sample size (*n*) and family mean ± SEM (min–max).

Table 7. Orthogonal PCA loadings of limb dimensions for 12 populations of laboratory-reared side-blotched lizards

	Factor loadings	
Variable	PC1	PC2
Residual femur length	**0.819**	0.275
Residual tibia length	0.114	**0.887**
Residual pes length	0.322	**0.770**
Residual fourth-toe length	**0.880**	0.142
Eigenvalue	1.563	1.476
% Variation explained	39.1	36.9

Note: Primary factor loadings are indicated in **bold**.

8.1 ± 2.27 families; range: 3–10 families). Using PCA we reduced the four limb-dimension traits to two orthogonal factors explaining 76.0% of the total variation (Table 7). PC1 loaded primarily with the femur and fourth-toe lengths. PC2 loaded primarily with the tibia and pes lengths.

Multiple regression analyses relating metabolism-scaled estimates of predation environment to size-adjusted side-blotched lizard limb dimensions revealed that predation environment could not explain variation in limb PC1 ($F_{3,8} = 0.823$, $P = 0.517$, $R^2 = 0.236$), limb PC2 ($F_{3,8} = 1.708$, $P = 0.242$, $R^2 = 0.390$) or HLL ($F_{3,8} = 1.125$, $P = 0.395$, $R^2 = 0.297$). Examination of the individual predictor variables further supports the lack of relationship between predation environment and limb morphology. That is, the significant results detected using wild lizards were not supported using laboratory-reared animals.

DISCUSSION

The results of this study suggest that the hind-limb length of wild side-blotched lizards is related to predation environment, but we cannot reject the possibility that these results are due to phenotypic plasticity among populations. Specifically, we found that in natural populations the distal limb elements (pes and fourth-toe lengths) and total hind-limb length (HLL) are all positively related to the predation environment, in particular as it relates to predatory lizards. However, we also found that these differences are not retained when animals are reared in a common-garden environment.

While previous studies have reported selection on limb morphology (Losos *et al.*, 2006; Calsbeek and Smith, 2008; Calsbeek and Cox, 2010), our results do not unambiguously support a relationship between predation and limb dimensions. These previous studies used island settings to maintain distinct predation environments and create replicate study populations. Furthermore, they only focused on a single species of predator. For example, Losos and colleagues (2006) compared the morphology and behaviour of island populations after introducing a single species of predatory curly-tailed lizard (*Leiocephalus carinatus*). Considering that the suite of predators present in any environment contributes to the predation pressure experienced by prey (Case, 1975), we predicted that *Uta* populations at sites with higher predator abundances or with greater diversity of predators would possess longer hind limbs than those at sites experiencing less predation; however, we lack clear support for this idea.

Populations of side-blotched lizards found outside of the range of predatory lizards may experience less selection associated with this alteration to the predation environment. Although palaeoclimatological evidence suggests that the Great Basin and interior Pacific Northwest were warmer and drier 6000 years ago (Mehringer, 1985), we do not know how this affected the distributions of side-blotched lizards and their predators. One possibility is that *Uta* and its predators expanded throughout the Great Basin and that some of those predator species (particularly predatory lizards) have experienced a range contraction leading to relaxed selection. Another possibility is that side-blotched lizards only recently expanded their range beyond that of predatory lizards. However, the specifics of this study system suggest that in response to differences in the predation environment, the limbs of side-blotched lizards have not responded by shortening. That is, although we expected a greater locomotor performance facilitated by longer hind limbs to be advantageous in historical predator evasion (Bonine and Garland, 1999), in the absence of predatory lizards the expense of maintaining longer limbs does not appear to have led to a reduction in their length.

An unexpected result of this study is that only one type of predator, namely predatory lizards, was related to variation in limb morphology. This relationship may be associated with the type of foraging strategy used by predatory lizards and the escape response that strategy evokes. An escape response can be energetically expensive in terms of lost foraging and reproductive opportunities, and must be weighed against the risk of injury or mortality associated with a predator (e.g. Martín and López, 1999). Although some variation in foraging strategy can exist within a predator type (e.g. sit-and-wait vs. active foraging), the general morphological differences between the predator types (e.g. lizards vs. snakes vs. birds) likely produce unique foraging strategies that generate distinct selective pressures on prey. For example, ground-dwelling lizards overcome their prey using potentially long-distance pursuits that can involve relatively fast accelerations, high speeds, agility, and even prey excavation (Montanucci, 1965, 1978; Nussbaum *et al.*, 1983).

Uta can and do evade predators by locating and using a refuge that is inaccessible to their predators. While the terrestrial snake predators of *Uta* may also achieve relatively high speeds and actively pursue their prey (Jones and Whitford, 1989; Secor, 1995), a major difference from predatory lizards is that snakes more readily gain access to burrows or refuges due to their body shape. Thus, *Uta* may evade snakes by avoiding unsafe refuges, by attempting to put sufficient distance between themselves and the predator, and by using crypsis (Secor, 1995; Zani *et al.*, 2009). While both lizards and snakes locate and pursue prey terrestrially, avian predators use rapid aerial descent to ambush prey, which requires clear visual identification (Endler, 1978). Escape from birds is enhanced through the use of speed and agility and then immediately hiding from view in the nearest refuge (Stamps, 1983; Ito and Mori, 2012). Among the different types of predators included in this study, the foraging strategy of other lizard predators appears most likely to select for greater sprint speeds that would result in the evolution of longer limbs. Thus, predatory lizards may be the only predator type to exert sufficiently strong selective pressures to evoke a response in the limb morphology of *Uta* as we detected using wild populations.

Hind-limb length has been identified as a heritable trait for numerous lizards (Tsuji *et al.*, 1989; Vanhooydonck *et al.*, 2001). Yet, previous studies have indicated that variation in morphological and performance traits may be associated with phenotypic plasticity (Losos *et al.*, 2000; Van Buskirk, 2002; Irschick and Meyers, 2007). For example, Smith and Van Buskirk (1995) found environmentally induced variation in tail-fin height of tadpoles to be the result of phenotypic plasticity and not due to evolved differences.

As a further check on the effects of phenotypic plasticity, we reared animals in common-garden conditions in the lab. Our results show there was no suggestion that limb morphology differences persist in animals reared in the lab, which is consistent with phenotypic plasticity causing the pattern we observed in the wild. However, lack of evolved differences in the lab does not automatically prove that limb morphology is phenotypically plastic in this species. For example, even after artificial selection for high levels of voluntary wheel running in mice, Middleton *et al.* (2008) failed to detect widespread effects of wheel access on limb morphology. Similarly, Husak *et al.* (2015) reported that sprint-trained *Anolis* lizards had larger areas of oxidative muscle fibres, but that these changes did not result in improved maximal sprint speed. Thus we cannot reject the hypothesis that environmentally induced filtering in the wild resulted in an altered distribution of limb morphology.

To account for potential environmentally induced phenotypic plasticity or environmental filtering, we attempted to measure populations inhabiting similar environmental conditions (i.e. shrub-steppe habitat). Yet relevant differences inevitably exist among sites (see Table 1). Aspects of the environment that could influence limb morphology include food availability, rainfall, substrate type, and habitat structure, but we did not attempt to determine which environmental variables are responsible for the apparent pattern in wild-caught animals.

In conclusion, by comparing populations of wild-caught side-blotched lizards, we found a relationship between limb morphology and predatory lizards that suggests that predatory lizards are a cause of limb morphology differences among populations. However, the absence of this pattern in lab-reared lizards fails to support that the differences among populations are evolved. Yet neither can we clearly implicate phenotypic plasticity in limb morphology. Thus, the results of this study should serve as a caution against inferring evolutionary patterns without also testing for non-inherited sources of variation, such as those caused by phenotypic plasticity.

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