

# Fire-disturbed landscapes induce phenotypic plasticity in lizard locomotor performance

K. H. Wild<sup>1,2</sup> & C. M. Gienger<sup>1</sup>

<sup>1</sup> Department of Biology and Center of Excellence for Field Biology, Austin Peay State University, Clarksville, TN, USA

<sup>2</sup> Institute for Applied Ecology, University of Canberra, Canberra, ACT, Australia

## Keywords

phenotypic plasticity; locomotor performance; prescribed fire; temperature; *Sceloporus undulatus*; thermal quality; acclimation; reptile.

## Correspondence

C.M. Gienger, Department of Biology and Center of Excellence for Field Biology, Austin Peay State University, Clarksville, TN 37044 USA.

Email: giengerc@apsu.edu

Editor: Nigel Bennett

Received 7 September 2017; revised 4 January 2018; accepted 10 January 2018

doi:10.1111/jzo.12545

## Abstract

Phenotypic plasticity can occur in response to environmental fluctuation and can bring about pronounced changes in behavioral, physiological, or morphological traits. Anthropogenic habitat modifications, such as prescribed fire, can provide insight on the phenotypic response of ectotherms to structural habitat change. Our objective was to quantify the effect of fire-altered landscapes on the locomotor performance of the eastern fence lizard (*Sceloporus undulatus*). Lizard sprint performance was compared among three habitats with different fire histories: a control habitat, which had not experienced fire in more than 60 years, a recovering habitat that had not experienced fire in 4 years, and a recent burn habitat that burned less than 6 months prior to the study. There were significant differences in locomotor performance among lizards from the different habitats (indicative of phenotypic plasticity), and lizards in the recent burn habitat had significantly higher maximum sprint speeds than lizards in recovering and control habitats. To measure the consistency of locomotor performance within individuals, lizards were captured and raced during the field seasons of 2014 and again in 2015. Locomotor performance was significantly repeatable across years, suggesting lizard populations contain considerable individual variation, despite this trait being closely tied to fitness. To the best of our knowledge, this is the first study to observe individual between-year repeatability in performance of free-ranging *S. undulatus*. Lizards had similar body condition among habitats suggesting that nutritional status did not play a role in performance plasticity. Habitats differed both structurally and thermally, and less restrictive thermal regimes in recently burned habitats appear to be the underlying mechanism permitting increased lizard locomotor performance.

## Introduction

Variation in phenotypic traits is common in natural populations and may be attributed to underlying influences of natural selection among individuals (Price, Qvarnström & Irwin, 2003; Piersma & Van Gils, 2011). Investigating how individual variation is maintained requires an understanding of how genotypes and phenotypes interact with the surrounding environment. Phenotypic pathways can be either irreversible responses to abiotic factors experienced during ontogeny, or they can be reversible in response to fluctuating environmental factors (Dewitt, Sih & Wilson, 1998; Sarre, Georges & Quinn, 2004; Warner & Shine, 2008). Plasticity can be induced by biotic factors, such as the presence of predators or competitors (Weisser, Braendle & Minoretti, 1999; Mondor, Rosenheim & Addicott, 2005) or by abiotic factors such as temperature, salinity, or habitat structure (Tomkins, 1999; Neufeld & Palmer, 2008; Shaw *et al.*, 2014). Thus, phenotypic changes in

response to habitat alteration can be responsible for pronounced differences in behavioral, physiological, morphological, and/or life-history traits. Evidence of phenotypic plasticity in response to anthropogenic habitat alterations have been well described in plants, but less so for vertebrates that are highly sensitive to thermal regimes (Van Kleunen & Fischer, 2005; Rubio de Casas *et al.*, 2009). For example, predicted shifts in thermal regimes, caused by climate change, can induce variation in plasticity across geographic ranges of a single species (Valladares *et al.*, 2014). It is appropriate to assume that the ability to adapt *in situ* may have potential fitness consequences (Matesanz, Gianoli & Valladares, 2010; Chevin, Lande & Mace, 2010).

Locomotor ability is a common metric used to assess whole-animal performance (Arnold, 1983; Husak, 2006), and the ability to effectively traverse the environment can play an important role in individual fitness (Irschick & Losos, 1998; Warner & Andrews, 2002; Miles, 2004). Studies focusing on

ectothermic vertebrates have shown that individuals with high locomotor performance also tend to have higher success in fitness-related activities including prey acquisition (Ayers & Shine, 1997), predator escape (Lailvaux, Alexander & Whiting, 2003), social dominance (Husak & Fox, 2006), and reproductive success (Phillips *et al.*, 2006). Environmental temperature directly influences the body temperature of ectotherms, which in turn strongly affects their behavior, physiology, and performance (Huey, 1982). Reptiles generally use behavioral thermoregulation to achieve and maintain body temperatures that permit performance near optimal levels (Angilletta, Niewiarowski & Navas, 2002), but thermoregulatory strategies vary considerably by species and environment (Adolph, 1990). Different scales of environmental thermal heterogeneity may potentially lead to considerable differences in phenotype (Johnston & Temple, 2002; Shine, 2004; Clusella-Trullas, Terblanche & Chown, 2010).

Thermal heterogeneity induced by habitat alteration (e.g., vegetation removal by fire, herbicide applications, logging) can affect local microclimates available to animals and landscapes experiencing fire may have improved thermal habitat quality (Webb *et al.*, 2005; Hossack *et al.*, 2009; Greenberg, Forrest & Waldrop, 2010). Fire alters forest communities by reducing canopy cover, leaf litter, and coarse woody debris (Hutchinson *et al.*, 2005), and effectively interrupts natural vegetative community succession (Driscoll *et al.*, 2010). As a result of effective fire suppression by resource management agencies, large-scale naturally occurring wildfires have largely been replaced with smaller scale prescribed burning (Fernandes & Botelho, 2003). Typically, prescribed fires burn at varying intensities across the landscape (Turner, Romme & Tinker, 2003), creating a patchy mosaic of different habitats that provide new establishment opportunities for both plants and animals (Fisher & Wilkinson, 2005). Increased structural habitat complexity in recently burned landscapes can provide new microhabitat opportunities such as increased burrowing habitats for reptiles (Yager *et al.*, 2007), increased nesting habitats for birds (Saab *et al.*, 2005), and increase prey abundances for mammals (Lacki *et al.*, 2009). Previous studies have shown that fire disturbances can benefit species that prefer earlier successional forests, such as heliothermic reptiles (Perry, Rudolph & Thill, 2009; Howey, Dickinson & Roosenburg, 2016). However, species that depend on successional processes to provide specific habitat features, such as accumulated layers of leaf litter for refuge, may be more susceptible to the impacts of fire (Fenner & Bull, 2007; Howey & Roosenburg, 2013).

Here, we test the effects of habitat alteration by fire on locomotor performance and body condition of eastern fence lizards (*Sceloporus undulatus*) across a chronosequence of recovering eastern deciduous forest. The eastern fence lizard is a nearly ubiquitous forest-dwelling lizard occurring across much of the eastern US (Tinkle & Ballinger, 1972). Fire disturbance is common throughout the species range and because fire creates pronounced physical changes in habitat structure, we hypothesize that increased habitat heterogeneity may induce a phenotypic response in body condition and in locomotor performance of *S. undulatus*. Both are traits that have been used as proxies for measuring individual fitness (Stevenson

& Woods, 2006; Husak *et al.*, 2006). We predict that recently burned sites, with higher habitat heterogeneity, should provide new foraging opportunities to lizards, and thus increase body condition. We also expect habitat heterogeneity created by fire will provide increased thermal opportunities and elicit a plastic response in locomotor performance in lizards. Our goal is to understand the responses of ectotherms to structurally altered environments using locomotor performance and body condition indices as possible proxies for flexible phenotypes that are fitness related.

## Materials and methods

Study sites were located at the Land Between the Lakes National Recreation Area (LBL) in Trigg County, Kentucky, USA. Historically, LBL was a native oak-savanna, but after many decades of fire suppression, the dominant vegetative community has changed to secondary oak-hickory forest (Close, Fralish & Franklin, 2002). Recently, prescribed fire has been used as a management tool in attempts to restore the historic oak-grasslands of LBL. During Spring and Summers of 2014 and 2015, adult ( $\geq 1$  year of age) eastern fence lizards were captured by hand or by noosing (Fitzgerald, 2012). Sex was determined using morphological characteristics including enlarged base of the tail, femoral pores, post-anal scales, and ventral coloration. Reproductive condition of females was noted in the field, and gravid females were not used for locomotor performance trials. Capture locations were recorded with a handheld GPS and percent canopy cover at the location of capture was measured for a subset of captured lizards ( $n = 34$ ) with a spherical densiometer. Lizards were placed in cloth bags and transported to Hancock Biological Station (Murray, KY; ~16 km from study sites) for laboratory locomotor performance trials. After completion of locomotor trials lizards were marked with a unique toe clip and released back at the location of capture.

To measure the effects of habitat alteration on performance, three study areas with different fire histories (prescribed burns) were selected. The first was a control site (control) which had not experienced fire in more than 60 years and was at a climax community state (Close *et al.*, 2002); the second site was burned in March 2010 (recovering; 4 years since burning) and the third was burned in February 2014 (recent burn; < 6 months since burning). Sites ranged from 160 to 1000 hectares and were surrounded by mixed oak-hickory forest. Because of the considerable size of the burn areas, fire treatments were not replicated, and we consider the study a natural experiment (Oksanen, 2001) with individuals experiencing the fire-alteration of habitat simultaneously.

Each habitat type was surveyed for lizards at least twice a week, and locomotor performance trials occurred within 24 h of capture. Before each locomotor trial, lizards were placed individually into copper containers (repurposed autoclave pipette boxes; 4 cm  $\times$  6 cm  $\times$  25 cm) that were housed inside a lighted incubator (Percival I30-BLL). Incubator temperature was maintained at 33°C, which is the preferred body temperature of *S. undulatus* in a laboratory thermal gradient (Angilletta, 2001) and near the thermal optima for sprinting in this species (34.1°C; Angilletta

*et al.*, 2002). After 30 min of thermal equilibration, lizards were placed on a  $2.4 \times 0.2$  m racetrack and encouraged to sprint the length of the track by prodding with a soft-bristle paintbrush. Races were recorded using a Midland XTC 720p High Definition Action Camera recording at 35 frames per second. The camera was mounted 3 m above the center of the racetrack, such that the entire length of the track was visible on the recording. The racetrack floor was covered by Astroturf that was marked into 25 cm segments.

Lizards were raced three times with trials separated by at least 30 min for recovery. The quality of each sprinting trial was classified as 'poor' if the lizard paused or reversed direction while sprinting, or 'good' when a continuous run was made (Van Berkum *et al.*, 1989). A minimum of two 'good' trials were needed for an individual to be included in analyses. The same researcher (K.W.) conducted all trials and video analysis. Videos were analyzed using Tracker Video Software (version 4.85; [www.cabrillo.edu/tracker](http://www.cabrillo.edu/tracker)) following standard video protocols for measuring sprint speed (Tulli, Abdala & Cruz, 2012). Lizard performance was measured in two ways: (1) maximum sprint speed; defined as the fastest 25-cm interval, representing a 'burst' reaction frequently observed in the field, and (2) maximum 2-m run speed; determined as the fastest 2-m total-track run speed, representing lizard's ability to actively forage and engage in territory defense (Tulli *et al.*, 2012). After locomotor trials, morphological measurements were recorded for each individual including snout-to-vent length (SVL), body mass, and hind limb length (HLL was defined as the greatest distance on the outstretched leg from the distal tip of the fourth toe to the point of insertion in the body wall; Pianka, 1969). Lizards were measured to the nearest 0.1 mm for length and 0.25 g for mass.

A general linear model (GLM) was used to compare individual performance measurements (maximum sprint speed and 2-m run) among the habitats with different fire histories (< 6 months since burn, 4 years since burn, and 60+ years since burn). The main effects for the GLM were sex and site, on both performance measurements, with hind limb length (HLL) and body condition index (BCI) used as covariates. Hind limb length was used to remove the potential allometric effects of body size on sprint performance (Tsuji *et al.*, 1989) and BCI was used as a proxy of individual health. The BCI was calculated from the residuals of an ordinary least squares linear regression of mass (g) on length (SVL). If main effects of the model were significant, they were followed with a Tukey HSD post hoc test; LS Means are reported to account for slight differences in body size among groups. An ANOVA was used to compare BCI measurements of *S. undulatus* among recent burn, recovery and control treatments. Any individuals with missing tails were excluded from BCI analysis.

To determine whether habitats with different burn histories differed in thermal opportunities available to lizards, environmental data loggers (Hobo Pendant Loggers) were randomly placed along a 100 m transect at the recent burn, recovering, and control sites (11 loggers at each site). Data loggers recorded temperatures every 10 minutes over a 3-day period (early July 2015). For analysis, the maximum and minimum temperatures of each site were calculated for each hour of the

day. For estimating differences in thermal opportunities among the burn and control habitats, the duration in which environmental temperatures were within the 95% performance breath interval for locomotor performance ( $B_{95}$ : 31.3–37.0°C; Angilletta, 2001) were summed over the 72-h sample period. Vegetative canopy cover of lizard capture locations was compared among sites with ANOVA and a Tukey HSD post hoc test for pairwise comparisons among sites.

We estimated the repeatability (R) of locomotor performance across years using lizards captured and measured in 2014 and again in 2015. Lizards were individually marked with toe clips after the first measurement in 2014, and recaptured lizards in 2015 were identified and re-assessed for sprint performance. For both years, lizards were subjected to the same performance measurement protocol described above. To calculate the repeatability of locomotor performance (maximum sprint speed and 2-m run), we followed the general linear mixed-effects frameworks of Nakagawa & Schielzeth (2010) and Dingemanse & Dochtermann (2013). We used the rptGaussian function of the package rptR (Stoffel, Nakagawa & Schielzeth, 2017) to fit a linear mixed model for sprint performance holding year as a fixed effect and site and lizard ID as random effects. This model controls for possible conflation of site and individual differences and for repeated measurements of each individual. We used 1000 parametric bootstraps and permutations to estimate uncertainty in the repeatability estimate (standard error). Due to the difficulty in capturing the same animals across years, samples from the recovering and control treatments were pooled for repeatability analysis.

## Results

A total of 80 lizards were captured and tested for locomotor performance during the 2014 field season, 28 in control habitat (mean SVL of  $62.7 \pm 1.3$  mm), 26 in recovering habitat (mean SVL of  $65.1 \pm 1.3$  mm), and 26 lizards in the burn habitat (mean SVL of  $67.3 \pm 1.3$  mm). Snout-to-vent length did not vary among the three habitats ( $F_{2,77} = 2.92$ ;  $P = 0.06$ ) and there was also no difference in body condition ( $F_{2,76} = 0.16$ ;  $P = 0.86$ ). In comparing maximum sprint speeds of all lizards captured at the three habitats, there was no difference in speeds between males (LS mean =  $2.80 \text{ m sec}^{-1}$ ) and females (LS mean =  $2.59 \text{ m sec}^{-1}$ ;  $F_{1,73} = 0.28$ ;  $P = 0.60$ ; Table 1). The body condition covariate (BCI) did not have an effect on maximum sprint speed ( $F_{1,73} = 0.05$ ;  $P = 0.82$ ), however, the hind limb length covariate (HLL) did exert an effect on maximum sprint speed ( $F_{1,73} = .37$ ;  $P = 0.01$ ). Once the effects of sex, BCI, and HLL were accounted for, habitat type had an effect on maximum sprint speed ( $F_{2,73} = 24.59$ ;  $P < 0.01$ ; Table 1; Fig. 1). Pairwise comparisons showed that lizards in the recent burn habitat had higher maximum sprint speed (LS mean =  $3.14 \text{ m sec}^{-1}$ ) than those captured in control habitat ( $P < 0.01$ ; LS mean =  $2.31 \text{ m sec}^{-1}$ ) or recovering habitat ( $P < 0.01$ ; LS mean =  $2.58 \text{ m sec}^{-1}$ ). There was no difference between the maximum sprint speeds of lizards captured at recovering and control habitats ( $P = 0.09$ ).

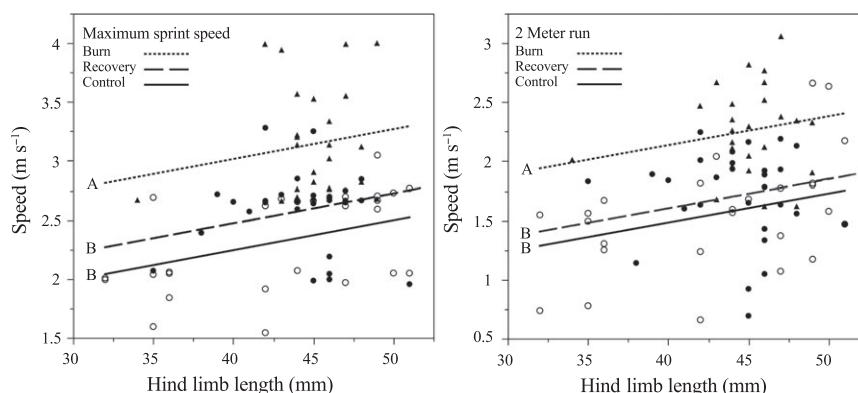
In comparing 2-m runs of lizards from all three habitats, there was no difference between males (LS mean =  $1.76 \text{ m}$

**Table 1** Effects of sex and site (habitats with contrasting fire histories) on lizard sprint performance

Performance Metric	Sex			Site				Covariate	
	Male	Female	<i>P</i> -value	Burn	Recovery	Control	<i>P</i> -value	HLL	BCI
Maximum sprint speed (m s <sup>-1</sup> )	2.70 (2.58-2.82) <sup>A</sup>	2.65 (2.50-2.79) <sup>A</sup>	0.60	3.12 (2.96-3.28) <sup>A</sup>	2.57 (2.42-2.72) <sup>B</sup>	2.32 (2.16-2.49) <sup>B</sup>	<0.01	<0.01	0.82
2-m run speed (m s <sup>-1</sup> )	1.86 (1.73-1.98) <sup>A</sup>	1.81 (1.66-1.96) <sup>A</sup>	0.65	2.24 (2.07-2.40) <sup>A</sup>	1.70 (1.54-1.86) <sup>B</sup>	1.56 (1.39-1.73) <sup>B</sup>	<0.01	<0.02	0.78

Hind limb length (HLL) and body condition index (BCI) were used as model covariates in a GLM.

Data are least square means (LS Mean) with 95% confidence intervals; groups with differing superscript letters indicate least square means being different on a pairwise basis.



**Figure 1** Maximum sprint speed (left) and 2-m run speed (right) of lizards captured at three habitats with contrasting fire histories. Triangles represent lizards captured at burn habitat (<6 months since burned). Solid circles represent lizards captured at recovery habitat (4 years since burn). Open circles represent lizards captured at control habitat ( $\geq 60$  years since burn). Lines with different letters indicate least square means differing on a pairwise basis.

sec<sup>-1</sup>) and females (LS mean = 1.95 m sec<sup>-1</sup>;  $F_{1,73} = 0.21$ ;  $P = 0.65$ ; Table 1). The body condition covariate (BCI) did not have an effect on 2-m run speed ( $F_{1,73} = 0.08$ ;  $P = 0.78$ ), but the hind limb length covariate (HLL) influenced 2-m run speed ( $F_{1,73} = 5.40$ ;  $P < 0.05$ ). Once the effect of sex, BCI, and HLL were accounted for, habitat type had an effect on 2-m run speed ( $F_{2,73} = 24.59$ ;  $P < 0.01$ ; Table 1; Fig. 1). Pairwise comparisons showed that lizards in the recent burn habitat had faster 2-m run speeds (LS mean = 2.26 m sec<sup>-1</sup>) than those captured in control habitat (LS mean = 1.73 m sec<sup>-1</sup>;  $P < 0.01$ ) or recovering habitat (LS mean = 1.86 m sec<sup>-1</sup>;  $P < 0.01$ ). There was no difference between the 2-m run speeds of lizards in recovering and control habitats ( $P = 0.53$ ).

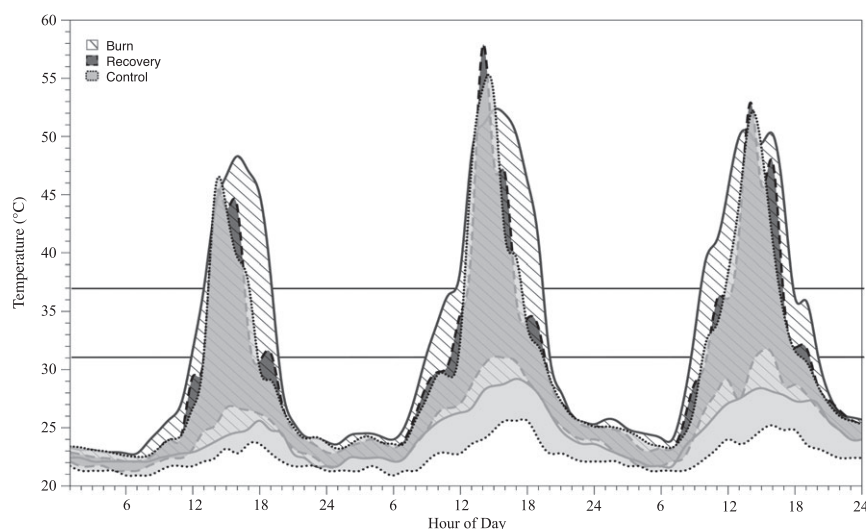
In comparing the repeatability of maximum sprint speed and 2-m run, 14 individuals were measured during both 2014 and 2015 (eight males and six females). Maximum sprint speeds were repeatable among individuals between 2014 (LS mean =  $2.54 \pm 0.43$  m sec<sup>-1</sup>) and 2015 (LS mean =  $2.44 \pm 0.47$  m sec<sup>-1</sup>; repeatability ( $R$ ) = 0.80 (SE = 0.22);  $D = 11.1$ ;  $P = 0.0004$ ). Also, 2-m run speeds were repeatable among individuals between 2014 (mean =  $1.79 \pm 0.54$  m sec<sup>-1</sup>) and 2015 (mean =  $1.79 \pm 0.47$  m sec<sup>-1</sup>; repeatability ( $R$ ) = 0.40 (SE = 0.25);  $D = 3.36$ ;  $P = 0.03$ ).

Thermal opportunities for lizards to maintain body temperatures within the optimal sprint performance range, 31.3–37.0°C, varied among the three habitats (Fig. 2). Over the 3-day measurement period, the recent burn habitat offered more thermal opportunities to maintain body temperature within the optimal sprint performance range ( $9.3 \pm 1.0$  SE hours per day) than recovery habitats ( $7.0 \pm 1.3$  SE hours per day), or control habitats ( $6.7 \pm 1.2$  SE hours per day). The vegetative canopy cover for lizard capture locations differed among habitats ( $F_{2,31} = 20.42$ ;  $P < 0.01$ ; Fig. 3) and pairwise comparisons showed that recent burn habitats had lower canopy cover ( $55.4 \pm 3.1\%$ ) than recovering ( $78.7 \pm 3.6\%$ ;  $P < 0.01$ ) and control habitats ( $82.4 \pm 3.4\%$ ;  $P < 0.01$ ). There was no pairwise difference in canopy cover between control and recovering habitats ( $P = 0.74$ ).

## Discussion

This study demonstrates that locomotor performance in *S. undulatus* can be plastic among habitats with varying fire histories, and that thermal differences resulting from habitat alteration by prescribed fire likely underlie the phenotypic plasticity. Lizards captured in recently burned habitats (burned 3–6 months previous) had higher maximum sprint speeds and



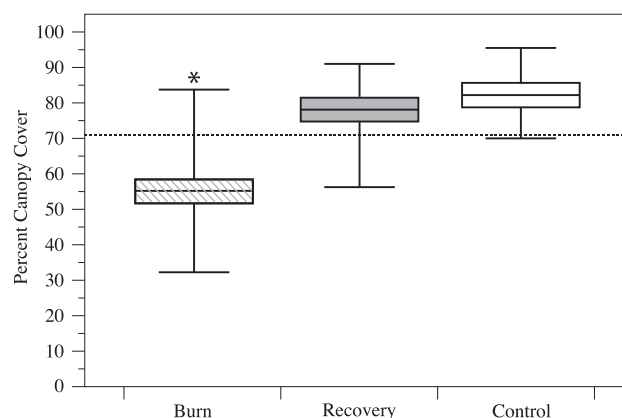


**Figure 2** Environmental thermal opportunities among three sites with contrasting fire histories. Minimum/maximum temperature envelopes were calculated for each habitat over a 72-h period in July 2015. Horizontal lines represent the 95% performance breadth interval ( $B_{95}$ : 31.3–37.0°C) of *Sceloporus undulatus* (Angilletta, 2001). The recent burn habitat had more opportunities to maintain body temperature within the  $B_{95}$  performance breadth ( $9.3 \pm 1.2$  SE hours day<sup>-1</sup>) than recovery ( $7.0 \pm 1.5$  SE hours day<sup>-1</sup>) and control habitats ( $6.7 \pm 1.3$  SE hours day<sup>-1</sup>).

higher 2-m run speeds than lizards from recovery or control habitats (Fig. 1). Prescribed fire leads to increased habitat structural heterogeneity, lower vegetative canopy, and an increased range of environmental temperatures available to lizards (Fig. 2). Environmental temperatures at recently burned sites allowed lizards to maintain body temperatures within the 95% optimal sprint performance range ( $B_{95}$ ) for approximately 2.3 h more per day (a 32.9% increase) than recovering or control habitats (Fig. 2).

The most likely explanation for the observed phenotypic plasticity in lizard locomotor performance is thermal acclimatization, a rapid physiological change (typically within days or months) in response to an environmental cue (Angilletta, 2009; Schulte, Healy & Fanguie, 2011). Lizard muscle power output has been shown to have a strong thermal dependence (Putnam & Bennett, 1982; Bennett, 1984). The gastrocnemius muscle plays an important role in locomotion and power output and is an important determinant of sprint performance in *Sceloporus* lizards (Higham, Korchari & McBrayer, 2011). Glucose transporter type four (GLUT-4) facilitates glucose transport to the gastrocnemius and can be significantly upregulated in only a few days (Garland & Kelly, 2006; Gomes *et al.*, 2009). Enzyme activities can be altered in response to changes in temperature by the expression of allozymes and isozymes with different thermal sensitivities (Dahlhoff & Rank, 2000; Podrabsky & Somero, 2004), or by changing rates of enzyme transcription (Guderley, Leory & Gagne, 2001; Schnurr, Yin & Scott, 2014). Thus, differences in locomotor performance among habitat types could result from differing thermal environments influencing the regulatory pathways of muscle function, which would in turn influence performance.

Several examples from the literature support the contention that thermal acclimatization (or acclimation) enhances



**Figure 3** Vegetative canopy cover among lizard habitats with differing fire histories. Burn habitats had lower mean canopy cover ( $55.4\% \pm 3.1$  SE) than recovering ( $78.7\% \pm 3.6$  SE), and control habitats ( $82.3\% \pm 3.4$  SE). Horizontal lines in each box represents mean per cent canopy cover for each site; boxes represent  $\pm 1$  SE; whiskers show minimum and maximum values. Dotted line represents grand mean of all sites (70.9%). Asterisk indicates significant difference ( $P < 0.05$ ) in pairwise comparison.

performance abilities across various taxa; filtration in mollusks (Newell, Johnson & Kofoed, 1977), fighting success in crustaceans (Seebacher & Wilson, 2006), swimming in fishes (Temple, Wakeling & Johnston, 2000), jumping in amphibians (Renaud & Stevens, 1983), and swimming performance in reptiles (Glanville & Seebacher, 2006). The short time scale over which acclimatization or acclimation occurred in these examples (days to months) suggests that ectotherms can rapidly adjust physiological performance in novel thermal environments. Our data suggest that lizards occupying recently burned

habitats could routinely achieve temperatures that permit optimal performance for longer, and that this could allow the conditions necessary for thermal acclimatization. This could create a shift in performance within a short period (Glanville & Seebacher, 2006), allowing lizards from burn sites to run faster than lizards from recovery and control sites, even when tested at the same temperature in a laboratory setting.

Wider ranges of environmental temperatures, as we have observed in fire-altered landscapes, may also allow higher rates of energy assimilation. Angilletta (2001), found that *S. undulatus* populations from South Carolina and New Jersey differed in metabolizable energy intake (MEI) because populations in South Carolina had more opportunities to maintain body temperature within their preferred temperature range. These results suggest that there is appreciable variation in physiological phenotype among populations that may be driven, in part, by differences in thermal quality of different habitats (Sørensen, Dahlgaard & Loeschke, 2001; Sears, 2005).

Differences in performance could also be driven by other factors associated with fire disturbance. Lizards in recently burned habitats could be subjected to different rates of predation due to the structural changes following fire (Carter, Rollins & Scott, 2002; Wilgers & Horne, 2007; Hovick *et al.*, 2017). Fire can contribute to increased abundance of predators that favor disturbed habitats, such as mammalian meso-predators, predatory birds, or actively foraging and thermophilic snakes (Carter *et al.*, 2002; Fontaine & Kennedy, 2012; Howey *et al.*, 2016). If lizards in burn sites were exposed to increased predation pressures, then faster lizards should be better able to escape predation (Snell *et al.*, 1988; Husak, 2006). If slower lizards are then being removed from the population disproportionately to faster lizards, then selection may be acting (potentially in concert with phenotypic plasticity) to produce higher locomotor performances in recently burned habitats (Miles, 2004; Irschick *et al.*, 2008). There is substantial literature linking selective pressures to locomotor performance, and some of the best examples come from populations experiencing novel predators or increased predation risk (Jayne & Bennett, 1990; Losos, 1990; Langerhans *et al.*, 2004; Calsbeek & Irschick, 2007). However, Crowley (1985) found that *S. undulatus* from two populations with different predation pressures showed no difference in relative sprint speed and that performance similarities were largely attributable to a similar (conserved) thermal physiology. Lizards in burn sites may have an additional advantage in avoiding predation because of their increased ability to select temperatures near the performance optimum for sprinting, thus likely maximizing their ability to avoid predation (Christian & Tracy, 1981; Huey, 1982; Angilletta *et al.*, 2002).

Analyzing the repeatability of phenotypic traits across time has been used to understand the heritability of performance traits such as speed and endurance (Putnam & Bennett, 1981; Van Berkum *et al.*, 1989; Austin & Shaffer, 1992). Our measurements for individual maximum sprint speed and 2-m run speed were significantly repeatable between years. These repeatabilities demonstrate that individuals can maintain consistency in locomotor performance across long time periods and suggests that the phenotypic plasticity may have a genetic

component (Husak *et al.*, 2006; Dochtermann, Schwab & Shi, 2015). Between-year repeatability in locomotor performance has been documented in other *Sceloporus* species (Van Berkum *et al.*, 1989; *S. occidentalis*; Huey *et al.*, 1990; *S. merriami*); however, these studies compared the population-level repeatabilities of locomotor performance or trait repeatabilities of individual lizards reared in a captive setting. Our results are noteworthy due to the difficulty of capturing the same individuals over the course of two study seasons, and to the best of our knowledge, is the first study to observe individual between-year repeatability in performance of free-ranging *S. undulatus*. Bell, Hankison and Laskowski (2009) performed a meta-analysis on studies that calculated repeatabilities of individual behaviors over time, and concluded that cross-year repeatabilities were significantly lower than repeatabilities calculated over shorter intervals (<1 year). Repeatability in the expression of a phenotypic trait may suggest how intensively natural selection is acting on the trait, and generally selection is expected to remove variation from populations, lowering the ability to detect significant among-individual variation (Brodie & Russell, 1999). Our results support the notion that lizard populations can contain considerable variation in locomotor performance despite the trait being closely tied to fitness.

We failed to detect differences in body condition of lizards among habitat types. The use of body condition indices as a surrogate measure for energetic state and nutritional status has been the subject of considerable debate (Labocha, Schutz & Hayes, 2003; Schulte-Hostedde, Healy & Fangue, 2005; Barnett *et al.*, 2015; Wilder, Raubenheimer & Simpson, 2016). It is assumed that an animal in good condition would have higher relative energy reserves than an animal in poor condition, potentially resulting in important survival and fitness-related consequences. Studies investigating how habitat disturbance influences body condition of reptiles and amphibians have reported mixed results (Karraker & Welsh, 2006; Amo, López & Martín, 2007). Griffiths & Christian (1996) found higher body condition for frilled-neck lizards (*Chlamydosaurus kingii*) in recently burned habitats than those in unburned habitats. They attributed the differences to increased prey abundance and to favorable foraging habitat created by opening of the vegetative community (tropical savannah) after fire disturbance. Although the mixed-hardwood forest habitats in our study showed pronounced structural differences associated with fire history, we found no distinguishable differences in body condition among lizards in the three habitats.

We tested whether body condition influenced locomotor performance, and our results indicate that body condition was also not an informative covariate related to either of our performance measurements (Table 1). These results are consistent with other studies that tested the functional relationship between condition indices generated from morphological measurements and their relation to various performance metrics (Amo *et al.*, 2007; Vervust *et al.*, 2008). Vervust *et al.* (2008) tested six commonly used morphological condition indices to predict locomotor performance abilities (maximum sprint speed and maximum exertion) in *Podarcis sicula*, and found that no condition index consistently predicted locomotor performance ability.

Understanding phenotypic reactions of ectotherms in response to habitat alteration can provide insight into the relationship between temperature, physiology, and ecology of reptiles, and how changing habitats may result in flexible phenotypes (the raw material for adaptation). Our study shows how a fitness-related measurement, locomotor performance, can rapidly change in response to environmental alteration. We suggest that structural changes in the environment as a result of fire creates increased thermal opportunities for lizard thermoregulation, and the acclimatization of *S. undulatus* to different thermal regimes results in measurable differences in locomotor performance. Our results suggest that there are physiological and, possibly, fitness-related benefits for acclimatization. However, more research is needed to explain the underlying mechanisms, and the costs associated with phenotypic plasticity.

## Acknowledgments

Support was provided by the Center of Excellence for Field Biology and Department of Biology at APSU. We thank the US Forest Service and Land Between the Lakes National Recreation Area for access to study sites. Logistical support and research facilities were provided by Hancock Biological Station (Murray State University). We thank Bryan Gaither for assistance in constructing research equipment. For help in both the laboratory and field, we thank James Flaherty, Amanda Mosher, Brooke Bedal, Savannah Price, Dustin Owen and Andy Mueller. John Roe and Ned Dochtermann provided helpful feedback on early drafts of the manuscript. Clint Collins and an anonymous reviewer provided valuable suggestions for clarification and critical review. Research was conducted under approved APSU IACUC protocol #14.005.

## References

- Adolph, S.C. (1990). Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* **71**, 315–327.
- Amo, L., López, P. & Martín, J. (2007). Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammotromus algirus* lizards. *Can. J. Zool.* **85**, 743–751.
- Angilletta, M.J. Jr (2001). Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* **82**, 3044–3056.
- Angilletta, M.J. Jr (2009). *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.
- Angilletta, M.J. Jr, Niewiarowski, P.H. & Navas, C.A. (2002). The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249–268.
- Arnold, S.J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347–361.
- Austin, C.C. & Shaffer, H.B. (1992). Short-, medium-, and long-term repeatability of locomotor performance in the tiger salamander *Ambystoma californiense*. *Funct. Ecol.* **6**, 145–153.
- Ayers, D.Y. & Shine, R. (1997). Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Funct. Ecol.* **11**, 342–347.
- Barnett, C.A., Suzuki, T.N., Sakaluk, S.K. & Thompson, C.F. (2015). Mass-based condition measures and their relationship with fitness: in what condition is condition? *J. Zool.* **1**, 1–5.
- Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behav.* **77**, 771–783.
- Bennett, A.F. (1984). Thermal dependence of muscle function. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **247**, 217–229.
- Brodie III, E.D. & Russell, N.H. (1999). The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes. *Animal Behav.* **57**, 445–451.
- Calsbeek, R. & Irschick, D.J. (2007). The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. *Evolution* **61**, 2493–2503.
- Carter, P.S., Rollins, D. & Scott, C.B. (2002). Initial effects of prescribed burning on survival and nesting success of northern bobwhite in west-central Texas. *Proc. Nat. Quail Symposium* **5**, 129–134.
- Chevin, L.M., Lande, R. & Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e100357.
- Christian, K.A. & Tracy, C.R. (1981). The effect of thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* **49**, 218–223.
- Close, D.D., Fralish, J.S. and Franklin, S.B. (2002) The climate, soil, and vegetation of Land Between the Lakes. In *Land Between the Lakes, Kentucky and Tennessee: four decades of Tennessee Valley Authority Stewardship*: 53–68. Chester, E.W. and Fralish, J.S. (Eds). Kentucky: Gerald Printing. The Center for Field Biology, Austin Peay State University.
- Clusella-Trullas, S., Terblanche, J.S. & Chown, S.L. (2010). Phenotypic plasticity of locomotion performance in the seed harvester *Messor capensis* (Formicidae). *Physiol. Biochem. Zool.* **83**, 519–530.
- Crowley, S.R. (1985). Thermal sensitivity of spring-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia* **66**, 219–225.
- Dahlhoff, E.P. & Rank, N.E. (2000). Functional and physiological consequences of genetic variation at phosphoglucose isomerase: heat shock protein expression is related to enzyme genotype in montane beetle. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 10056–10061.
- Dewitt, T.J., Sih, A. & Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81.
- Dingemanse, N.J. & Dochtermann, N.A. (2013). Quantifying individual variation in behavior: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54.
- Dochtermann, N.A., Schwab, T. & Shi, A. (2015). The contribution of additive genetic variation to personality and variation: heritability of personality. *Proc. Biol. Sci.* **282**, 2014–2201.

- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J. & York, A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biol. Conserv.* **143**, 1928–1939.
- Fenner, A.L. & Bull, C.M. (2007). Short-term impact of grassland fire on the endangered Pygmy Bluetongue lizard. *J. Zool.* **272**, 444–450.
- Fernandes, P.M. & Botelho, H.S. (2003). A review of prescribed burning effectiveness in fire hazard reduction. *Int. J. Wildland Fire* **12**, 117–128.
- Fisher, J.T. & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mamm. Rev.* **35**, 51–81.
- Fitzgerald, L.A. (2012). Finding and capturing reptiles. In *Reptile biodiversity standard methods for inventory and monitoring*: 77–88. McDiarmid, R.W., Foster, M.S., Guyer, C., Gibbons, J.W. & Chernoff, N. (Eds). Los Angeles: University of California Press.
- Fontaine, J.B. & Kennedy, P.L. (2012). Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecol. Appl.* **22**, 1547–1561.
- Garland, T. Jr & Kelly, S.A. (2006). Phenotypic plasticity and experimental evolution. *J. Exp. Biol.* **209**, 2344–2361.
- Glanville, E.J. & Seebacher, F. (2006). Compensation for environmental change by complementary shifts of thermal sensitivity and thermoregulatory behaviour in an ectotherm. *J. Exp. Biol.* **209**, 4869–4877.
- Gomes, F.R., Rezende, E.L., Malisch, J.L., Lee, S.K., Rivas, D.A., Kelly, S.A., Lytle, C., Yaspelkis, B.B. & Garland, T. Jr (2009). Glycogen storage and muscle glucose transporters (GLUT-4) of mice selectively bred for high voluntary wheel running. *J. Exp. Biol.* **212**, 238–248.
- Greenberg, C.H., Forrest, T.G. & Waldrop, T. (2010). Short-term response of ground-dwelling arthropods to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. *For. Sci.* **56**, 112–121.
- Griffiths, A.D. & Christian, K.A. (1996). The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Aust. J. Ecol.* **21**, 386–398.
- Guderley, H., Leory, P.H. & Gagne, A. (2001). Thermal acclimation, growth and burst swimming of threespine stickleback: enzymatic correlates and influence of photoperiod. *Physiol. Biochem. Zool.* **74**, 66–74.
- Higham, T.E., Korchari, P.G. & McBrayer, L.D. (2011). How muscles define maximum running performance in lizards: an analysis using swing- and stance-phase muscles. *J. Exp. Biol.* **214**, 1685–1691.
- Hossack, B.R., Eby, L.A., Guscio, C.G. & Corn, P.S. (2009). Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. *For. Ecol. Manage.* **258**, 1414–1421.
- Hovick, T.J., McGranahan, D.A., Elmore, R.D., Weir, J.R. & Fuhlendorf, S.D. (2017). Pyric-carnivory: raptor use of prescribed fires. *Ecol. Evol.* **7**, 9144–9150.
- Howey, C.A.F. & Roosenburg, W.M. (2013). Effects of prescribed fire on the eastern box turtle (*Terrapene carolina carolina*). *Northeast Nat.* **20**, 493–497.
- Howey, C.A.F., Dickinson, M.B. & Roosenburg, W.M. (2016). Effects of a landscape disturbance on the habitat use and behavior of the black racer. *Copeia* **104**, 853–863.
- Huey, R.B. (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the reptilia*. Vol. 12: 25–91. Gans, C. & Pough, F. (Eds). New York: Academic Press.
- Huey, R.B., Dunham, A.E., Overall, K.L. & Newman, R.A. (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiol. Zool.* **63**, 845–872.
- Husak, J.F. (2006). Does speed help you survive? A test with collared lizards of different ages. *Funct. Ecol.* **20**, 174–179.
- Husak, J.F. & Fox, S.F. (2006). Field use of maximal sprint speed by collard lizards (*Crotaphytus collaris*): compensation and sexual selection. *Evolution* **60**, 1888–1895.
- Husak, J.F., Fox, S.F., Lovern, M.B. & Van Den Buzzche, R.A. (2006). Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* **60**, 2122–2130.
- Hutchinson, T.F., Boerner, R.E., Sutherland, S., Sutherland, E.K., Ortt, M. & Iverson, L.R. (2005). Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Can. J. For. Res.* **35**, 877–890.
- Irschick, D.J. & Losos, J.B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219–226.
- Irschick, D.J., Meyers, J.J., Husak, J.F. & Le Galliard, J.F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.* **10**, 177–196.
- Jayne, B.C. & Bennett, A.F. (1990). Selection on locomotor performance capacity in a natural-population of garter snakes. *Evolution* **44**, 1204–1229.
- Johnston, I.A. & Temple, G.K. (2002). Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behavior. *J. Exp. Biol.* **205**, 2305–2322.
- Karraker, N.E. & Welsh, H.H. Jr (2006). Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians of Northwestern California. *Biol. Cons.* **131**, 132–140.
- Labocha, M.K., Schutz, H. & Hayes, J.P. (2003). Which body condition index is best? *Oikos* **123**, 111–119.
- Lacki, M.J., Cox, D.R., Dodd, L.E. & Dickinson, M.B. (2009). Response of Northern bats (*Myotis septentrionalis*) to prescribed fires in Eastern Kentucky forests. *J. Mammal.* **90**, 1165–1175.
- Lailvaux, S.P., Alexander, G.J. & Whiting, M.J. (2003). Sex-based differences and similarities in locomotor performance,



- thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiol. Biochem. Zool.* **76**, 511–521.
- Langerhans, R.B., Layman, C.A., Shokrollahi, A.M. & DeWitt, T.J. (2004). Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* **58**, 2305–2318.
- Losos, J.B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**, 1189–1203.
- Matesanz, S., Gianoli, E. & Valladares, F. (2010). Global change and the evolution of phenotypic plasticity in plants. *Ann. N. Y. Acad. Sci.* **2**, 35–55.
- Miles, D.B. (2004). The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evol. Ecol. Res.* **6**, 63–75.
- Mondor, E.B., Rosenheim, J.A. & Addicott, J.F. (2005). Predator-induced transgenerational phenotypic plasticity in the cotton aphid. *Oecologia* **142**, 104–108.
- Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev.* **85**, 935–956.
- Neufeld, C.J. & Palmer, A.R. (2008). Precisely proportioned: intertidal barnacles alter penis form to suit coastal wave action. *Proc. Biol. Sci.* **275**, 1081–1087.
- Newell, R.C., Johson, L.G. & Kofoed, L.H. (1977). Adjustment of the components of energy balance in response to temperature change in *Ostrea edulis*. *Oecologia* **30**, 97–110.
- Oksanen, L. (2001). Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* **94**, 27–38.
- Perry, R.W., Rudolph, D.C. & Thill, R.E. (2009). Reptile and amphibian responses to restoration of fire-maintained pine woodlands. *Restoration Ecol.* **17**, 917–927.
- Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006). Invasion and the evolution of speed in toads. *Nature* **439**, 803–803.
- Pianka, E.R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* **50**, 1012–1030.
- Piersma, T. & Van Gils, J.A. (2011). *The flexible phenotype*. Oxford, England: Oxford University Press.
- Podrabsky, J.E. & Somero, G.N. (2004). Changes in gene expression associated with acclimation to constant temperature and fluctuating daily temperatures in annual killifish *Austrofundulus limnaeus*. *J. Exp. Biol.* **207**, 2237–2254.
- Price, T.D., Qvarnström, A. & Irwin, D.E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proc. Biol. Sci.* **270**, 1433–1440.
- Putnam, R.W. & Bennett, A.F. (1981). Thermal dependence of behavioural performance of anuran amphibians. *Anim. Behav.* **29**, 502–509.
- Putnam, R.W. & Bennett, A.F. (1982). Thermal dependence of isometric contractile properties of lizard muscle. *J. Comp. Physiol. B.* **147**, 11–20.
- Renaud, J.M. & Stevens, E.D. (1983). The extent of long-term temperature compensation for jumping distance in the frog, *Rana pipiens*, and the toad, *Bufo americanus*. *Can. J. Zool.* **61**, 1284–1287.
- Rubio de Casas, R., Vargas, P., Perez-Corona, E., Manrique, E., Garcia-Verdugo, C. & Balaguer, L. (2009). Variation in sclerophylly among Iberian populations of *Quercus coccifera* L. is associated with genetic differentiation across contrasting environments. *Plant Biol. (Stuttg)* **11**, 464–472.
- Saab, V.A., Powell, H.D.W., Kotliar, N.B. & Newlon, K.R. (2005). Variation in fire regimes of the Rocky Mountains: implications for avian communities and fire management. *Stud. Avian Biol.* **30**, 76–96.
- Sarre, S.D., Georges, A. & Quinn, A. (2004). The ends of a continuum: genetic and temperature sex determination in reptiles. *BioEssays* **26**, 639–645.
- Schnurr, M.E., Yin, Y. & Scott, G.R. (2014). Temperature during embryonic development has persistent effects on metabolic enzymes in the muscle of zebrafish. *J. Exp. Biol.* **217**, 1370–1380.
- Schulte, P.M., Healy, T.M. & Fangue, N.A. (2011). Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integr. Comp. Biol.* **51**, 691–702.
- Schulte-Hostedde, A.I., Zinner, B., Millar, J.S. & Hickling, G.J. (2005). Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**, 155–163.
- Sears, M.W. (2005). Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. *Oecologia* **143**, 25–36.
- Seebacher, F. & Wilson, R.S. (2006). Fighting fit: thermal plasticity of metabolic function and fighting success in the crayfish *Cherax destructor*. *Funct. Ecol.* **20**, 1045–1053.
- Shaw, J.R., Hampton, T.H., King, B.L., Whitehead, A., Galvez, F., Gross, R.H., Keith, N., Notch, E., Jung, D., Glaholt, S.P., Chen, C.Y., Colbourne, J.K. & Stanton, B.A. (2014). Natural selection canalizes expression variation of environmentally induced plasticity-enabling genes. *Mol. Biol. Evol.* **31**, 3002–3015.
- Shine, R. (2004). Seasonal shifts in nest temperature can modify the phenotypes of hatchling lizards, regardless of overall mean incubation temperature. *Funct. Ecol.* **18**, 43–49.
- Snell, H.L., Jennings, R.D., Snell, H.M. & Harcourt, S. (1988). Intrapopulation variation in predator-avoidance performance of Galápagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol.* **2**, 353–369.
- Sørensen, J.G., Dahlgaard, J. & Loeschcke, V. (2001). Genetic variation in thermal tolerance among natural populations of *Drosophila buzzatii*: down regulation of Hsp70 expression and variation in heat stress resistance traits. *Funct. Ecol.* **15**, 289–296.
- Stevenson, R.D. & Woods, W.A. Jr (2006). Condition indices for conservation: new uses for evolving tools. *Integr. Comp. Biol.* **46**, 1169–1190.
- Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effect models. *Methods Ecol. Evol.* **8**, 1639–1644.
- Temple, G.K., Wakeling, J.M. & Johnston, I.A. (2000). Seasonal changes in fast-starts in the short-horn sculpin: integration of

- swimming behavior and muscle performance. *J. Fish Biol.* **56**, 1435–1449.
- Tinkle, D.W. & Ballinger, R.E. (1972). *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* **53**, 570–584.
- Tomkins, J.L. (1999). Environmental and genetic determinants of the male forceps length dimorphism in the European earwig *Forficula auricularia* L. *Behav. Ecol. Sociobiol.* **47**, 1–8.
- Tsuji, J.S., Huey, R.B., Van Berkum, F.H., Garland, T. Jr & Shaw, R.G. (1989). Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol. Ecol.* **3**, 240–252.
- Tulli, M.J., Abdala, V. & Cruz, F.B. (2012). Effects of different substrates on the sprint performance of lizards. *J. Exp. Biol.* **215**, 774–784.
- Turner, M.G., Romme, W.H. & Tinker, D.B. (2003). Surprises and lessons from the 1988 Yellowstone fires. *Front. Ecol. Environ.* **1**, 351–358.
- Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzon, M., Cornwell, W., Gianoli, E., Kleuden, M., Naya, D.E., Nicotra, A.B., Poorter, H. & Zavala, M.A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* **17**, 1351–1364.
- Van Berkum, F.H., Huey, R.B., Tsuji, J.S. & Garland, T. Jr (1989). Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Funct. Ecol.* **3**, 97–105.
- Van Kleunen, M. & Fischer, M. (2005). Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytol.* **166**, 49–60.
- Vervust, B., Lailvaux, S.P., Grbac, I. & Van Damme, R. (2008). Do morphological condition indices predict locomotor performance in the lizard *Podarcis sicula*? *Acta Oecol.* **34**, 244–251.
- Warner, D.A. & Andrews, R.M. (2002). Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biol. J. Linn. Soc.* **76**, 105–124.
- Warner, D.A. & Shine, R. (2008). The adaptive significance of temperature-dependent sex determination in a reptile. *Nature* **451**, 566–568.
- Webb, J.K., Shine, R., Pringle, R.M. & Lannoo, M.J. (2005). Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. *Copeia* **2005**, 894–900.
- Weisser, W.W., Braendle, C. & Minoretti, N. (1999). Predator-induced morphological shift in the pea aphid. *Proc. Biol. Sci.* **266**, 1175–118.
- Wilder, S.M., Raubenheimer, D. & Simpson, S.J. (2016). Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Funct. Ecol.* **30**, 108–115.
- Wilgers, D.J. & Horne, E.A. (2007). Spatial variation in predation attempts on artificial snakes in a fire-disturbed tallgrass prairie. *Southwest Nat.* **52**, 263–270.
- Yager, L.Y., Heise, C.D., Epperson, D.M. & Hinderliter, M.G. (2007). Gopher tortoise response to habitat management by prescribed burning. *J. Wildl. Manage.* **71**, 428–434.