

## RESEARCH ARTICLE

# Reciprocally transplanted lizards along an elevational gradient match light environment use of local lizards via phenotypic plasticity

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**Abstract**

1. Thermoregulatory behaviour enables ectotherms to maintain preferred body temperatures across a range of environmental conditions, and it may buffer individuals against the effects of climate warming. In lizards, the mechanism underlying variation in thermoregulatory behaviour has long been assumed to be phenotypic plasticity, and while this assumption has been difficult to test using wild populations in their natural habitat, it has critical implications as to how variation in thermoregulation is incorporated in models designed to predict outcomes of climate change on ectotherms.
2. We continuously recorded one component of thermoregulatory behaviour, light-environment use, by two wild populations of desert short-horned lizards *Phrynosoma hernandesi* occurring at low (warm) and high (cool) elevations. We then reciprocally transplanted lizards and recorded their light-environment use when exposed to a novel climate at the transplant site.
3. Immediately following the reciprocal transplant to a novel climate, lizards from both populations adjusted their light-environment use and matched the light-environment use exhibited by local lizards at that site.
4. This study provides direct empirical evidence that lizards can immediately adjust light-environment use, one component of thermoregulatory behaviour, via phenotypic plasticity to match the local environment. Our results provide hope that lizards may have some capacity to buffer against climate change by adjusting their light-environment use to compensate for warmer environmental temperatures.

**KEYWORDS**

Abajo Mountains, basking, horned lizard, light-level geolocator, *Phrynosoma hernandesi*, thermoregulation

## 1 | INTRODUCTION

Predicting how organisms will be affected by climate change is a complex but critical challenge in contemporary ecology. The rapid rate at which human-induced climate change is occurring will likely outpace

the capacity of many species to adapt (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Lavergne, Mouquet, Thuiller, & Ronce, 2010), meaning that such species must instead disperse to track their climate envelope, respond to climate change through phenotypic plasticity, or face extinction. Ectotherms have been the focus

of many studies on the impacts of climate change because their physiological and behavioural traits are highly dependent on environmental temperatures (e.g. Buckley, 2008; Cooper, Hammad, & Montooth, 2014; Kearney, Shine, Porter, & Wake, 2009; Sinervo et al., 2010), and such studies have provided empirical evidence for a variety of responses to climate change across ectothermic taxa. For example, genetic adaptation to warmer temperatures has been demonstrated in species with short generation times such as *Drosophila* (Balanyá, Oller, Huey, Gilchrist, & Serra, 2006; Reed, Lowe, Briscoe, & Frankham, 2003) and *Daphnia* (Du Meester, van Doorslaer, Geerts, Orsini, & Stoks, 2011), while phenotypically plastic responses have been observed in longer-lived species such as frogs (Blaustein et al., 2001) and turtles (Refsnider & Janzen, 2012). Finally, some highly mobile species such as butterflies (Hill et al., 2002; Parmesan et al., 1999) and dragonflies (Hickling, Roy, Hill, & Thomas, 2005) have shifted their ranges poleward in response to recent climate change.

Species that are unable to respond to climate change through adaptive evolution, phenotypic plasticity, or range shifts likely face extinction. Such species tend to have relatively long generation times, low genetic variability and low dispersal ability; these life-history traits characterize many reptile species and may make reptiles as a taxon particularly vulnerable to human-induced climate change (Mitchell & Janzen, 2010). A tool that is widely employed to predict locations where range contractions and local extinctions are likely for a given species is biophysical modelling. Biophysical (or mechanistic) models assess habitat suitability under climate warming in terms of a species-specific physiological process that may constrain a species' range. Local extinctions predicted in areas where, for example, increased environmental temperatures will reduce the number of hours per day that are within the range of a species' thermal tolerance, thereby reducing the time available for critical activities such as foraging and courting mates. Biophysical models are particularly common in predicting effects of climate warming on lizards (Buckley, 2008; Kearney & Porter, 2009). As a worst-case scenario, Sinervo et al. (2010) predicted that climate change will result in the extinction of 20% of the world's lizard species due to climate warming-induced reduction in activity time.

Preferred body temperatures are strongly conserved within lizard species, even across diverse thermal environments (Bogert, 1949; Buckley, Ehrenberger, & Angilletta, 2015; Sears & Angilletta, 2004). To maintain preferred body temperatures despite substantial climatic differences, local lizard populations vary behaviours directly associated with thermoregulation, such as microhabitat use, activity timing and basking frequency (Huey, Hertz, & Sinervo, 2003; Huey & Webster, 1976; Rand, 1964). Light-environment use is an additional component of thermoregulatory behaviour, with effects on lizards' thermoregulation that are distinct from those of temperature (Sievert & Hutchison, 1988, 1989). Despite its influence on thermoregulation in ectotherms, light environment has been largely ignored in the literature in favour of temperature. Importantly, an ectotherm's body temperature depends not only on convection with the surrounding environment, but also on conduction, evaporation, metabolism and solar radiation, the latter being directly affected by

light environment (Sunday et al., 2014). Lizards can directly affect the amount of solar radiation they receive through their use of light environment, such as shuttling between shade and sun (Kearney et al., 2009). The ability of lizards to adjust various components of thermoregulatory behaviour may buffer populations from some of the effects of climate change (Kearney et al., 2009). For example, cool microhabitats such as shade or burrows may act as thermal refugia, substantially offsetting activity restrictions imposed by high temperatures in unshaded, open microhabitats (Kearney, 2013; Kearney et al., 2009; Sunday et al., 2014). Biophysical models incorporating availability of shaded microhabitats predict that in areas with high shade availability, many lizard species will experience substantially less activity restriction than that predicted by Sinervo et al. (2010), assuming that lizards can shift their microhabitat use appropriately (Kearney, 2013). The importance of shade availability in predicting population persistence underscores the need to understand not only the temperatures selected by lizards in their natural habitat, but also their use of the light environment.

Thermoregulatory behaviour in general is widely assumed to occur via phenotypic plasticity (Buckley et al., 2015; Cowles & Bogert, 1944; Huey et al., 2003). While there are many examples of plasticity in thermoregulatory behaviour occurring within the range of normal, predictable fluctuations in either an individual's physical condition or that of the environment (e.g. reproductive status, nutritional status, time of year; Gatten, 1974; Isaac & Gregory, 2004; Van Damme, Bauwens, & Verheyen, 1987), whether plasticity in thermoregulatory behaviour will also allow ectotherms to cope with larger or more unpredictable changes outside the normal range of conditions, such as extreme heat waves or continual climate warming, remains to be seen. One behavioural component of thermoregulation, perch height, was phenotypically plastic in *Sceloporus* lizards, using a common garden design (Adolph, 1990). However, among-population variation in thermoregulatory behaviour could also be due to local adaptation matching different components of thermoregulatory behaviour to local climates. Either mechanism—phenotypic plasticity or local adaptation—could explain the common observation that lizard populations from widely divergent thermal environments nevertheless maintain similar preferred body temperatures.

To fully understand the capacity of behavioural thermoregulation to buffer lizards against the effects of climate change, we must conclusively demonstrate whether among-population differences in thermoregulatory behaviour are due to local adaptation or phenotypic plasticity. As pointed out by Huey et al. (2003), common garden or reciprocal transplant designs are necessary to test the widespread assumption that "plasticity of thermoregulatory behaviour is almost certainly ancestral for lizards." A major obstacle in testing this assumption, however, is the difficulty of accurately assessing thermoregulatory behaviour of wild lizards in their natural habitat. Previous studies have estimated thermoregulation either by measuring lizards' preferred body temperatures in a laboratory thermal gradient (Aguado & Braña, 2014; Christian & Weavers, 1996; Lara-Reséndiz, Gadsden, Rosen, Sinervo, & Méndez-De la Cruz, 2015), or by measuring the body temperature of wild lizards captured while actively

basking (Christian, 1998; Hertz, Huey, & Stevenson, 1993; Williams et al., 2010); these body temperatures are then compared to environmental temperatures available in their natural habitat. While useful as input in biophysical models, and even allowing for individual differences in activity phenotypes (Gunderson & Leal, 2016), this approach does not directly demonstrate how an individual is using its natural habitat. These shortcomings demonstrate the need for a method that directly assesses behavioural thermoregulation in natural habitat to determine (1) how wild lizards exploit environmental variation across available microhabitats, and (2) whether the mechanism underlying behavioural thermoregulation is phenotypically plastic or genetically controlled.

Here, we adapt light-level data-logger technology, first proposed by Wilson et al. (1992) and now widely used in tracking migratory birds (Shaffer et al., 2005; Streby et al., 2015; Stutchbury et al., 2009), to continuously record one component of thermoregulatory behaviour, light-environment use, in wild reptiles in their natural habitat. We conducted a reciprocal-transplant experiment to determine whether light-environment use is a phenotypically plastic trait in lizards. We reciprocally transplanted lizards from different home climates on an elevational gradient and quantified how they adjusted one component of thermoregulatory behaviour, light-environment use, when exposed to a novel climate. If light-environment use is a phenotypically plastic trait, we predicted that transplanted lizards would demonstrate light-environment use similar to that exhibited by local lizards, but differing from what the transplanted lizards exhibit at their home site. In contrast, if light-environment use is a genetically controlled, locally adapted trait, we predicted that lizards would exhibit similar light-environment use in both their home site and when transplanted, despite differences in local climate between their home and transplanted sites.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and species

We conducted this study using a low- and high-elevation population of greater short-horned lizards *Phrynosoma hernandesi* (formerly *P. douglasii*). Both study sites were on North Peak in the Abajo Mountains, San Juan Co., Utah, USA. *Phrynosoma hernandesi* is considered a high-elevation species and generally occurs between 600 and 3,200 m (Hodges, 2009). Our study sites were an east-facing slope in sagebrush habitat at 2,080 m (low site) and a northeast-facing slope in a piñon-juniper shrubland interspersed with sagebrush patches at 2,550 m (high site); we have never observed *P. hernandesi* below 2,000 m in our study area. Field-active body temperatures for 71 lizards did not differ between the two sites (low site = 32.55°C, high site = 31.71°C,  $t = -1.58$ ,  $p = .12$ ; J. M. Refsnider, unpubl. data).

### 2.2 | Microhabitat characterization

We characterized the temperatures available in various microhabitats at each study site, using Thermochron iButton data loggers

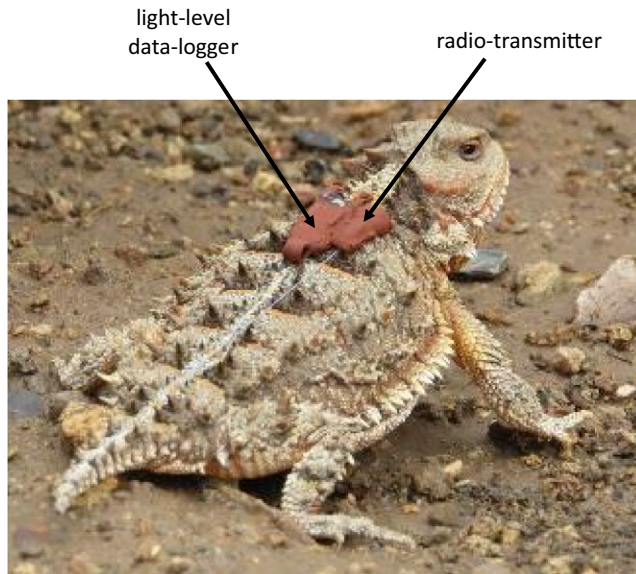
(Embedded Data Systems, Lawrenceburg, Kentucky). We placed two data loggers wrapped in parafilm in each of five microhabitats at each study site: buried 5 cm underground; on the soil surface under a cover object (i.e. a naturally occurring flat piece of bark); on the soil surface in full shade at the base of a dense sagebrush shrub; on the soil surface in full sun; and hanging 1 m off the ground against the trunk of a small shrub. The data loggers recorded temperature hourly throughout the entire experimental period (9–26 July 2016).

### 2.3 | Quantifying light-environment use

We captured *P. hernandesi* at each study site by hand, and housed them individually in plastic terraria (Kritter Keepers, LLL Reptile and Supply Company, Inc., Oceanside, California) with sand substrate and a handful of local vegetation for shelter. We transported all lizards to our field laboratory at Canyonlands Research Center, where they were housed at 24–28°C under ambient lighting. We collected standard morphological measurements (mass, snout-vent length, tail length, head depth and width) for all individuals. We determined sex based on the presence of enlarged post-anal scales and orange femoral pores in adult males.

We then attached a “backpack” to each lizard. The backpack consisted of a 0.35 g radio transmitter (Blackburn Transmitters, Inc., Nagadoches, Texas) and a 0.32-g light-level geolocator (Intigeo-W30Z11, Migrate Technology Ltd, Cambridge, UK). Geolocators are commonly used to track migrating birds by recording the ambient light level every minute, recording the maximum light level at 5-min intervals, and using sunrise and sunset times to estimate a marked animal's location on the planet on that day. Importantly, geolocators only record data but do not transmit it, and must be recovered to download the data. While relatively common at our study sites, *P. hernandesi* are cryptic and labour-intensive to capture in large numbers. Therefore, to ensure that we would be able to later recapture lizards carrying geolocators (hereafter, light-level data-loggers), we also included radio-transmitters in the backpacks so lizards could be relocated, using radio-telemetry. The geolocator models used here did not include an on-board thermometer, although this feature will become available on future geolocator models.

To construct a backpack, we first glued the transmitter to the light-level data-logger, using fast-drying superglue (Loctite Super Glue Gel Control), and we then painted the entire backpack (except for the light sensor on the data-logger) rust-brown using acrylic paint to approximate the dorsal surface of the lizards. Once the paint had dried, we glued the backpack directly to the skin of the lizard along the dorsal midline between the forelimbs, with the transmitter antenna pointing posteriorly down the centre of the lizard's back (Figure 1). We used fast-drying superglue to attach the backpack to the lizard, and were careful not to leave any gaps between the front of the backpack and the lizard's skin which could become entangled in vegetation and allow the backpack to be pried off. After gluing the backpack to the lizard, we gently held it in place for 2 min to allow the glue to dry. We then placed the lizard into an individual terrarium and allowed the glue to further dry overnight. We released lizards at



**FIGURE 1** Female greater short-horned lizard *Phrynosoma hernandesi* in the Abajo Mountains, San Juan County, Utah, USA outfitted with a “backpack” made up of a light-level data-logger and a miniature radio-transmitter

the site of capture the morning following initial capture. Backpacks averaged 0.04% of lizard body mass (range 0.01%–10.0%), and during daily radio tracking we never observed any instances of abnormal or impaired movement, entanglements in vegetation, or injuries attributable to the backpacks or attachments.

## 2.4 | Reciprocal transplant experiment

For the first half of the experiment, following backpack attachment, we released all lizards at their exact site of capture (Home treatment). We located all lizards once daily using radio-telemetry. Each time a lizard was radio-tracked, we recorded its location, using a hand-held GPS unit and noted its behaviour and microhabitat use. We monitored all lizards at their home site for 5–7 days during the period of 9–21 July. On the last day of each individual's Home treatment, we recaptured the individual, downloaded data from the light-level data-logger without removing the backpack and then released the individual at the other study site. That is, low-elevation lizards were transplanted to the high-elevation site and high-elevation lizards were transplanted to the low-elevation site. We then monitored all lizards daily during the Transplant treatment using radio telemetry, as described above, for a further 5–7 days during the period of 16–26 July. At the end of each individual's Transplant treatment, we again captured the lizard, downloaded data from the light-level data-logger and returned the lizard to its home site. We released lizards at their last observed location in their home site. We did not remove the backpacks but allowed them to fall off naturally in the next shed. (approximately monthly at our study sites; J. M. Refsnider, unpubl. data). The exact dates of transplant and the total length of the experiment varied among individuals because individuals that were captured early during our search effort were monitored for 7 days at

their home site, transplanted, monitored for 7 days at the transplant site, and returned to their home site 14 days after original capture. In contrast, individuals captured towards the end of our search effort were monitored for 5 days at their home site, transplanted, monitored for 5 days at their transplant site, and returned to their home site 10 days after original capture.

## 2.5 | Statistical analyses

To characterize local climates at the two study sites, we used the mean temperature recorded by each pair of iButton data loggers placed in a given microhabitat. We compared mean temperatures during the day (sunrise–sunset), at night (sunset–sunrise) and overall at the low and high elevation sites in each microhabitat using *t* tests, and we compared the temperature variances at the low- and high-elevation sites in each microhabitat, using Levene's tests.

Light intensities recorded by light-level data-loggers ranged from 0.1 (complete darkness) to 74,419 (full sun) lx. To quantify the use of light environments by low- and high-elevation lizards at their home site and when transplanted, we binned all light-level readings into six categories of light environment: buried under the soil surface (<100 lx), sheltered under a cover object (100–1,000 lx), full shade (1,001–1,500 lx), part shade (1,501–10,000 lx), part sun (10,001–50,000 lx) and full sun (>50,000 lx). These categories translated light readings from the light-level data-loggers into light-environment use by lizards. We defined the width of these light-level bins after placing light-level data-loggers into each of the six light environments for 24 hr for calibration; however, only light-level readings after sunrise and before sunset were used to describe light-environment use by lizards, as light levels recorded at night were indistinguishable from light levels recorded from buried lizards. We also excluded light-level readings between twilight and sunrise, and between sunset and twilight, because the level of ambient light changes quickly during these periods, complicating the relationship between light-level readings and our predetermined behaviour categories. These pre-sunrise and post-sunset transitional light-level readings are critical in studies using light-level geolocators to determine an animal's position on the planet (Rakhimberdiev et al., 2016), but are not relevant for this study.

We quantified a lizard's daytime light-environment use, using the number of light-level readings recorded for a lizard in each of the six light environment categories. The proportions of time a lizard spent in each of the six light environment categories were used as the basis for inference about a lizard's light-environment use. We quantified the proportion of time spent in each light environment category overall, as well as at different times of the day (morning: sunrise–1,100 hr; afternoon: 1,101–1,600 hr; evening: 1,601 hr–sunset). The categorization of the light-level readings leads to a multivariate count response variable  $y = \{n_1, n_2, \dots, n_6\}$ , where  $n_1, n_2, \dots, n_6$  are the number of light-level readings in each of the six categories. The probability distribution of these counts is the multinomial distribution, or  $\{n_1, \dots, n_6\} \sim \text{multinom}(p_1, \dots, p_6; N)$ . The parameters  $p_1, \dots, p_6$  are the proportions of time a lizard spends in these six light-environment

categories. We modelled these proportions as a function of site of origin, treatment, sex and their interactions through the generalized logit transformation

$$\log(p_j/p_1) = \beta_{1H} \times \beta_{2T} \times \beta_{3S}$$

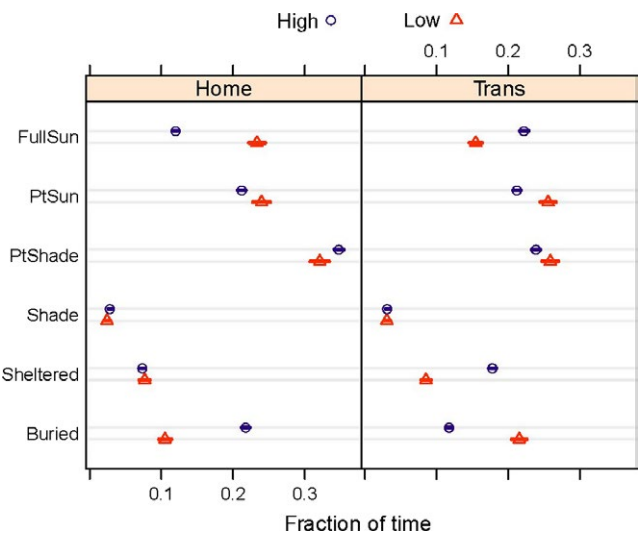
for  $j = 2, \dots, 6$ , where  $\beta_{1H}$  is site of origin effect (i.e. low vs. high elevation),  $\beta_{2T}$  is treatment effect (i.e. home vs. transplant), and  $\beta_{3S}$  is sex effect. The full model has a total of 40 parameters representing both main effects and their interactions and we fit the model in R (R Core Team, 2013), using the `multinom` function in the package `nnet` (Venables & Ripley, 2002). We evaluated our model's goodness-of-fit and over-dispersion using both hypothesis testing and residual plots as outlined in section 8.5.2 of Qian (2016). The generalized logit transformation  $\log(p_j/p_1)$  is the log-odds ratio with, in this case,  $p_1$  as the baseline. Which proportion is used as the baseline is irrelevant to computation; however, the model-estimated effects ( $\beta$ 's) are baseline specific. Consequently, the model-reported statistical significance with respect to these effects is meaningless. We therefore converted the uncertainty of the estimated effects from the log-odds ratio scale to the proportions scale, using a Monte Carlo simulation algorithm (Qian, 2016). Comparisons are based on the 95% confidence intervals of the estimated proportions. Computational details can be found in our on-line supplement at <https://github.com/songsqian/lizards>.

### 3 | RESULTS

The low-elevation site was warmer during the day, at night, and overall than the high-elevation site in all five microhabitats tested (all  $p$ -values  $< .001$ ; Tables 1; Figure S1), with the exception that the daytime temperature under a cover object did not differ between low and high elevation ( $t = -0.96$ ,  $p = .34$ ). The magnitude of overall temperature variation also differed between sites for some microhabitats: the temperature under a cover object was more variable at the high-elevation site than at the low-elevation site ( $F_{1,812} = 23.3$ ,  $p < .0001$ ), while the temperature 1 m off the ground in a tree was

more variable at the low-elevation site than at the high-elevation site ( $F_{1,812} = 13.8$ ,  $p < .001$ ).

We recorded light-environment use at both elevations for 19 lizards originating from the low site, and 6 lizards originating from the high site (Figure S2). Site of origin (i.e. low vs. high elevation), treatment (i.e. home vs. transplant site), sex and their interactions all had significant effects on the light environment used by lizards (Figure 2). All effects (main effects of site of origin, treatment, sex and two-way and three-way interactions) are statistically different from 0 at a significance level of .01. (Because the model-estimated effects are in log-odds scale, the statistical significance information is irrelevant. In our online supplement [<https://github.com/songsqian/lizards>], we provide more details of model fitting and interpretation, as well as alternative plots of the result for emphasizing the comparisons of different factors included in the model.) At their home site, high-elevation lizards spent more time in the full sun, and less time buried, than did low-elevation lizards. When transplanted, however, lizards



**FIGURE 2** Mean and 95% confidence intervals of proportion of time spent in each of six light environments by low- (red triangles) and high-elevation (blue circles) lizards at their home site (left panel) and when transplanted to a novel climate (right panel)

**TABLE 1** Mean daily temperature  $\pm$  SD of microhabitats in *Phrynosoma hernandesi* habitat at low- and high-elevation sites on North Peak, Abajo Mountains, San Juan County, Utah, USA, and comparison of means and variances between sites. Temperatures were recorded hourly during 9–26 July 2016 by two Thermochron iButtons in each microhabitat at each elevation, paired readings from the two iButtons were averaged hourly, and hourly readings were averaged to give an overall daily mean temperature in each microhabitat (separate daytime and nighttime temperature comparisons not shown)

	Low elevation (2,080 m)	High elevation (2,550 m)	Comparison of means	Comparison of variances (Levene's test)
Buried underground	24.0 $\pm$ 7.2	21.8 $\pm$ 7.5	Welch's $t = -4.42$ $p < .001$	$F_{1,812} = 0.9$ $p = .33$
Under cover object	24.9 $\pm$ 6.6	22.5 $\pm$ 8.6	Welch's $t = -4.32$ $p < .0001$	$F_{1,812} = 23.3$ $p < .0001$
Under sagebrush shrub	22.4 $\pm$ 7.8	19.9 $\pm$ 6.4	Welch's $t = -5.00$ $p < .0001$	$F_{1,812} = 2.2$ $p = .14$
Soil surface, full sun	24.4 $\pm$ 11.1	21.6 $\pm$ 10.6	Welch's $t = -3.67$ $p < .001$	$F_{1,812} = 0.5$ $p = .48$
In tree	23.2 $\pm$ 5.6	19.4 $\pm$ 4.9	Welch's $t = -10.26$ $p < .0001$	$F_{1,812} = 13.8$ $p < .001$

Bold indicates differences significant at  $\alpha = .05$ .



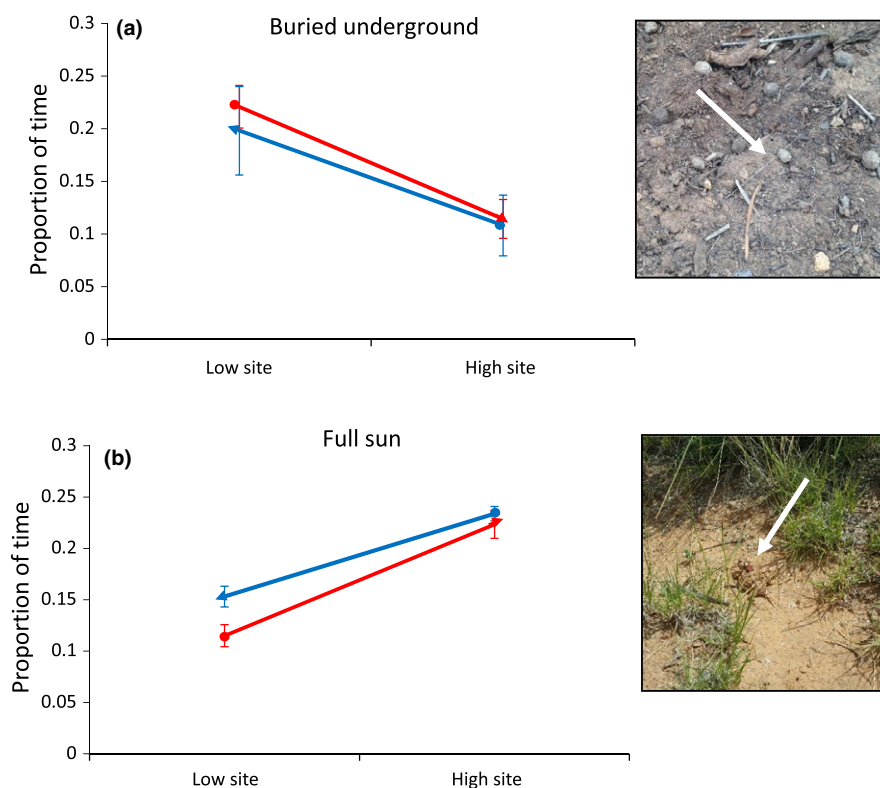
from both sites adjusted their light-environment use by changing the proportion of time spent in different light environments. In particular, low-elevation lizards transplanted to the high-elevation site increased the proportion of time spent in full sun ( $M = 0.223$ ) compared to the proportion of time spent in full sun when at their home site ( $M = 0.115$ ). Similarly, high-elevation lizards transplanted to the low-elevation site increased the proportion of time they spent buried under the soil surface ( $M = 0.198$ ) compared to the proportion of time spent buried when at their home site ( $M = 0.108$ ). Critically, when transplanted, lizards from both sites adjusted the proportion of time spent in the sun and buried under the soil surface to match the proportions used by lizards local to each site, both in direction and magnitude (Figure 3). In other words, lizards demonstrated sufficient phenotypic plasticity in their light environment use when transplanted to almost perfectly match the light environment use of local lizards.

The pattern of plasticity in light-environment use displayed by lizards following a transplant to a novel habitat differed depending on home site (Figure S3). High-elevation lizards only demonstrated plasticity in the proportion of time spent buried (slope of population mean reaction norm =  $-0.090$ ) and in full sun (slope =  $0.081$ ) following transplant to the low-elevation site. High-elevation lizards did not change the proportion of time spent sheltered (slope =  $-0.010$ ), in full shade (slope =  $-0.007$ ), in partial shade (slope =  $0.046$ ), or in partial sun (slope =  $-0.020$ ) following transplant to the low-elevation site. Low-elevation lizards also demonstrated plasticity in the proportion of time spent buried (slope =  $-0.106$ ) and in full sun (slope =  $0.108$ ) following transplant to the high-elevation site (although in the opposite direction to that demonstrated by high-elevation lizards

transplanted to the low-elevation site). In addition, following transplant to the high-elevation site, low-elevation lizards increased the proportion of time spent sheltered (slope =  $0.100$ ) and in partial shade (slope =  $-0.103$ ). They did not adjust the proportion of time spent in full shade (slope =  $0.001$ ) or in partial sun (slope =  $0.001$ ). Finally, at the high-elevation site, local and transplanted lizards did not differ in the proportion of time spent basking in the full sun at different times of day. At the low-elevation site, however, local lizards spent more time basking in the morning, and less time basking in the evening, than did the transplanted lizards (Figure S4).

## 4 | DISCUSSION

Thermoregulatory behaviour is assumed to be a phenotypically plastic trait that enables ectotherms to achieve preferred body temperatures despite mean environmental temperatures that differ from the preferred body temperature (Buckley et al., 2015). Studies seeking to predict the consequences of global climate change on ectotherms rely on the assumption that thermoregulation is phenotypically plastic to determine whether animals will have sufficient microhabitats available to achieve preferred body temperatures, and whether the time per day during which they are able to achieve preferred body temperatures is sufficient to complete necessary activities such as foraging or breeding (Kearney, 2013; Sunday et al., 2014). Some models predicting the outcome of various climate warming scenarios on lizard populations demonstrate that plasticity in thermoregulatory behaviour is critical if populations are to avoid extinction (Kearney, 2013). Although lizards may be able to buffer against



**FIGURE 3** Population reaction norms for mean proportion  $\pm$  SE of time spent buried underground (a;  $<100$  lx) and in full sun (b;  $>50,000$  lx) at low- and high-elevation sites as recorded by light-level data-loggers. Red lines are lizards whose home site was low elevation ( $N = 19$ ), and blue lines are lizards whose home site was high elevation ( $N = 6$ ). Closed circles are phenotypic means from local lizards at their home sites, arrows are phenotypic means from lizards transplanted to the other site, and slopes show degree of phenotypic plasticity exhibited between home and transplant sites. Arrow in (a) shows a buried lizard's radio transmitter antenna projecting above the soil surface; arrow in (b) shows a lizard on the soil surface in full sun

the effects of climate change through behavioural thermoregulation in general, and by exploiting cool microhabitats in particular, several problems remain unresolved. First, the availability of cool microhabitats depends critically on how climate change will alter vegetation structure and shade cover (Kearney & Porter, 2009; Refsnider, Warner, & Janzen, 2013). Second, behavioural modification of habitat use or timing of critical activities likely entail energetic or fitness costs, such as narrower activity windows or increased predation risk (Basson, Levy, Angilletta, & Clusella-Trullas, 2017; Sears et al., 2016; Sunday et al., 2014); moreover, such costs will likely differ substantially across life stages (Levy, Buckley, Keitt, & Angilletta, 2016). Finally, species must possess the ability to modify behaviours associated with thermoregulation (Sunday et al., 2014), which has been difficult to demonstrate due to challenges associated with accurately quantifying thermoregulatory behaviour of wild lizards in their natural habitat.

We provide direct empirical evidence that thermoregulatory behaviour is a phenotypically plastic trait in a wild population of lizards. Horned lizards adjusted one component of thermoregulatory behaviour, light-environment use, to compensate for a novel climate following a reciprocal transplant by specifically adjusting the proportion of time they spent buried under the soil surface and basking in full sun. Importantly, this behavioural adjustment in time spent in different light environments occurred immediately following the transplant. Moreover, each population adjusted their light-environment use in the new environment to almost perfectly match the behaviour exhibited by local lizards. The transplant portion of our experiment lasted up to 7 days for any given individual, yet a significant change in the proportion of time spent in different light environments was evident during this relatively short time period. Such an immediate response to a novel climate demonstrates that light-environment use has a phenotypically plastic basis, and provides hope that ectotherms may have some capacity to buffer against climate change by adjusting their light-environment use to compensate for warmer environmental temperatures. The mean temperature difference between our study sites ranged from 2.2 to 3.8°C, depending on microhabitat (Figure S1), which falls within the range of likely future climate warming scenarios (IPCC, 2013). Within this temperature range, transplanted lizards in our experiment demonstrated nearly perfect matching of light-environment use to that of local lizards. Our estimate of lizards' adjustment of light-environment use likely underestimates their ability to adjust their behaviour to match new environmental conditions, as our light-level data loggers were unable to account for fine-scale adjustments such as a lizard's posture or orientation with respect to the sun. Future research should endeavour to quantify the full range of possible plasticity by transplanting lizards to a broader range of climatic conditions to determine at what point they can no longer match light-environment use to local environmental conditions.

Behavioural phenotypic plasticity is increasingly being recognized as an important mechanism by which ectotherms may compensate for a warming climate (Caldwell, While, & Wapstra, 2017; Refsnider & Janzen, 2016; Urban, Richardson, & Freidenfelds,

2014). Plasticity is particularly important in long-lived species that may evolve too slowly to keep pace with the rapid pace of climate change, such as many reptiles (Hoffmann & Sgrò, 2011; Janzen, 1994; McGaugh, Schwanz, Bowden, Gonzalez, & Janzen, 2010). For example, plasticity in nest-site choice prevents sex ratio skews potentially caused by increased environmental temperatures in reptiles with temperature-dependent sex determination (Doody et al., 2006; Refsnider & Janzen, 2012; Telemeco, Elphick, & Shine, 2009). Importantly, however, even if a species has a large capacity for behavioural plasticity, constraints may exist that prevent that plasticity from being expressed. In the previous example of nest-site choice compensating for sex ratio skews, individuals in some populations may be unable to express the necessary plasticity in nest-site choice if their habitat lacks, for example, suitable shade cover (Refsnider et al., 2013) or soil depth (Mitchell, Kearney, Nelson, & Porter, 2008). Climate change is already altering community composition and vegetation structure, in some cases resulting in decreased habitat quality and declines in lizard populations (Schreuder & Clusella-Trullas, 2016; Stellatelli, Vega, Block, & Cruz, 2013). The plasticity in light-environment use demonstrated by lizards in our study depends on the availability of suitable microhabitats in which to achieve preferred body temperatures. If vegetation structure or soil conditions change as a result of climate change such that suitable microhabitat is no longer available, lizards with the phenotypic plasticity to adjust their light-environment use may not be able to express that plasticity and could still be subject to population declines due to climate change. If lizards alter the time of day during which they bask in open habitats to compensate for ambient temperature changes, as observed here, they may become vulnerable to a different suite of predators, which could paradoxically increase mortality risk. It is also possible that populations locally adapted to different climatic conditions may have diverged in their extent of phenotypic plasticity, such that populations from more stable thermal environments have evolved a lower magnitude of plasticity in their thermoregulatory behaviour (sensu Cooper et al., 2014). Species or populations with a lower capacity for phenotypic plasticity may therefore be more vulnerable to climate warming than those from more variable thermal environments, where phenotypically plastic responses may be greater (Caldwell et al., 2017).

The presence of phenotypic plasticity in thermoregulatory behaviour has been suggested to limit local adaptation of thermal physiology in lizards, thereby increasing their vulnerability to climate change (Bogert, 1949; Buckley et al., 2015; Muñoz et al., 2014). Alternatively, phenotypic plasticity has been hypothesized to act as a "place-holder," allowing favoured phenotypes to be expressed in a novel environment until evolution can "catch up" (Ghalambor, McKay, Carroll, & Reznick, 2007). An experiment reciprocally transplanting *Anolis* lizards to a novel thermal environment in the tropics demonstrated strong selection on transplanted lizards' thermal performance, despite their ability to behaviourally thermoregulate (although phenotypic plasticity for behavioural thermoregulation was not directly assessed; Logan,

Cox, & Calsbeek, 2014). Similarly, in a study where behavioural phenotypic plasticity in habitat use was directly quantified, tropical lizards exposed to a novel predator experienced selection on foraging height despite ongoing operation of plasticity for that trait (Losos, Schoener, & Spiller, 2004). Finally, differences in time spent basking by lizards in a thermal gradient suggest that divergence in thermoregulatory behaviour between populations and species may have been facilitated by adaptive behavioural plasticity within populations historically exposed to different climates (Caldwell et al., 2017). Although these studies seem to support the “phenotypic plasticity as a place-holder” hypothesis (Ghalambor et al.’s (2007) “incomplete phenotypic plasticity”), we do not yet have empirical evidence that phenotypic plasticity in thermoregulatory behaviour will partially compensate for climate change while allowing time for directional selection to act on thermal tolerance traits. No lizards experienced mortality during the brief reciprocal transplant period in our experiment, so we were unable to assess selection on light-environment use itself or on plasticity of light-environment use. A critical next step is to quantify the selection on thermal tolerance operating under the known magnitude of phenotypic plasticity for light-environment use in these populations. If selection on thermal tolerance is strong despite the presence of substantial phenotypic plasticity in light-environment use, then these lizards may have considerable adaptive potential for compensating for effects of climate change, in addition to the phenotypic plasticity measured here. As geolocator technology continues to advance and models with on-board thermometers become available, we will soon be able to correlate a lizard’s light-environment use with its operative temperature, thereby further refining biophysical models and more accurately predicting how climate change-induced shifts in vegetation communities and shade structure might impact lizard populations.

Continental- and global-scale models of climate change are very useful for predicting large-scale patterns in temperature and precipitation, but it is difficult to downscale these models to the spatial extent relevant to individual animals with small home ranges, such as lizards. Here, we continuously recorded one component of thermoregulatory behaviour, light-environment use, of wild lizards in their natural habitat and we developed a statistical framework for describing the light environment used by lizards as recorded by light-level geolocators. Lizards have become a model taxon for predicting local effects of global climate change, yet our ability to accurately measure local effects of climate change on individual thermoregulatory behaviour has been limited (Wilmers et al., 2015). Quantifying additional components of thermoregulatory behaviour beyond temperature selection, such as light-environment use, is feasible across a wide range of ectotherm taxa and habitat types, and would allow us to parameterize biophysical models with species-specific data on multiple components of thermoregulatory behaviour and their capacity for plasticity. Overall, incorporating multiple axes of thermal ecology into biophysical models will dramatically increase their accuracy at scales relevant to individual animals.

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## AUTHORS’ CONTRIBUTIONS

J.M.R. designed the research, collected data, analysed data and wrote the paper; S.S.Q. analysed data and wrote the paper; H.M.S., S.E.C., I.T.C., A.D.S. and T.K.V. collected data and contributed to writing the paper.

## DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.8jr0b76> (Refsnider et al., 2018). Annotated R code for the statistical analyses are available at <https://github.com/songsqian/lizards>.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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