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Degrees of change: between and within population variation in thermal reaction norms of phenology in a viviparous lizard

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Abstract

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Degrees of change: between and within population variation in thermal reaction norms of phenology in a viviparous lizard

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Abstract. As the earth warms, populations will be faced with novel environments to which they may not be adapted. In the short term, populations can be buffered against the negative effects, or maximize the beneficial effects, of such environmental change via phenotypic plasticity and, in the longer term, via adaptive evolution. However, the extent and direction of these population-level responses will be dependent on the degree to which responses vary among the individuals within them (i.e., within population variation in plasticity), which is, itself, likely to vary among populations. Despite this, we have estimates of among-individual variation in plastic responses across multiple populations for only a few systems. This lack of data limits our ability to predict the consequences of environmental change for population and species persistence accurately. Here, we utilized a 16-yr data set from climatically distinct populations of the viviparous skink *Niveoscincus ocellatus* tracking over 1,200 litters from more than 600 females from each population to examine inter- and intrapopulation variability in the response of parturition date to environmental temperature. We found that these populations share a common population-mean reaction norm but differ in the degree to which reaction norms vary among individuals. These results suggest that even where populations share a common mean-level response, we cannot assume that they will be affected similarly by altered environmental conditions. If we are to assess how changing climates will impact species and populations accurately, we require estimates of how plastic responses vary both among and within populations.

Key words: climate change; development; intraspecific variation; life history; phenotypic plasticity; random regression; reptile.

INTRODUCTION

Climate change is affecting the ecological and climatic context within which species exist. A common response of species to rising environmental temperatures is a shift in the timing of life history events (i.e., phenology). Such changes, including the timing of flowering (e.g., Anderson et al. 2012), migration (e.g., Anderson et al. 2013), laying or spawning (e.g., Beebe 1995, Crick et al. 1997, While and Uller 2014), birth or hatching (e.g., Visser and Holleman 2001, Husby et al. 2010), and the length of growing seasons (e.g., Menzel and Fabian 1999) have been reported for a range of species. Importantly, these effects can have a range of consequences for population persistence. For example, differences in the magnitude of phenological shifts between animals and their food sources can lead to mismatches between periods when

resource requirements are high (e.g., during periods of parental provisioning) and the availability of those resources (e.g., Mayor et al. 2017, Noble et al. 2018). In extreme cases, such phenological mismatches can lead to population collapse (Visser and Both 2005). Conversely, changes in phenology can enhance population growth. For example, earlier parturition dates or increased length of activity seasons may provide more time to juveniles for condition building and growth (McCaffery and Maxwell 2010).

Because of the potential effects of altered phenology on population persistence, an increasing number of studies that assess the responses of populations and species to climate change take shifts in phenology into account (e.g., Mitchell et al. 2008, Chapman et al. 2017, Vicenzi et al. 2017). However, in so doing, these studies often assume, explicitly or implicitly, that responses (conceptualized as a reaction norm; Nussey et al. 2007) will be homogeneous among populations, and among the individuals within them. There are several reasons, however, that these assumptions may not hold, especially where

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populations are distributed across broad climatic or geographical ranges (Valladares et al. 2014, Noble et al. 2018). Population-mean and among-individual variation in reaction norms (both slopes and elevations) can be expected to differ among populations primarily because of variation in environmental conditions, but also because of genetic factors, including differences in the strength and direction of selection, degrees of interpopulation connectivity, founder effects, past population bottlenecks, and/or genetic drift (e.g., Valladares et al. 2014). Indeed, populations located at the core and periphery of a species' range, which are likely to differ in many, or all, of these factors (Mägi et al. 2011), have been shown to differ in both mean-level reaction norms and the degree of among-individual variation in individual reaction norms (Volis et al. 1998, Mägi et al. 2011). In general, plasticity (i.e., the slope of reaction norms) should be favored where environmental conditions affecting fitness are both variable and predictable (Scheiner and Holt 2012), provided its benefits are not outweighed by its costs (e.g., DeWitt et al. 1998, Valladares et al. 2007). However, plasticity may also be favored in populations under stable conditions if there is sufficient migration among populations that differ in the environmental conditions faced (Sultan and Spencer 2002). Furthermore, random processes, such as genetic drift, founder effects, and population bottlenecks, may outweigh selection, especially in small, isolated populations, such as those at the periphery of a species range (Mägi et al. 2011). How patterns of plasticity will vary among and within populations is difficult to predict a priori because predictions may be altered depending on what component of reaction norms selection is primarily acting on. For example, selection for earlier birth, arising from the amount of time available to offspring for growth and condition building before the onset of winter (i.e., time-limited selection), is likely to be stronger in populations in colder locations than in populations in warmer locations (e.g., Uller et al. 2011). Such selective differences, however, can result in different responses with respect to reaction norm evolution. Time-limited selection could result in differences in reaction norm elevations, and/or shallower or steeper reaction norm slopes, depending on whether selection is primarily acting on reaction norm slopes or elevations, or whether there is a genetic correlation between slopes and elevations (see Edge et al. 2017).

It is important that we understand how reaction norms differ among populations because different patterns can alter predictions of how species will respond to climate change (Valladares et al. 2014). Similarly, among-individual variation in reaction norms within populations may have substantial ecological consequences (Bolnick et al. 2011). Greater variation among individuals in their expressed phenotypes, where plasticity is adaptive, is likely to enhance population persistence in the short term. Where there is little among-individual variation in reaction norms, individuals will

be affected similarly by altered environmental conditions, which could lead to population collapse if environmental change results in detrimental effects (Fig. 1a, e). In contrast, when individuals vary in reaction norm elevations (i.e., the phenotype in the mean environment), but not slope (i.e., plasticity) of reaction norms (Fig. 1b), phenotypes will vary among individuals, but to a similar extent across the environmental gradient (Fig. 1f). Where slopes vary among individuals (Fig. 1c, d), among-individual variation of phenotypes will differ among individuals to different extents across the environmental gradient (Fig. 1g, h). Thus, in extreme environmental conditions, where responses predicted by knowledge of population-mean-level reaction norms may be maladaptive, information about the level of among-individual variation may lead to alternative predicted outcomes. This is because responses of some individuals in populations with greater among-individual variation in reaction norms will differ from the population mean. Thus, some individuals may be less negatively affected by, or even benefit from, the environmental change. The level of among-individual variation in reaction norms will, additionally, determine the capacity of populations to respond to changed conditions through adaptive evolution, depending on the extent to which reaction norms are underpinned by genetics (and are, therefore, heritable) and the extent to which plastic responses affect fitness in novel conditions (Gavrilets and Scheiner 1993).

Although some studies have investigated how mean-level phenological reaction norms vary among populations (e.g., Porlier et al. 2012, Rutschmann et al. 2016, Lindestad et al. 2019) and individual reaction norms vary within populations (e.g., McGaugh et al. 2010, Ljungström et al. 2015), few have been able to compare among-individual variability among populations (but see Husby et al. 2010, Edge et al. 2017). This lack of information is, perhaps, unsurprising, because data of this type exist for few species and require long-term longitudinal data sets that include repeated measures of individuals across a range of conditions and across multiple populations. Thus, our understanding of the degree to which reaction norms of phenology vary within and among populations is limited. This is especially true for some taxa, such as reptiles, where long-term data for multiple populations are rare but for which altered environmental conditions are predicted to have significant effects. Here, we address this shortcoming using an extensive long-term data set, tracking births of the viviparous skink *Niveoscincus ocellatus* in two populations located at the species' extreme climatic limits (i.e., in warm lowland and cold alpine areas) across 16 seasons. We used this data set to investigate how thermal reaction norms of parturition date vary within and between populations. To do this, we first characterized population-mean-level reaction norms. We then tested for significant among-individual variation in the elevation and slope of thermal reaction norms of parturition date

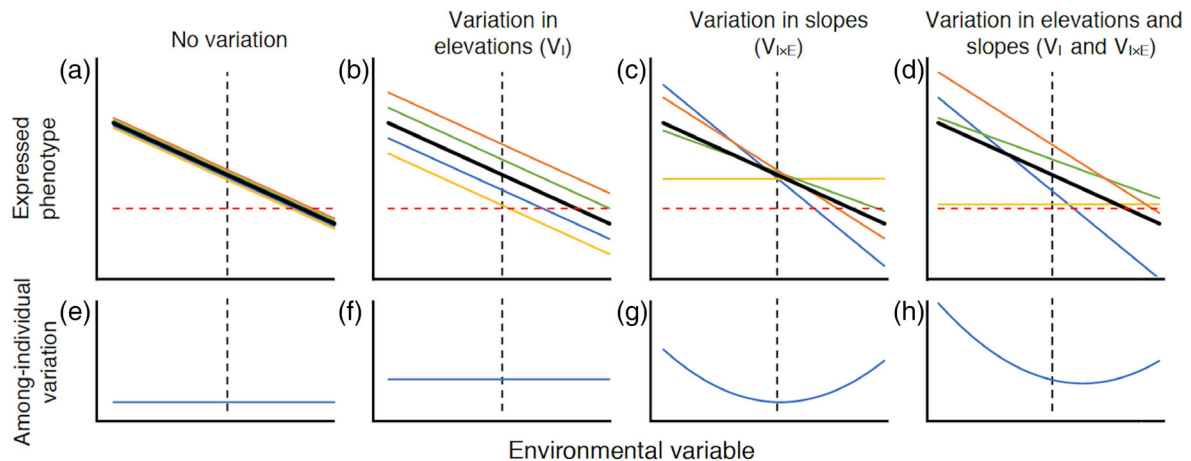


FIG. 1. Conceptual figure showing the effect of among-individual variation in reaction norms (a–d) on phenotypic variation across an environmental gradient (e–h) in populations with identical population-mean-level reaction norms (solid black line). The black dashed line represents the mean value of the environmental variable, and the red dashed line represents a phenotypic value, below which individual fitness falls to 0 (e.g., individuals fail to breed or fail to survive). Plots represent situations in which there is no among-individual variation in either the elevations or slopes of reaction norms (a and e) and all individuals are similarly affected by extreme conditions, potentially leading to population collapse. Where there is variation in elevations (b and f), slopes (c and g), or both elevations and slopes (d and h), the effect of extreme conditions varies among individuals, which may alter predictions of the effects of extreme events.

within populations using a random regression approach. Finally, by expanding this approach into a bivariate framework, we tested whether among-individual variation in the elevations and slopes of reaction norms differed between populations.

MATERIALS AND METHODS

Study system and population monitoring

Niveoscincus ocellatus (Gray 1845) is a small viviparous skink, (3–10 g, 60–80 mm snout–vent length) endemic to Tasmania, Australia. The species is a trophic generalist (Wapstra and Swain 1996) and inhabits areas of rocky scree across a wide altitudinal range from sea level to 1,200 m (Uller et al. 2011, Cadby et al. 2014). After reaching maturity, females give birth to a single litter each year. Populations are found across a broad range of climates, from comparatively warm coastal locations to cold subalpine/alpine areas. Across this range, there is evidence of local adaptation, including behavioral, physical, and physiological differences (Wapstra et al. 2001, Cadby et al. 2014, Caldwell et al. 2017), and evidence of among-population genetic isolation and differentiation (Cliff et al. 2015, Hill et al. 2018).

Annually, from the 2000/2001 to the 2015/2016 austral summer season, we monitored births in populations located at the extreme altitudinal and thermal limits of the species' range, according to a standard field and laboratory protocol (Wapstra et al. 2009, Uller et al. 2011, Cadby et al. 2014, Cunningham et al. 2017). The cold highland site is located on Tasmania's Central Plateau

(41°86' S, 146°53' E, elevation: 1,150 m), and the warm lowland site is on Tasmania's East Coast (42°55' S, 147°87' E, elevation: 30 m). Both sites are surrounded by either unsuitable habitat or road and there is, consequently, little immigration or emigration in either population (Cadby et al. 2010, Uller et al. 2011, Cunningham et al. 2018). Each year the majority (90–95%) of pregnant females were captured late in the gestation period but prior to birth (mid-December and mid-January for the lowlands and highlands, respectively, because of differences in the timing of birth; Cadby et al. 2010, Uller et al. 2011, Gruber et al. 2018). Females were identified using existing toe clips, and their capture location was recorded (± 5 m). Females were then returned to a temperature-controlled facility (ambient temperature 16°C) at the University of Tasmania, where they were weighed (± 1 mg) and housed in individual terraria (600 cm²) with a shelter, a basking rock and a basking light provided for 8 hr per day. This provided a thermal gradient from approximately 35°C directly below the basking light to 14°C in the remainder of the terrarium. Water was available ad libitum and lizards were fed 3–4 times per week on mealworms (*Tenebrio* larvae) and Heinz baby food, supplemented with protein powder (Nature's Way). Terraria were checked twice daily for newborns.

Following birth, mothers and offspring were weighed and measured and offspring were sexed and toe clipped for future identification. Within 1 week of birth, offspring were released at 1 of 12 random release locations within each site, and mothers were released at the release location closest to where they were captured. Thus, we avoided conflating the effects of subclimates within sites

with heritable or maternal effects because, following birth, offspring did not occupy the same location within sites as their mothers or siblings (see Wapstra et al. 2010). This data set now covers 16 yr of uninterrupted data, consisting of records for over 1,200 litters, from over 600 unique females, from each population (see Appendix S1: Table S1).

Statistical analysis

Population-level patterns.—To explore population-mean-level response of parturition dates to temperature, we first fit a linear mixed model (LMM) with mean cohort parturition date as a response variable. We have previously shown that factors other than temperature, including environmental variables (humidity, cloud cover, and wind speed; Cadby et al. 2010), food quality during gestation (Cadby et al. 2011), females' condition at ovulation and food availability during gestation and their interactions with temperature (Gruber et al. 2018) do not affect birth dates in *N. ocellatus*. We, therefore, included the site-specific mean maximum daytime temperature during the gestation period (October 1–December 31 and October 15–January 15 for the lowland and highland sites, respectively (Pen et al. 2010).), site (highland or lowland), and their interaction as fixed factors. We additionally included year as random factor to model interannual variation not explained by temperature. Gestation periods differed for each site because ovulation dates differ among sites but are highly synchronized among females within them (Wapstra et al. 2009). Temperature data were obtained from Australian Bureau of Meteorology weather stations located close (<11 km) to the sites (Orford South (42°36' S, 147°55' E) and Liawenee (41°54' S, 146°40' E) meteorological stations for the lowland and highland sites, respectively).

Within-population patterns.—To explore patterns of among-individual variation in the effect of temperature on parturition date within populations, we used a random regression framework. Using univariate random regression models, we estimated among-individual variation in mean parturition dates and their response to temperature during gestation for each population by fitting constant ($x = 0$) and linear ($x = 1$) polynomial functions (Φ). A first-order function estimates a linear reaction norm for individual parturition dates across temperature. Thus, among-individual variance in intercepts (V_I) and slopes ($V_{I \times E}$) of reaction norms is estimated, as well as the covariance between slopes and intercepts, resulting in a 2×2 variance-covariance matrix. In our analysis, we used Legendre polynomials, which are only defined within the range -1 to $+1$. We, therefore, standardized site-specific measurements of temperature (see Population-level patterns, above) to be within this range using the equation

$$T = -1 + 2(T_{\text{gest}} - \min T_{\text{gest}}) / (\max T_{\text{gest}} - \min T_{\text{gest}}).$$

Our full model was

$$PD_i = XT_i + Z_1\varphi(I_i, n_1, T) + Z_2Yr_i + e_i.$$

In this model, PD_i is the vector of individual parturition dates and X is the design matrix relating to the fixed effect of standardized yearly mean maximum daytime temperature during gestation (T on the range -1 to 1). Z_1 and Z_2 are the design matrices relating to the random effects of individual female (I_i), and year (Yr_i) observations, respectively. Year (Yr_i vector) was included as a random effect to model variation among years not explained by environmental temperature. Thus, $\varphi(I_i, n_1, T)$ is the random regression function of order n_1 of individual i . We modeled both homogeneous and heterogeneous by-year residual error variances (i.e., we first estimated a common within-individual variance across years and then 16 year-specific within-individual residual variances; see Nicolaus et al. 2013). For both sites, all models fit with a heterogeneous structure gave a better fit than equivalent models fit with a homogenous structure (lowland: $\chi^2_{15} = 90.18$, $P < 0.0001$; highland: $\chi^2_{15} = 90.30$, $P < 0.0001$ comparing model 4; see Table 1). We, therefore, present results from models fit with heterogeneous error variances. To test the significance of model fit and random factors, we fit models of increasing variance structure complexity (see Table 1) and tested the significance of variance and covariance components using likelihood ratio tests with degrees of freedom equal to the difference in degrees of freedom between the models being compared.

Between-population comparison.—To test explicitly whether among-individual variation in thermal reaction norms of parturition date differed between populations, we modeled the response of parturition date to temperature during gestation in a bivariate random regression model following Husby et al. (2010). We combined the data sets from both populations, treated parturition date in each population as a separate trait, and included population-specific scaled standardized environmental temperature (see Within-population patterns, above) as a fixed effect. In these models, we constrained the covariance between population-specific traits to be zero since, given the distance between sites and the limited dispersal ability of *N. ocellatus* (Atkins et al. 2007), gene flow is likely to be negligible (see Cliff et al. 2015 for evidence of population genetic isolation). As in the univariate models above, we fit these models with heterogeneous, by-year, error variances. Thus, the residual variation was modeled as 16 (year-specific for each population) 2×2 unstructured matrices with covariances constrained to be zero. Residual variance in these models was, therefore, the same as for the univariate models, above. To compare among-individual variation between

TABLE 1. Results from site-specific univariate regression analyses of the effect of environmental temperature during the gestational period on parturition dates in lowland and highland populations of the viviparous skink *Niveoscincus ocellatus* across 16 yr.

Model	Variance components	df	Lowland			Highland		
			LogL	χ^2	<i>P</i>	LogL	χ^2	<i>P</i>
1	Null	–	–3,952.34	–	–	–2,846.18	–	–
2	Year	1	–3,815.11	274.46	<0.0001	–2,525.83	640.70	<0.0001
3	Year+ V_I	1	–3,664.63	300.96	<0.0001	–2,451.56	148.54	<0.0001
4	Year + V_I + I×E	2	–3,662.00	5.26	0.072	–2,450.27	1.29	0.275

Notes: Degrees of freedom, χ^2 values are for comparison with the previous model of log likelihoods from which *P* values are calculated. All models were fitted with year-specific error variance (see Methods). V_I is the between-individual variance; I×E is the phenotypic variance–covariance plasticity matrix. Variance components for model 4 are presented in Table 2. Variance components for models 1–3 are shown in Appendix S1: Tables S2 and S3.

populations, we used a likelihood ratio test to compare models in which we optimized the likelihood with the variance components for the two populations constrained to be equal to one in which they were unconstrained (see Husby et al. 2010). Random regression analyses were performed using ASReml v 4.1 (Gilmore et al. 2015). The GLMM model and likelihood ratio tests were performed in R (R Development Core Team 2014).

RESULTS

Population-level patterns

Over the 16-yr field study, temperatures differed substantially between the two sites. Mean maximum temperatures during the gestation period varied between 17.4 and 20.8°C (mean = 19.0°C) at the lowland site, and between 12.8 and 17.4°C (mean = 15.58°C) at the highland site. Despite this, population-mean-level reaction norms were similar between sites. There was no interaction effect between site and temperature ($F_{(1,20.8)} = 0.48$, $P = 0.495$; $\sigma_{\text{Year}} = 0.60 \pm 0.78$ SD; $\sigma_{\text{resid}} = 18.34 \pm 4.29$ SD) or an independent effect of site ($F_{(1,29.3)} = 0.17$, $P = 0.685$) on mean cohort parturition date. There was, however, a significant main effect of temperature on mean parturition date ($F_{(1,21.1)} = 55.09$, $P < 0.0001$). Thus, temperature had a similar effect on parturition dates at both sites, advancing 5.96 ± 0.81 SD days for each 1°C increase in temperature (Fig. 2). Because of differences in temperatures, mean cohort parturition dates were later and varied more among years in the highlands than in the lowlands.

Within-population patterns

Univariate models for both populations revealed significant among-individual variation in parturition date at mean temperatures (i.e., V_I the intercept of reaction norms) in both populations ($P < 0.0001$ in both populations: model 3 in Table 1). In the lowlands, we found some evidence that individuals varied in the effect that temperature had on parturition dates (i.e., I×E; the slope

of reaction norms (plasticity); model 4 in Table 1), although this failed to reach significance ($P = 0.072$). In the highland population, we found no evidence for among-individual variation in plasticity ($P = 0.275$). In models where both random individual intercepts and slopes were fitted (Model 4, Table 1), the estimated size of the individual variance components for slope was 1.3 in the lowland population and 0.18 in the highland population (Table 2). When visualized according to a character-state view, the lowland population showed a qualitative (though nonsignificant) pattern of increasing V_I with increasing temperature (Fig. 3a), whereas the highland population showed no evidence of a change in V_I across the range of temperatures observed (Fig. 3b). See Appendix S1: Table S4 for variance components evaluated at standardized temperatures; that is, from a character-state view.

Between-population comparison

Results from the bivariate models explicitly comparing among-individual variation in reaction norms between populations were consistent with the results from the univariate, within-population patterns. These tests showed that there was a significant difference between the populations in patterns of among-individual variation in reaction norm intercepts (V_I ; $\chi^2_1 = 60.85$, $P < 0.0001$) and slopes ($V_{I \times E}$; $\chi^2_3 = 51.45$, $P < 0.0001$; see Fig. 3). Thus, this test supports the conclusion that the I × E pattern differs between populations, despite among-individual variation in the lowland population failing to reach statistical significance.

DISCUSSION

Within species, climatically distinct populations have experienced historically different selective pressures and demographic patterns. Thus, it is not clear that such populations should necessarily share a common phenotypically plastic response to environmental conditions. Likewise, within populations, reaction norms may vary among individuals, and the degree of among-individual variation may vary among populations. Here, we

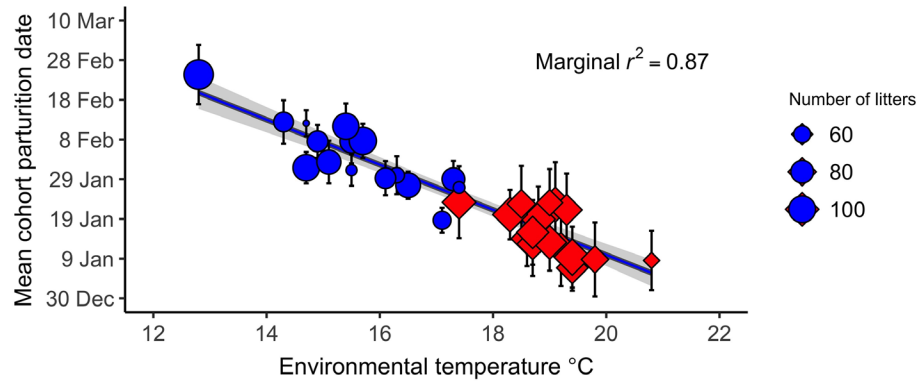


FIG. 2. Relationship between mean cohort parturition date and environmental mean maximum daytime temperature during the gestation period in highland (blue circles) and lowland (red diamonds) populations of the spotted snow skink *Niveoscincus ocellatus* between 2000/2001 and 2015/2016. Error bars show standard deviations from the mean. Point size indicates the number of litters born within years.

TABLE 2. Variance components of site-specific univariate random regression models of the effect of environmental temperature during the gestational period on parturition dates in lowland and highland populations of *Niveoscincus ocellatus* across 16 yr (2000/2001–2015/2016), fit with random effects for year and individual variation in intercept (V_I), slope ($V_{I \times E}$) and their covariance (COV) with heterogeneous by-year error variance (Model 4 from Table 1).

Variance component	Lowland	Highland
Year	21.71 ± 8.38	21.38 ± 8.16
2000/2001	10.71 ± 5.15	21.38 ± 8.16
2001/2002	56.60 ± 11.74	5.83 ± 1.87
2002/2003	57.05 ± 10.97	44.26 ± 8.02
2003/2004	67.95 ± 11.36	20.93 ± 4.10
2004/2005	20.28 ± 4.63	9.43 ± 1.87
2005/2006	28.52 ± 5.58	7.77 ± 1.84
2006/2007	28.55 ± 5.68	22.74 ± 3.86
2007/2008	31.29 ± 7.14	16.68 ± 3.29
2008/2009	25.31 ± 4.87	22.18 ± 4.73
2009/2010	22.04 ± 4.63	5.35 ± 2.09
2010/2011	15.88 ± 3.68	3.69 ± 1.69
2011/2012	32.03 ± 6.34	11.44 ± 2.89
2012/2013	44.97 ± 8.98	11.34 ± 2.77
2013/2014	51.24 ± 10.09	7.05 ± 2.12
2014/2015	21.07 ± 5.59	11.78 ± 2.50
2015/2016	1.93 ± 9.18	6.35 ± 2.07
V_I	76.85 ± 6.32	16.44 ± 2.16
Cov	9.25 ± 3.66	-1.34 ± 1.30
$V_{I \times E}$	1.30 ± 4.19	0.18 ± 1.29

Notes: Variances are presented ± standard error. Variance components for models 1–3 for each site are presented in Appendix S1: Tables S2 and S3.

explicitly tested whether patterns of the plastic response of parturition date to temperatures experienced during gestation (i.e., thermal reaction norms of parturition) varied within and between climatically distinct populations of the viviparous skink *Niveoscincus ocellatus*. Population-mean reaction norms of parturition date were

the same between populations, but the degree of among-individual variation in reaction norms was different. This suggests that, despite having similar population-mean reaction norms, highland and lowland populations may respond differently to changing climates, in both in the short and the long term.

Environmental temperature during the gestation period affected parturition dates in both the highlands and the lowlands. Birth dates advanced to the same extent with increasing temperatures in both populations. Because of differences in temperatures between sites during this period, this contributed to parturition occurring later in the highlands than in the lowlands across years. An effect of temperature on parturition date is not surprising in this species because, as ectotherms, snow skink metabolism and, therefore, development rates are temperature dependent (Wapstra 2000, Cunningham et al. 2017, 2018). Indeed, for this reason, birth or hatching dates generally advance with increasing environmental temperatures in reptilian taxa (Noble et al. 2018). It is unlikely that other environmental factors contributed to this effect, as previous research has demonstrated that such factors, including maternal condition at ovulation, and food availability and quality during gestation, do not affect parturition date in this species. (Cadby et al. 2011, Gruber et al. 2018).

When we examined the extent to which individuals within both populations varied in their individual thermal reaction norms, we found that individuals of both populations varied in the elevation of reaction norms (V_I). We also found evidence that individuals in the lowlands, but not the highlands, varied in the slope of reaction norms ($V_{I \times E}$) although this failed to reach statistical significance. This suggests considerable among-individual variation in thermal reaction norms of parturition, and that among-individual variation differed between the two populations. Indeed, despite a consistent mean-level reaction norm across both highland and lowland populations, when we explicitly compared individual-

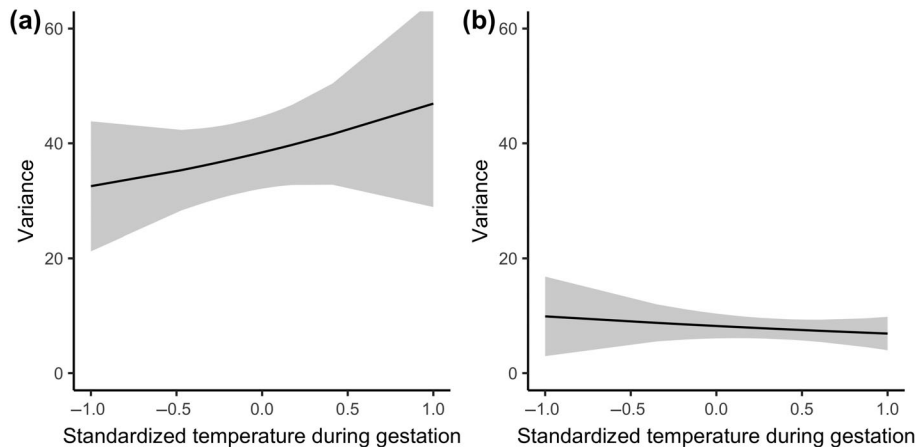


FIG. 3. Change in among-individual variance (V_1) in parturition date in relation to standardized mean temperature during gestation in (a) lowland and (b) highland populations of *Niveoscincus ocellatus* over 16 yr (2000/2001 to 2015/2016). Shaded areas indicate the approximate 95% confidence interval. Standardized temperatures correspond to mean temperatures on the range 17.4 to 20.8 in the lowland population and 12.8 to 17.4 in the highland population (see Methods).

level variation in reaction norm intercepts and slopes between populations in our bivariate model, we found significantly more among-individual variation in the lowland than the highland population in both parameters, and a qualitative pattern of increasing variation with increasing temperature in the lowland population, but not the highland population. Combined, these results suggest that thermal reaction norms of parturition vary more among females in the lowlands than among females in the highlands.

What might account for these differences between populations? Because *N. ocellatus* is viviparous, observed reaction norms of parturition (both slopes and intercepts) are the result of interactions between the effects of underlying physiology and behavioral thermoregulation. Both of these factors are likely to differ among populations. For example, *N. ocellatus* captured from highland populations bask significantly more, and maintain higher body temperatures, than those from lowland populations when maintained under the same thermal conditions in the laboratory (Cadby et al. 2014, Caldwell et al. 2017). This may explain lower among-individual variation in the elevation and, possibly, the slopes of thermal reaction norms of parturition in the highlands, compared to the lowlands, because in the highlands there is a tighter link between environmental temperatures and the temperatures experienced by females (and, thus, developing embryos). Lower among-individual variation (i.e., canalization) of reaction norms of parturition in the highlands than the lowlands may also be the result of selection. In the highlands, newborns have a shorter period for growth and condition building between birth and the onset of winter than those in the lowlands (Atkins et al. 2007, Uller et al. 2011). Birth dates may, therefore, be under stronger selection in the highlands than the lowlands, leading to canalization of reaction norms. The canalization of developmental

reaction norms (which influence birth date) may, alternatively, be a concomitant result of selection on other developmental traits affected by temperature. For example, we have previously found that increased size at birth enhances survival in the highlands, but not in the lowlands (Uller et al. 2011). Alternatively, the patterns we observed may have arisen because of variation among the environmental conditions to which individuals are exposed at a microscale. The lowland site is more heterogeneous than the highlands, with areas of suitable rocky scree overshadowed to different extents by vegetation. In contrast, highland populations are restricted to exposed rocky outcrops without significant vegetation. Increased vegetation cover affects both mean temperatures and their variation at fine scales (Suggitt et al. 2011). Females show high within-site fidelity among years (see Atkins et al. 2007). Higher among-individual variation in the elevation of measured reaction norms at our lowland site may, therefore, have resulted from greater differences between individuals between the environment actually experienced and the environment we measured (i.e., the broad-scale, population-mean temperature), rather than variation in thermal reaction norms of physiology and/or behavior per se. Finally, to the extent that reaction norms are underpinned by genetics, any factor that reduces genetic variation will result in reduced among-individual variation in reaction norms. Thus, differences in among-individual variation of reaction norm elevation between populations may result from differences in a range of demographic factors including founder effects, population bottlenecks, interpopulation connectivity, or genetic drift (Valladares et al. 2014).

Clearly, more work is required to disentangle these alternative hypotheses. For example, holding pregnant females at controlled temperatures during gestation would allow the effects of mothers' thermoregulatory behavior and small-scale environmental variation to be

disentangled, whereas genetic profiling of populations would enable an estimation of how overall genetic variation differs among them. The genetic contribution to plasticity could also be estimated using common garden transplant or controlled mating experiments. Where data on paternity are available, or with additional years of female phenology data, a random regression animal modeling approach (see Kruuk 2004) could be used to estimate the degree to which reaction norm slopes and elevations are heritable and the extent to which the heritability of these traits vary within and among populations. Finally, long-term data and experimental manipulations from additional populations across the climatic and environmental gradient of the species distribution, although logistically very difficult to collect, would also help disentangle these effects and ultimately allow for a more thorough assessment of how and why reaction norms vary within and among populations.

Independent of the mechanisms responsible for the differences in among-individual variation in reaction norms between populations, our results have a number of important consequences for how these populations might respond to environmental change. Because climatically distinct populations share a common population-mean-level reaction norm, we can project the short-term effect of rising temperatures on mean cohort parturition dates across the full distributional range of the species with some confidence. We found that, in climatically distinct populations, parturition dates advanced 5.96 ± 0.84 SE days for each 1°C increase in mean maximum daytime temperature over the gestation period. Mean maximum temperatures in Tasmania are projected to rise by between 1.6°C (low emissions scenario) and 2.9°C (high emissions scenario) over the course of the 21st century, and this rise is likely to be relatively uniform across the landscape (Grose et al. 2010). Thus, in the absence of other factors, the inter-annual mean of mean cohort parturition dates can be expected to advance by as much as 17 d by 2,100 across the species' range. Indeed, in extreme warm years mean cohort dates of birth may advance by as much as a full month (i.e., from mid-January to mid-December and from early February to early January in the lowlands and the highlands, respectively). Shifts in phenology, such as this, have been widely reported for many species across both ectothermic and endothermic taxa and are one of the most consistently predicted and observed consequences of warming climates (e.g., Root et al. 2003, Cohen et al. 2018).

Whether altered climate and its effects on parturition dates have a positive or negative effect on population persistence in *N. ocellatus* in the short term will depend on the net effect of a range of factors. These include the frequency, duration, and magnitude of extreme temperatures, the extent to which advanced phenology allows for increased time for growth and survival (Uller et al. 2011, Cunningham et al. 2018), rates of temperature-induced developmental stress, the extent to which increased

temperatures select for responses to avoid thermal extremes (e.g., Monasterio et al. 2011) and differences in the effect of temperature on the phenologies of other components of the ecosystem, which may lead to the emergence of trophic mismatches (e.g., Mayor et al. 2017, Noble et al. 2018). Importantly, the differences between populations we found in among-individual variation in the elevation and, possibly, the slopes of reaction norms suggest that the consequences of altered phenology may differ among populations. This is likely because the effects of altered parturition phenology will vary more among individuals in our lowland population than among those in our highland population. In the longer term, changes in environmental conditions are likely to provoke an evolutionary response as selective pressures change. The potential of a population for evolutionary adaptation in a trait, including plasticity itself, is partially determined by the degree to which among-individual variation in that trait has a heritable basis (e.g., Franks and Hoffmann 2012). Although we were unable to test this in our study, if among-individual variation in reaction norms is due to heritable variation, lowland populations may have a greater capacity to respond to changed conditions in the long-term through adaptive evolution. Thus, in *N. ocellatus*, greater among-individual variation in reaction norms at the phenotypic level, whether or not it has a heritable component, suggests that lowland populations have a greater capacity to respond to changed climatic conditions than highland populations. Researchers should be cautious of predicting that populations will be similarly affected by changes in phenology arising from altered environmental conditions, even where populations share a common mean-level reaction norm.

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