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Recurrent sublethal warming reduces embryonic survival, inhibits juvenile growth, and alters species distribution projections under climate change

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Abstract

The capacity to tolerate climate change often varies across ontogeny in organisms with complex life cycles. Recently developed species distribution models incorporate traits across life stages; however, these life-cycle models primarily evaluate effects of lethal change. Here, we examine impacts of recurrent sublethal warming on development and survival in ecological projections of climate change. We reared lizard embryos in the laboratory under temperature cycles that simulated contemporary conditions and warming scenarios. We also artificially warmed natural nests to mimic laboratory treatments. In both cases, recurrent sublethal warming decreased embryonic survival and hatchling sizes. Incorporating survivorship results into a mechanistic species distribution model reduced annual survival by up to 24% compared to models that did not incorporate sublethal warming. Contrary to models without sublethal effects, our model suggests that modest increases in developmental temperatures influence species ranges due to effects on survivorship.

INTRODUCTION

For organisms with complex life cycles, ecological consequences of climate change may be driven by responses to warming that vary across ontogeny (Kingsolver *et al.* 2011; Radchuk *et al.* 2013). With rapid warming, a major goal for ecologists is to determine thermally-sensitive processes that underlie shifts in range dynamics (Pacifici *et al.* 2015; Urban *et al.* 2016). Recent advances in species distribution models (SDMs) incorporate biological mechanisms to predict climate-driven range shifts (Helmuth *et al.* 2005; Buckley *et al.* 2010; Riddell *et al.* 2017) but often rely upon adult life stages to make predictions (e.g., Sykes *et al.* 1996; Buckley 2008; Deutsch *et al.* 2008; Randin *et al.* 2009; Kearney 2013). Downstream effects from early life have

consequences for growth, survival, and reproduction (reviews in Lindström 1999; Podolsky & Moran 2006; Harrison *et al.* 2011). Thus, ecological projections might hinge on responses across ontogeny for many species (Lindström 1999; De Block & Stoks 2005).

Sensitive stages of early ontogeny drive ecological responses to environmental change (Radchuk *et al.* 2013). Sessile stages are sensitive to fluctuating conditions due to limited behaviors and the small range of microclimatic conditions experienced over small spatial extents (e.g., an egg; Refsnider & Janzen 2010; Telemeco *et al.* 2016; but see Du & Shine 2015). Embryos consequently rely on physiological responses to developmental conditions that can alter growth and development rates and increase mortality (e.g., Castro *et al.* 2005; Georges *et al.* 2005; Hepp *et al.* 2006; Oufiero & Angilletta 2006; Potter *et al.* 2011). In turn, developmental conditions may influence population dynamics through changes in maturation rates, reproductive success, and survival (e.g., Haywood & Perrins 1992; Lumey & Stein 1997; Warner & Andrews 2002; DuRant *et al.* 2010; Larios *et al.* 2014), particularly in short-lived species (Tinkle 1969; Overall 1994). Downstream effects of warming also increase risk of extirpation by reducing reproductive performance and survival (Edmunds 2005; Neilson *et al.* 2005; Crozier *et al.* 2008). Impacts of thermal fluctuations in early ontogeny should thus be considered in the development of physiologically-explicit models (Levy *et al*. 2015; Urban *et al*. 2016).

The lasting effects of warming during early ontogeny may be underestimated by ignoring impacts of fluctuating thermal conditions. Recurrent sublethal stressors—exposures to suboptimal conditions that are not acutely lethal—are increasingly likely as climate warming increases daily temperature variance and frequencies of extreme weather events (Meehl & Tebaldi 2004; IPCC 2013). Modest increases in temperature can benefit growth and development (Angilletta *et al.* 2004b; Refsnider & Janzen 2010), particularly in environments where low

temperatures limit growth (Deutsch *et al.* 2008; Randin *et al.* 2009; Paaijmans *et al.* 2013). However, in warmer environments, increased incubation temperatures may result in recurrent sublethal extremes that lead to chronic stress (Campbell *et al.* 1998; Badyaev 2005), which can inhibit development, increase embryo mortality, and influence lifetime fitness (e.g., Shine & Elphick 2001; Fly & Hilbish 2013; Marshall & Sinclair 2015). Recent SDMs incorporate ontogenetic variation of thermotolerance for some well-studied species (e.g., Crozier *et al.* 2008; Levy *et al.* 2015). Clearly, lethal thresholds influence fitness; however, physiologically-explicit SDMs based solely on lethal limits ignore consequences of recurrent sublethal fluctuations (Woodin *et al.* 2013). Unfortunately, the preponderance of constant-temperature treatments in physiological studies has left little focus on fluctuating developmental regimes (Niehaus *et al.* 2012; Bowden *et al.* 2014). Constant incubation temperatures have advanced research by elucidating thermal sensitivities of phenotypes across many oviparous taxa (reviews in Deeming & Ferguson 1991a; Booth 2006; Bowden *et al.* 2014). However, the applicability of that data to development under natural conditions is limited. By overlooking acute and recurrent thermal stressors, incubation under constant temperatures poorly predicts development under natural cycles (reviews in Bowden *et al.* 2014; Warner 2014; Wu *et al.* 2015). Thermal stress on anurans and *Manduca sexta* larvae reared under constant temperatures resulted in reaction norms that poorly predicted growth and development under naturalistic regimes (Niehaus *et al.* 2012; Kingsolver *et al.* 2015). Thermal impacts on development underscore the importance of experimental conditions for the embryonic environment.

Here, we use naturalistic thermal cycles to examine consequences of recurrent sublethal warming during incubation on embryonic and post-hatching phenotypes. We integrate these findings to predict the species distribution of *Sceloporus undulatus*, a widespread North

American lizard. Maternal behavior of *S. undulatus* suggest that females nest in the warmest parts of their environment, digging shallow nests where embryos experience diel thermal cycles (Fig. 1 a,b; Angilletta *et al.* 2000; Angilletta *et al*. 2009). Increases in temperature means and variances of *Sceloporus* embryos can speed growth and development without affecting survival (e.g., Sexton & Marion 1974; Andrews *et al.* 2000; Angilletta *et al.* 2000; Oufiero & Angilletta 2006). However, our study is the first to warm embryos throughout incubation beyond regimes experienced at contemporary nest sites in this system. In the laboratory, we reared embryos under treatments that simulated contemporary and potential future thermal conditions. In a complementary field experiment, we artificially warmed natural nests to simulate similar sublethal warming. We integrated embryonic responses to warming into a SDM using a life-cycle submodel of population dynamics (Levy *et al.* 2015). Model projections indicate that moderate warming during early ontogeny can limit species ranges. Our study highlights consequences of transient, but recurrent, exposure to warmer nests that may harm embryos and hatchlings, shaping ecological responses to environmental change.

METHODS

Laboratory Methods

Collection & husbandry

To examine impacts of sublethal warming during incubation, we conducted experiments using *S. undulatus* eggs from females collected in Edgefield County, South Carolina (SC) in May and June 2014 (UTM Easting 396467.43, Northing 3753517.85, Zone 17S). We housed adult lizards at Clemson University in terraria (8.48L; 30x19.5x14.5cm) with moist sphagnum for oviposition. Programmable environmental chambers (I-36VL; Percival Scientific, Perry, Indiana, USA)

maintained 14:10-hour light:dark cycles and kept lizards at preferred daytime (32°C) and approximate nighttime (24°C) temperatures (Niewiarowski 1992; Angilletta 2001). We replenished water daily and offered crickets *ad libitum* every two days.

Collection and care of eggs minimized exposure to conditions outside of treatment designs. We checked terraria hourly 0700-2100 to immediately weigh and place eggs in individual containers (59mL; 3cm-height-by-5cm-diameter) with a 1:100 water-to-silica-sand mixture (Angilletta *et al*. 2000). Environmental chambers (I-36VL; Percival Scientific) maintained eggs at 80% relative humidity and temperatures per treatment designs. We replaced water lost from containers every 3 days to maintain hydric conditions throughout incubation. We rotated treatment groups between chambers and rotated shelves in a balanced randomized design to control for potential effects of chamber or shelf location. Hatchlings were transferred to containers (474mL; 7.5cm-height-by-9cm-diameter) under the same conditions as adults, except pinhead crickets were offered daily.

Treatment design

We designed the treatments to create naturalistic thermal regimes based on soil temperatures recorded in simulated nests in Edgefield County, SC (Angilletta & Sears, unpublished data), which were constructed assuming nesting conditions consistent with those observed by Angilletta *et al.* (2009). The treatments included a thermal regime that estimated contemporary SC nest temperatures and two regimes that increased daily maximum temperature (T_{max}) to simulate warming scenarios (Fig. 1a). Angilletta *et al.* (2013) suggested that exposure to high T_{max} was not necessarily harmful to *S. undulatus* embryos below a lethal threshold (~41°C). However, they measured effects of acute exposure. To examine impacts of recurrent exposures

to high T_{max} throughout incubation, we increased T_{max} in the warming treatments by 3.5° and 7.0°C relative to the contemporary treatment (32.0°C). Thus, embryo T_{max} increased to suboptimal levels without reaching the lethal threshold. Though climate warming also increases nighttime minima (Donat & Alexander 2012; IPCC 2013), we held daily minimum temperature (T_{min}) at 19.0°C across treatments to specifically examine effects of increasing T_{max}. From 12 clutches (clutch size 7.67±0.39 (SEM), range 6-10), 29 embryos were reared under the contemporary treatment, 33 under +3.5°C, and 31 under +7.0°C.

To control for maternal effects, we randomly distributed each clutch evenly among treatments. In *S. undulatus*, oviposition occurs at about 18-26% of embryonic development (Sexton & Marion 1974; Parker *et al.* 2004). We maintained females under common conditions in the laboratory. So, assuming females maintained similar field body temperatures (T_b), embryos experienced the same temperatures *in utero*. Therefore, embryos were exposed to maternal T_b during the earliest stages of embryogenesis and to experimental temperatures during mid-to-late-development.

Embryonic survival & hatchling growth

We monitored survival daily by checking for heartrates using an infrared sensor (Buddy Egg Monitor; Avitronics, Cornwall, UK). If no heartrate was detected for three consecutive days, we marked the embryo as deceased on the first day. We measured hatchling mass to 0.1mg and snout-vent length (SVL) to 0.1mm. We then calculated scaled mass indices (SMI) from standard regressions of mass-to-SVL as outlined in Peig & Green (2009; 2010) to estimate hatchling body conditions. We chose SMI as a less biased measure than other indices (e.g., Fulton's index:

mass*length^{-3}) that do not account for changing allometry across growth stages (see Appendix S1 for details).

To examine downstream effects of warming treatments, we calculated juvenile growth rates. We repeated body size measurements for the first three weeks post-hatching. Then, we used the approach described by Dunham (1978) and Schoener & Schoener (1978) to estimate characteristic growth rates (r) for the interval form of von Bertalanffy growth models. We used SVL instead of mass to minimize potential variation due to nutritional state (Dunham 1978; Sears 2005). We fitted the growth model using Levenberg-Marquardt nonlinear least-squares regression from the *minpack.lm* library in R (Elzhov *et al.* 2015).

Field Methods

Tracking & collection

In May and June 2015, we tracked gravid females using radio telemetry to locate nests. We attached radio transmitters (Model BD-2X; Holohil Systems Ltd., Carp, Ontario, Canada) weighing <5% of a female's body mass to the dorsum with surgical adhesive. We located 8 nests (82 eggs, clutch size 10.2±0.36, range 9-12) and assigned clutches laid within five days of each other to nesting groups, within which we reciprocally transplanted eggs to control for maternal effects. We carefully excavated eggs and placed them in individual containers as in the laboratory methods for transport to Clemson University. We incubated eggs at 15°C for up to five days to allow collection of multiple clutches. This method suspends development without affecting growth and survival after development resumes (Christian *et al.* 1986; Andrews *et al.* 1997). We then reconstructed nests to contain a random sample including at least one egg from each clutch in the nesting group and totaling the original clutch size laid in that nest. iButton

loggers (DS1922L; Maxim Integrated, San Jose, California, USA) recorded hourly temperatures at mean nest depth.

Treatment design

We randomly assigned half the nests to a warming treatment, for which a 0.09m^2 section of black thermoplastic (TerraTexSF-D; Hanes Geo, Winston-Salem, North Carolina, USA) was stapled against the soil surface to decrease solar reflectance. There were 44 embryos among the natural nests and 38 among warmed. The material consisted of woven 2.0mm-wide-by-0.15mm-thick polypropylene filaments, forming a porous surface that increased daytime nest temperatures without retaining excess heat overnight and allowed for water and gas exchange. To ensure this method did not influence soil moisture or oxygen availability, we performed a validation experiment in which we measured soil temperatures, moisture, and oxygen in a grid of mock nests randomly assigned to the warmed or natural treatment (see Appendix S1 and Table S1 for details).

Embryonic survival & hatchling size

We monitored nests daily for emerging hatchlings. Steel wire cages with 3.0mm spacing placed over nests enabled collection. We calculated survival by counting hatchlings and confirmed results through excavation to count nonviable eggs and empty shells. We measured hatchling mass and SVL and calculated SMI as described above.

Data Analysis

We conducted statistical analyses in R v3.3.1 (R Core Team 2016). To test effects of laboratory warming treatments on embryonic survival, we used a Cox proportional hazard model from the *survival* library (Therneau 2014), which included an estimator of variance attributable to maternal identity to control for correlation of responses among siblings. To test effects of laboratory treatments on development time, hatchling sizes, SMI, and *r*, we constructed linear mixed effects (LME) models using the *lme* function (Pinheiro *et al.* 2016) with treatment as a categorical variable and maternal identity as a random effect. We added hatchling SVL as a continuous variable for *r* and initial egg mass as a continuous variable for development time and hatchling sizes. For the field data, we constructed LME models with treatment as a categorical variable and with assigned nest and nesting group as random effects for T_{max}, T_{min}, embryonic survival, development time, hatchling body sizes, and SMI. We could not include maternal identity in analyses of field data due to the reciprocal transplants. For each parameter in an LME model, we calculated effect sizes (ω^2) to determine the proportion of explained variance of each parameter included in an ANOVA (Olejnik & Algina 2003):

$$\omega^2 = (SS_{treatment} - (df_{treatment} \cdot MS_{error})) / (SS_{total} + MS_{error}) \quad [1]$$

where $SS_{treatment}$ = sum of squares, $df_{treatment}$ = degrees of freedom, MS_{error} = mean square error, and SS_{total} = total sum of squares.

Life-Cycle Model of Population Dynamics

Modeling embryonic and juvenile survival

We developed a SDM to explore how inclusion of our results affects projections of embryonic survival and population growth in North America. Our model was based on a population dynamic model developed by Buckley (2008) to incorporate biology of free-living *Sceloporus*

life stages into population growth projections under climate change and extended to include embryonic development and juvenile survival as in Levy *et al.* (2016b). Parameterization followed previous simulations, except where noted below.

We simulated activity by predicting T_b for female lizards of average size (10.7g; Angilletta 2001) across the geographic range on surfaces with 0-100% shade. We calculated T_b from operative temperatures (steady state temperature in a microclimate; Bakken 1992) using hourly microclimates (Levy *et al.* 2016a) covering the USA at 36x36-km resolution for the past (1980-2000) and future (2080-2100, assuming radiative forcing of +8.5W/m at year 2100). See Table S2 and Appendix S1 for parameter values and additional details. We assumed that lizards are active when T_b falls within the preferred range (central 80% of field body temperatures; Table S2) and that reproductive season begins after temperatures enable 30 days of activity (Tinkle & Ballinger 1972; Angilletta 2001). On each day of the reproductive season, we simulated oviposition by allocating nests to microhabitats with each combination of shade (0, 25, 50, 75, or 100%) and depth (3, 6, 9, or 12cm), which captured the range of microhabitats for natural nests (Angilletta *et al.* 2009; this manuscript).

Based on our empirical observations, we evaluated the impacts of warming nest temperatures on embryonic survival and population growth rates by comparing results of the model with and without effects of sublethal warming. We parameterized embryonic survival in the sublethal model using our laboratory survivorship results to provide conservative estimates based on experiments in which we controlled hydric conditions across treatments to isolate the impacts of incubation temperatures. See Appendix S1 for further details.

Modeling population growth

We computed population growth rates (r_0, lizards/day) per Buckley (2008):

$$r_0 = m \cdot e_{net} - \mu, \quad [2]$$

where e_{net} = net energy gain by an adult, μ = daily mortality ($197.36 \cdot 10^{-5}$ lizards/day; Buckley 2008), and m = eggs produced per Joule ($3.2 \cdot 10^{-4}$ eggs/J; Buckley 2008) multiplied by probability of surviving to adulthood. Net energy gain was estimated as the difference between energy gained from feeding and digestion and energy expended during resting and activity. For each location, we calculated the survival to adulthood component of m as the product of embryonic and juvenile survivorships (Levy *et al.* 2015). We then compared projections of population growth with and without effects of sublethal warming. See Appendix S1 for additional information.

To test how exposure of embryos to recurrent sublethal warming may alter projections through effects on later life stages, we ran the model with different hatchlings sizes and juvenile growth rates to calculate time to maturity. Assumptions built into the model—juvenile survivorship, juvenile growth, and size at maturity do not vary across geography, and all lizards mature by the next reproductive cycle—prevent incorporation of predicted time to maturity into projections. So, we estimated changes in intrinsic growth rates due to delayed maturity using life tables for northern (New Jersey (NJ)) and southern (SC) populations. See Appendix S1 for details.

RESULTS

Laboratory & Field Experiments

The field warming treatment increased T_{max} among warmed nests by 4.21±0.26°C compared to natural nests and did not alter T_{min} across treatments (Fig. 1b, Table 1). We used degree-day

calculations (Zalom *et al.* 1983) to compare the magnitudes of warming experienced by embryos due to changes in means and variances between treatments in both experiments (see Appendix S1 for details). Embryos under laboratory warming treatments accrued averages of 257.87 and 336.65 degree-days above the T_{max} of the contemporary treatment. In the field, embryos under the warming treatment accrued an average of 309.99 degree-days above the mean T_{max} of natural nests. Although absolute temperatures differed between experiments, the field warming treatment induced a magnitude of warming similar to that applied in the laboratory.

Recurrent sublethal warming increased embryonic mortality in both experiments. In the laboratory, embryonic survival decreased with increased warming (Fig. 1c). The proportional hazard model estimated 82.1% survival for the contemporary treatment versus 78.8% for +3.5°C and 58.1% for +7.0°C. Embryos in the +7.0°C treatment had lower survival probability than both the contemporary (ß=-2.84±1.05, z=2.81, p=0.005) and +3.5°C (ß=-1.01±0.47, z=2.12, p=0.034) treatments. Though survivorship decreased from the contemporary to the +3.5°C treatment, there was no significant difference between those survivorship curves (ß =-1.84±1.07, z=1.60, p=0.110). Embryonic survival in the field also decreased under warming with 36.9±9.3% survival among natural nests (typical of nest survivorship in SC, Tinkle & Ballinger 1972) versus 7.1±4.9% among warmed nests (Fig. 1d, Table 1). Lower survivorship in the field than in the laboratory was likely due to differences in hydric conditions. We maintained consistent hydric conditions in the laboratory, whereas embryos in the field experience natural variations in soil moisture that can impact survival (Tracy 1980; Packard *et al.* 1982).

Sublethal warming also led to shorter incubation times and smaller hatchling sizes in both experiments, lower body conditions of hatchlings in the field, and slower post-hatching growth in the laboratory. In the laboratory, hatchlings emerged 12.9% earlier from the +3.5°C treatment

(n=26, -8.93±0.37 days) and 15.4% earlier from +7.0°C (n=18, -10.72±0.63 days) compared to the contemporary treatment (n=23, 69.39±0.69 days; Fig. 1e, Table 1). In the field, hatchlings from warmed nests emerged 17.6% earlier (n=3, -13.30±1.20 days) than from natural nests (n=11, 75.64±1.90 days; Fig. 1f, Table 1). Lizards from laboratory warming treatments hatched at shorter SVL (contemporary: n=17, 24.91±0.22mm; +3.5°C: n=19, 24.40±0.19mm; +7.0°C: n=13, 23.80±0.27mm; Fig. 2a, Table 1), though hatchling mass and SMI did not differ (contemporary: n=17, 0.48±0.01g, 0.486±0.025 SMI; +3.5°C: n=19, 0.49±0.01g, 0.485±0.023 SMI; +7.0°C: n=13, 0.47±0.02g, 0.473±0.028 SMI; Fig. 2c, Table 1). In the field, hatchlings emerged from warmed nests at shorter SVL and lighter mass (natural: n=11, 25.60±0.10mm, 0.53±0.01g; warmed: n=3, 24.83±0.16mm, 0.45±0.01g; Fig. 2b,d, Table 1), which led to lower SMI (natural: 0.534±0.019, warmed: 0.447±0.046; Table 1). The growth model predicted 6.4% lower *r* from the +3.5°C treatment (n=8, 7.51+0.19µm/day) and 10.5% lower from +7.0°C (n=4, 7.18±0.14µm/day) compared to contemporary (n=6, 8.02±0.22µm/day; Fig. 2e, Table 1).

Model of Population Dynamics

Our SDM (herein "sublethal model") predicts more severe consequences of climate warming than those of a model based solely on lethal limits of embryonic thermotolerances (herein "lethal model"). The sublethal model accounts for the fact that nesting conditions avoiding lethal extremes still experience recurrent thermal stressors (Fig. 3; Fig. S1-S14). By accounting for moderate warming, we demonstrate that even small changes in temperature can lead to increased risk of extirpation under contemporary and future climates.

Predicted embryonic survival decreases under contemporary and future climates when incorporating our empirical observations. Under typical nesting conditions in July (6cm-depth

and 50%-shade, Angilletta *et al*. 2009; 4.4-8.0cm and 51.6-63.5%, this manuscript), the sublethal model predicts lower survival across 82.6% of the species range by -2.2% on average and by as much as -12.0% in locales that experience lower temperature variance, including portions of the southeast, the central plains, and the southwest (Fig. 4c). The magnitude and distribution of differences in predicted survival varies with nest depth, shade, and timing of oviposition (Fig. 4a-i, Fig. 5, Fig. S15-S42). For instance, incorporating the effects of sublethal warming alters survival across 96.8% of the range by -7.8% on average and by as much as -23.8% for nests laid in July at 12cm depth and 50% shade (Fig. 4i). Reduced embryonic survival then leads to decreased projected population growth.

Recurrent sublethal warming during incubation leads to decreased projected population growth. Both models show positive population growth across 96.0% of the species range under contemporary nesting conditions. Yet, when accounting for sublethal warming, the majority (84.7%) of those areas with positive growth experience increased risk of extirpation due to reduced population growth rates. Both models also agree on the geographic area of decreases in population growth under future warming (e.g., 51.4% and 50.5% of the range from the lethal and sublethal models respectively for typical nesting conditions). However, the magnitudes of reduced growth differ between the models. By overestimating embryonic survival, the lethal model underestimates negative impacts on population growth across 92.7% of the species range by 3.2% on average and by as much as 12.2% in locales that experience lower temperature variance (Fig. 4). Differences in population growth projections vary with nest depth, shade, timing, and geography similarly to embryonic survival (Fig 4j-r, Fig. S43-S46).

Sensitivity analyses examined how changes in hatchling sizes and juvenile growth rates affected projections of population growth via changes time to maturity. The growth model

indicated increased age at maturity by 32.4±7.6 days across the species range when incorporating slowed juvenile growth (Fig. S48). In SC, a predicted 26-day delay in maturity could reduce population growth rates up to an additional 39.7% over the 24.4% predicted by the sublethal model. In NJ, population growth rates could decrease by an additional 80.1% due to a 29-day delay in maturity, which would lead to population decline and likely extirpation. These results demonstrate potentially severe impacts of sublethal warming during incubation on population dynamics via downstream effects through ontogeny.

After comparing projections, we evaluated how well predictions match the contemporary species distribution. Both models predict the contemporary extent of the species range equally well if we treat positive embryonic survival and population growth as the only criteria. We also calculated sensitivity indices (proportion of presences predicted with positive survival, Manel *et al.* 2001; Buckley *et al.* 2010) and found no differences (see Appendix S1 for details). However, embryonic survival under the sublethal model decreased across 74.4% of occurrences to rates more consistent with demographic data (Tinkle & Ballinger 1972; Vinegar 1975; Tinkle & Dunham 1986). Thus, consideration of fluctuating developmental conditions reveals vulnerability to climate change that is not apparent without examination of sublethal warming.

DISCUSSION

We have demonstrated that organisms with thermally sensitive life stages do not have to experience lethal temperatures to undergo negative changes at the individual and population levels. Explicitly testing the effects of increasing T_{max} showed decreased embryonic survival under recurrent sublethal warming. The effects of warming extended through later life stages via reduced body condition and slowed growth. By integrating survivorship results into a SDM, we

show that consideration of moderate warming during vulnerable life stages alters predicted impacts of climate change. Shifts in distributions result from both lethal conditions (Jones *et al.* 2010; Wethey *et al.* 2011; Levy *et al.* 2015) and chronic exposure to sublethal fluctuations (Fly & Hilbish 2013; Woodin *et al.* 2013; Maynard *et al.* 2015). Numerous studies demonstrate that changing mean incubation temperatures affect phenotypes of oviparous ectotherms (e.g., reviews in Deeming & Ferguson 1991a; Booth 2006; Bowden *et al.* 2014), and variance of incubation temperatures affects traits across ontogeny as strongly or more than increasing means (e.g., Shine & Harlow 1996; Paaijmans *et al.* 2013). In the *Sceloporus* system, warming of constant and fluctuating incubation regimes can speed development without impacting hatchling sizes (review in Angilletta *et al.* 2004b). However, studies using fluctuating temperatures did not reach stressful highs (except Levy *et al.* 2015, but see below). In this study, survival decreased as the mean and variance of embryonic temperatures increased beyond that experienced in contemporary nests. We cannot partition the effects of temperature means and variances in our experiments. Yet, biological impacts of climate warming likely result from interactions between thermal means and variances, which are presumably not independent of one another in natural microclimates (Shine & Harlow 1996; Paaijmans *et al.* 2013; Bozinovic *et al.* 2015). By utilizing naturalistic thermal regimes, we demonstrate how impacts of warming on sensitive periods of ontogeny can affect ecological predictions.

Our SDM indicates that moderate warming during incubation can lead to reduced population growth compared to model predictions that do not incorporate sublethal fluctuations. Interestingly, the differences in laboratory survivorship that altered model predictions stemmed primarily from mortality in the first weeks post-oviposition. Running the survival analysis for the first 25% of the incubation period showed lower survival probability under the +7.0°C treatment

before any mortality events in the other treatments. Levy *et al.* (2015) suggested similar levels of warming had no effect on *S. undulatus* embryo survival, but they did not begin treatments until halfway through incubation. Our results suggest increased sensitivity to thermal stress in the earliest stages post-oviposition, during which incidences of developmental abnormalities increase as incubation temperatures near the lethal limits for reptiles and other ectotherms (reviews in Deeming & Ferguson 1991b; Farmer 2000). Therefore, *in situ* examinations of plasticity in nesting behavior could be critical to predicting the susceptibility of many ectotherms to climate change.

Plasticity of maternal behavior could buffer embryos from negative effects of climate change (Telemeco *et al.* 2009; Levy *et al.* 2015). However, the benefit of compensatory nesting behavior diminishes when accounting for effects of sublethal warming. Our model examines scenarios of altered nesting behavior by simulating oviposition across ranges of nest depths, shades, and days of the year beyond that exhibited among contemporary *S. undulatus* populations (Tinkle & Ballinger 1972; Niewiarowski 1994; Angilletta *et al.* 2009; this manuscript). Per the sublethal model, embryonic survival will decrease across much of the species range regardless of phenology (Fig. 5; though see Levy *et al.* 2016b). Nests with lower temperature variance could reduce negative impacts of warming by avoiding lethal extremes, but the impacts of sublethal warming may constrain that mitigation. For instance, if females nest 3cm deeper than contemporary averages, the sublethal model predicts a 17.4% lower increase in embryonic survival at the end of this century than the 179.2% benefit predicted by the lethal model. Repeated exposure to sublethal highs can be more detrimental to fitness than acute exposure to extreme temperatures for some species (Kearney *et al.* 2012; Marshall & Sinclair

2015). Thus, the effects of sublethal warming drive responses to warming through impacts on development and stage-specific mortality.

We demonstrate that warming during incubation could have significant impacts on demography via stage-specific survival and growth. Recurrent sublethal warming decreased embryo survival. Additionally, it led to smaller hatchlings and slowed juvenile growth, which could decrease survival to maturity via increased predation risk and reduced foraging success (Sinervo 1993; Stearns 2000; Sears & Angilletta 2004). One could argue that a longer growing season under warming mean temperatures could compensate for slowed juvenile growth. However, increased temperature variance would likely counteract such benefits via constrained activity time and more frequent potential for heat stress (Kingsolver *et al.* 2013; Levy *et al.* 2016b). Additionally, epigenetic effects could compensate for negative impacts of incubation conditions, such that exposure to warming during early ontogeny increases survival and performance of later stages. Though that is beyond the scope of this study, we incorporated predictions of embryonic survival and time to maturity into life tables to examine how slowed juvenile growth could negatively impact population persistence. Though assumptions in our model preclude life-history variation across geography, our life tables include such differences and highlight potentially severe downstream consequences of recurrent sublethal warming during incubation; results indicate particularly strong effects in northern populations that already exhibit delayed maturity compared to southern populations (Tinkle & Ballinger 1972, Niewiarowski 1994). Future integration of geographic variation of life-history traits will further improve model predictions.

According to life-history theory, faster growth should occur in environments where juveniles experience low survivorship (Stearns 2000), and *S. undulatus* juveniles grow more

quickly and experience higher mortality at more southern latitudes (Angilletta *et al.* 2004a; Sears & Angilletta 2004). Our novel nest temperature data demonstrate a counterintuitive pattern wherein southern embryos experience cooler temperatures than their northern conspecifics (Angilletta *et al.* 2009). Considering our results, one could hypothesize that variation in nest characteristics may be a mechanism underlying geographic variation in life-history traits in this species. Further research, such as reciprocal transplants of *S. undulatus* embryos across latitudes, could address hypotheses concerning plasticity of life-history traits (e.g., Stearns & Koella 1986) and elucidate impacts of nesting behavior and embryo thermal physiology on such variation. Accordingly, our work demonstrates the need for increased focus on ontogenetic and spatiotemporal variation of organismal responses to environmental fluctuations.

Our results should motivate researchers to expand efforts to examine life-cycle responses to local climates. If moderate warming during development can impede recruitment and decrease mean fitness, species in locations with lower thermal variance and relatively low frequencies of extreme events may suffer more than previously thought under climate warming. Unfortunately, data on responses to sublethal extremes are not sufficiently available to inform models beyond a few well-studied systems, such as corals (e.g., Edmunds 2005; Maynard *et al.* 2015), intertidal mussels (e.g., Miller *et al.* 2009; Fly & Hilbish 2013), and some insect species (e.g., Crozier & Dwyer 2006, Potter *et al.* 2011; Marshall & Sinclair 2015). The enduring impacts of sublethal environmental fluctuations is a largely unaddressed problem in ecological modeling. Future studies should examine responses to spatiotemporal variation in developmental conditions to further elucidate adaptive processes by which organisms handle environmental fluctuations.

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AUTHOR CONTRIBUTIONS

MAC and MWS designed the lab and field studies with consultation from EAR. OL designed the species distribution model. MAC collected data and analyzed model output. MAC wrote the first draft, and all authors contributed to revisions.

DATA ACCESSIBILITY

Data supporting the results in this paper are archived at Dryad (doi:10.5061/dryad.pr1h0).

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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SUPPORTING INFORMATION

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Legends

Figure 1. Thermal treatments in laboratory and field experiments and impacts of treatments on embryo development time and survival. Error bars indicate ±1 SE. (*a*) Laboratory treatments simulated contemporary thermal conditions at *S. undulatus* nest sites and warming scenarios designed to introduce recurrent sublethal thermal stressors via increased T_{max}. (*b*) In the field, the warming treatment induced sublethal warming of daytime nest temperatures without altering overnight minima. Recurrent sublethal warming reduced embryonic survival in (*c*) the laboratory and (*d*) the field. Among lizards that survived to hatching, development time (days from oviposition to hatching) decreased with increased warming in (*e*) the laboratory and (*f*) the field. For panels *c* and *e*, letters denote statistical relationships such that data with different letters are significantly different ($p<0.05$). In panel *f*, overlapping points are offset. See Table 1 for summary statistics.

Figure 2. Impacts of warming treatments on post-hatching sizes and projected growth rates. Error bars indicate ±1 SE. Hatchling SVL decreased with increased warming (*a*) in the laboratory and (*b*) in the field. Hatchling mass decreased with warming nest temperatures (*d*) in the field, but there was no significant difference in hatchling mass among (*c*) laboratory treatments. (*e*) In the laboratory, characteristic growth rates derived from von Bertalanffy growth models decreased with increased warming. For panels *a*, *c*, and *e*, letters denote statistical relationships such that data with different letters are significantly different ($p<0.05$). See Table 1 for summary statistics.

Figure 3. Spatial distributions of average maximum daily temperatures (T_{max}) during the month of July for the period 1980-2000 and predicted for the period 2080-2100. Black outlines within

maps indicate the extant *S. undulatus* range (IUCN 2017). Variation in T_{max} is displayed across (*a*) increasing nest depths under 50% shade and (*b*) across increasing shade levels at 6cm nest depth. See Fig. S1-S14 for plots based on all other combinations of nest depth (3, 6, 9, or 12cm) and shade (0, 25, 50, 75, or 100%) and for nests laid in April, May, June, August, September, and October.

Figure 4. Spatial distributions of embryonic survival and population growth rates generated by the sublethal model for the period 1980-2000, changes by 2080-2100, and differences between these projections and those generated by the lethal model. Negative model differences indicate the degree to which predictions are reduced by incorporating effects of moderate warming. Black outlines within maps indicate the extant *S. undulatus* range (IUCN 2017). Results are shown at three scenarios of nesting behavior: (*a-c, j-l*) 6cm depth and 50% shade typical of *S. undulatus* (Angilletta *et al.* 2009; this manuscript), (*d-f, m-o*) nest sites with 50% more shade, and (*g-i, p-r*) nests dug 6cm deeper. Survival results are based on simulations for nests laid in July. See Fig. S15-S42 for survival plots at all other combinations of nest depth (3, 6, 9, or 12cm) and shade (0, 25, 50, 75, or 100%) and for nests laid in April, May, June, August, September, and October. Also, see Fig. S43-S46 for population growth plots based on all other combinations of nest depth and shade.

Figure 5. Spatial distributions of predicted embryonic survival generated by the sublethal model for the period 1980-2000, predicted changes by 2080-2100, and differences between these projections and those generated by the lethal model. Negative model differences indicate the degree to which predictions are reduced by incorporating effects of moderate warming. Black

outlines within maps indicate the extant *S. undulatus* range (IUCN 2017). Results are shown across months in the breeding season to illustrate differences based on the timing of oviposition. These results are based on simulations for nests laid at 9cm depth and 50% shade. See Fig. S15-S42 for survival plots based on all other combinations of nest depth (3, 6, 9, or 12cm) and shade (0, 25, 50, 75, or 100%) and for nests laid in April, September, and October.

Figures

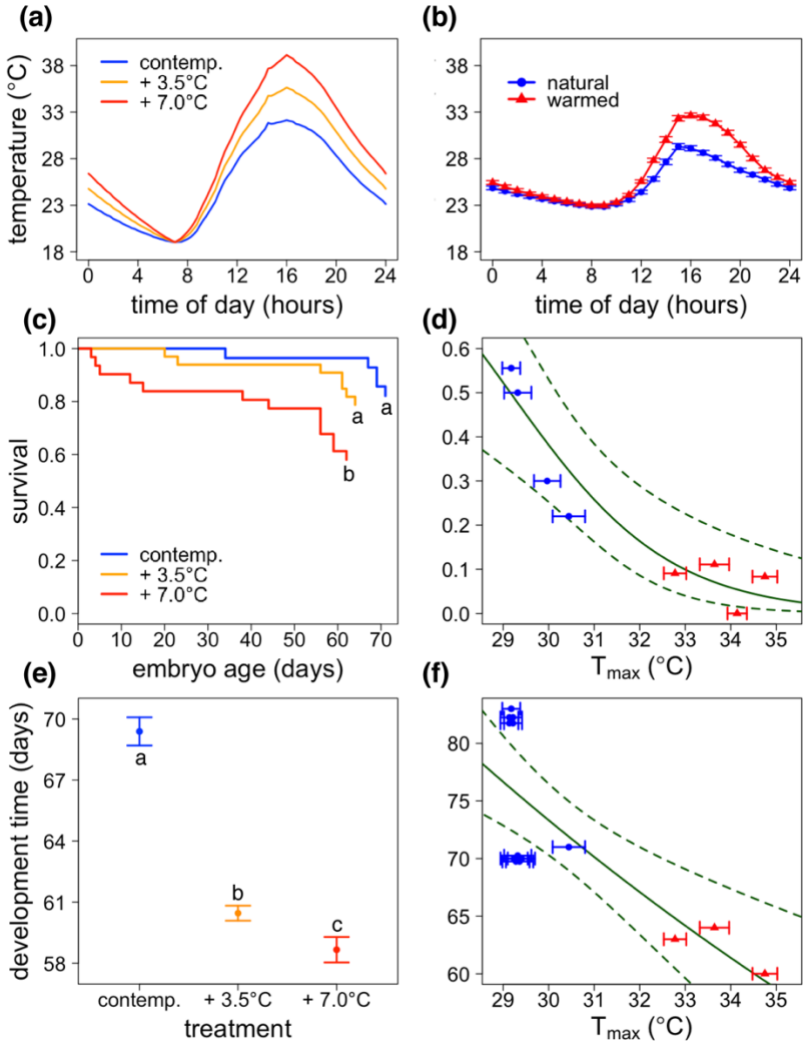


Figure 1

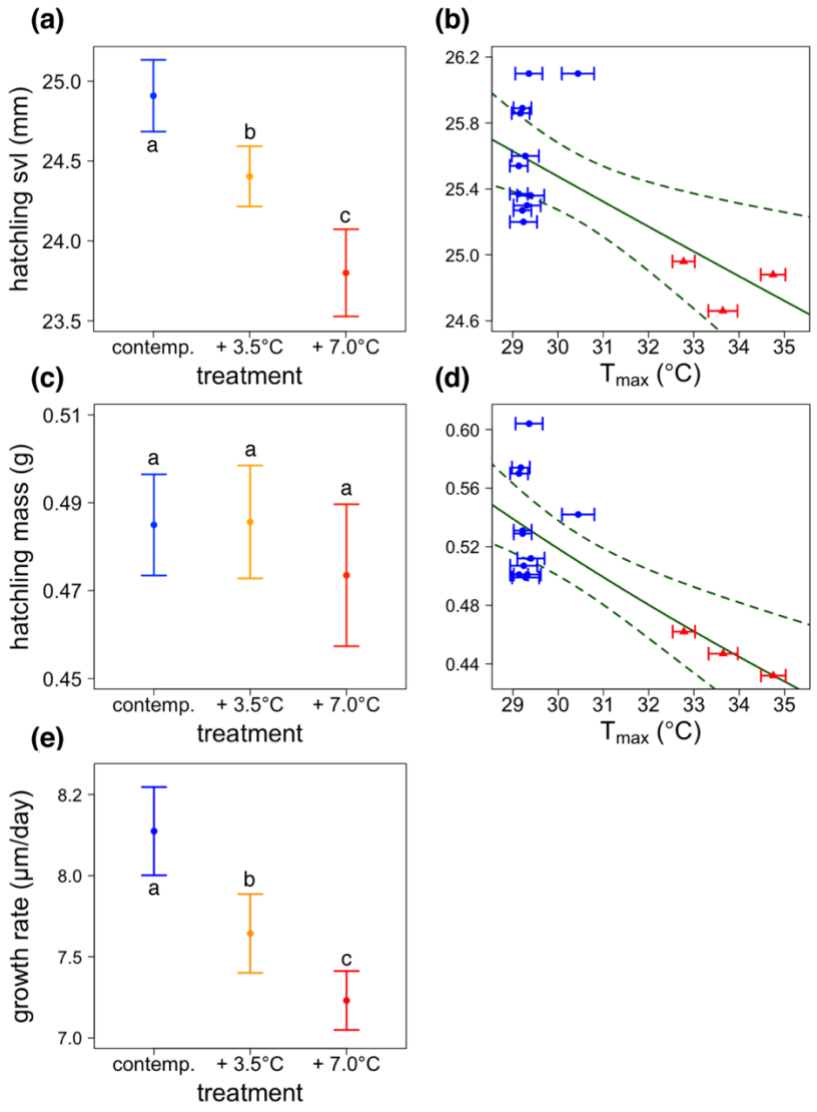
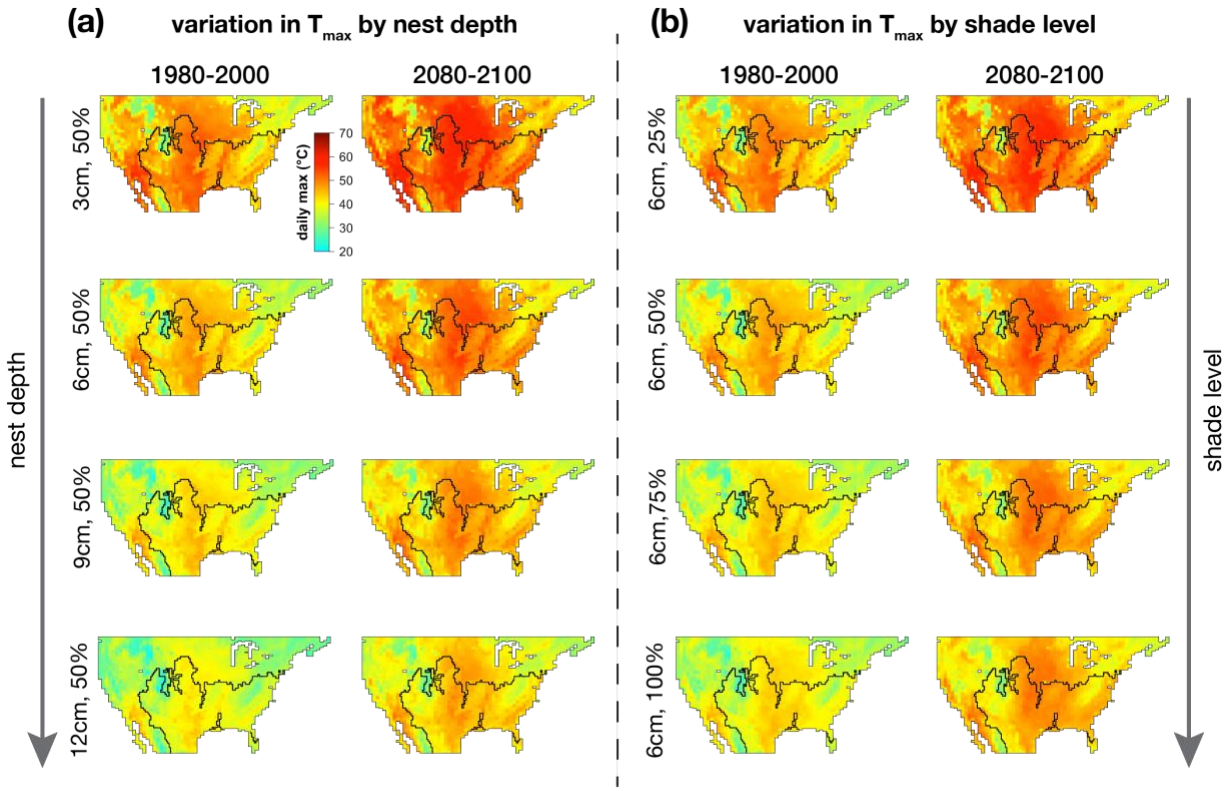

(a)
hatchling svl (mm)
25.0
24.5
24.0
23.5
a
b
c
contemp.
+ 3.5°C
+ 7.0°C
treatment
(b)
26.2
25.8
25.4
25.0
24.6
29
30
31
32
33
34
35
Tmax (°C)
(c)
hatchling mass (g)
0.51
0.49
0.47
0.45
a
a
a
contemp.
+ 3.5°C
+ 7.0°C
treatment
(d)
0.60
0.56
0.52
0.48
0.44
29
30
31
32
33
34
35
Tmax (°C)
(e)
growth rate (µm/day)
8.2
8.0
7.5
7.0
a
b
c
contemp.
+ 3.5°C
+ 7.0°C
treatment

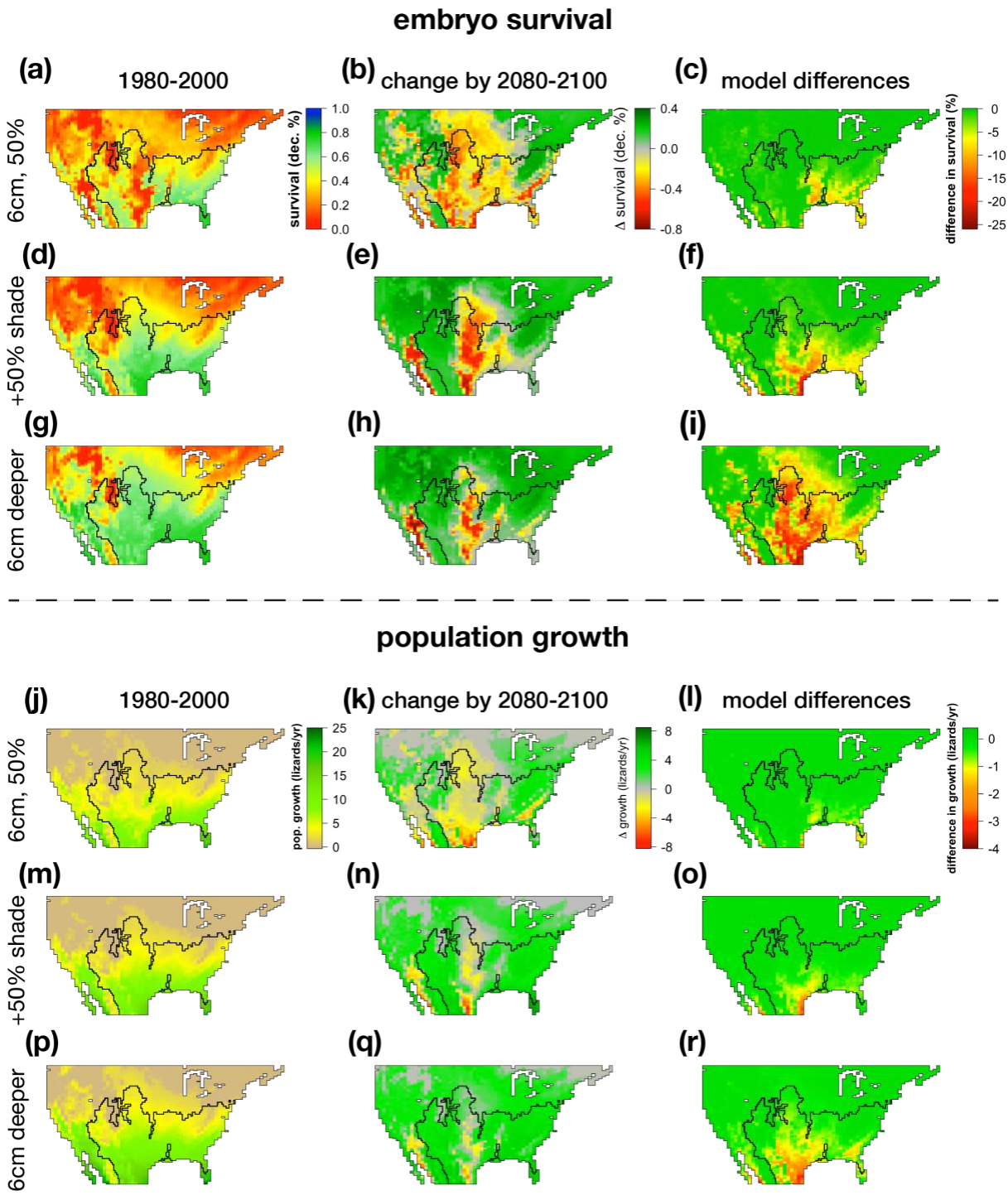
Figure 2


(a)
variation in T_{max} by nest depth
1980-2000
2080-2100
3cm, 50%
6cm, 50%
9cm, 50%
12cm, 50%
daily max (°C)
70
60
50
40
30
20
nest depth
(b)
variation in T_{max} by shade level
1980-2000
2080-2100
6cm, 25%
6cm, 50%
6cm,75%
6cm, 100%
shade level

1

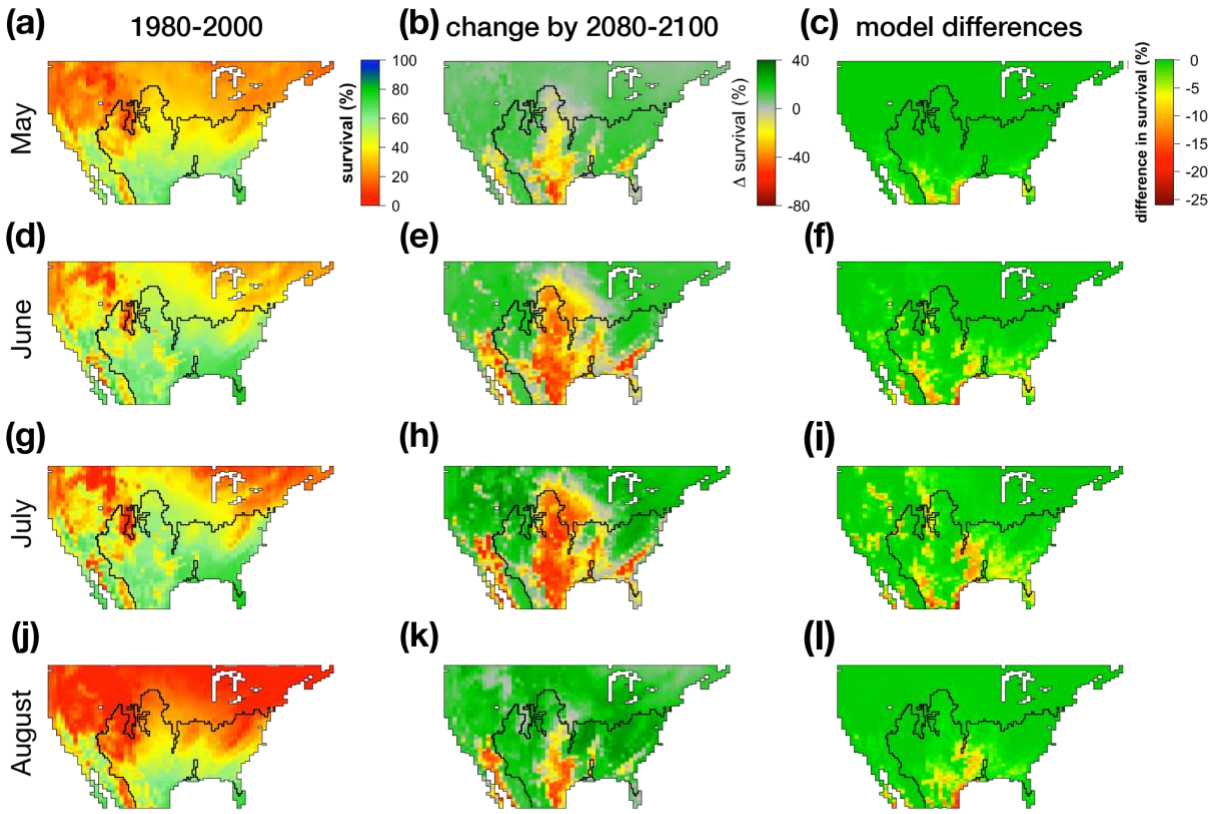
2 Figure 3

3


embryo survival
(a)
1980-2000
(b)
change by 2080-2100
(c)
model differences
6cm, 50%
survival (dec. %)
1.0
0.8
0.6
0.4
0.2
0.0
Δ survival (dec. %)
0.4
0.0
-0.4
-0.8
difference in survival (%)
0
-5
-10
-15
-20
-25
(d)
(e)
(f)
+50% shade
(g)
(h)
(i)
6cm deeper
population growth
(j)
1980-2000
(k)
change by 2080-2100
(l)
model differences
6cm, 50%
pop. growth (lizards/yr)
25
20
15
10
5
0
Δ growth (lizards/yr)
8
4
0
-4
-8
difference in growth (lizards/yr)
0
-1
-2
-3
-4
(m)
(n)
(o)
+50% shade
(p)
(q)
(r)
6cm deeper

1

2 Figure 4


(a)
1980-2000
(b)
change by 2080-2100
(c)
model differences
May
June
July
August
survival (%)
100
80
60
40
20
0
Δ survival (%)
40
0
-40
-80
difference in survival (%)
0
-5
-10
-15
-20
-25
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)

1

2 Figure 5

Tables

Table 1. Summary statistics for analyses of laboratory and field data using mixed effects ANOVA. Laboratory data include (*a*) time to hatching, hatchlings sizes in (*b*) SVL and (*c*) mass, (*d*) hatchling body conditions, and (*e*) characteristic growth rate derived from the Von Bertalanffy growth models. Laboratory analyses were performed using maternal identity as a random effect. Field data include (*f*) maximum and (*g*) minimum daily nest temperatures, (*h*) embryonic survival, (*i*) time to hatching, hatchling sizes in (*j*) SVL and (*k*) mass, and (*l*) hatchling body conditions. Analyses of field data included assigned nest and nesting group as a random effect. Bolded values indicate statistical significance.

Response	**Parameter**	**F**	**p**	**ω^2**
Lab Experiment				
(a) development time	treatment	**108.71**$_{2,63}$	**< 0.001**	**0.7521**
	initial egg mass	**5.01**$_{1,63}$	**0.029**	0.0140
(b) hatchling SVL	treatment	**7.16**$_{2,45}$	**0.002**	**0.1653**
	initial egg mass	**14.22**$_{1,45}$	**< 0.001**	**0.1774**
(c) hatchling mass	treatment	0.32$_{2,45}$	0.725	0.0000
	initial egg mass	**19.40**$_{1,45}$	**< 0.001**	**0.2784**
(d) hatchling SMI	treatment	0.34$_{2,45}$	0.713	0.0000
(e) characteristic growth rate (*r*)	treatment	**3876**$_{2,14}$	**< 0.001**	**0.3226**
	hatchling SVL	**16259**$_{1,14}$	**< 0.001**	**0.6769**
Field Experiment				
(f) T_{max}	treatment	**438.65**$_{1,792}$	**< 0.001**	**0.3553**
(g) T_{min}	treatment	1.35$_{1,792}$	0.245	0.0004

(h) embryonic survival	treatment	**14.93**$_{1,6}$	**0.008**	**0.6351**
(i) development time	treatment	**12.35**$_{1,12}$	**0.004**	**0.4477**
(j) hatchling SVL	treatment	**14.14**$_{1,12}$	**0.003**	**0.4842**
(k) hatchling mass	treatment	**16.38**$_{1,12}$	**0.002**	**0.5235**
(l) hatchling SMI	treatment	**24.11**$_{1,12}$	**<0.001**	**0.6228**

1 ω^2, effect size (Olejnik & Algina 2003)

2 SVL, snout-vent-length

3 SMI, scaled mass index (Peig & Green 2009; 2010)

4 *r*, post-hatching growth rate

5 T_{max}, maximum daily temperature

6 T_{min}, minimum daily temperature