

## LETTER

# Ontogeny constrains phenology: opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate

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## Abstract

As global warming has lengthened the active seasons of many species, we need a framework for predicting how advances in phenology shape the life history and the resulting fitness of organisms. Using an individual-based model, we show how warming differently affects annual cycles of development, growth, reproduction and activity in a group of North American lizards. Populations in cold regions can grow and reproduce more when warming lengthens their active season. However, future warming of currently warm regions advances the reproductive season but reduces the survival of embryos and juveniles. Hence, stressful temperatures during summer can offset predicted gains from extended growth seasons and select for lizards that reproduce after the warm summer months. Understanding these cascading effects of climate change may be crucial to predict shifts in the life history and demography of species.

## Keywords

Biophysical model, climate change, embryos, hatchlings, heat events, individual-based model, life cycle, lizards, phenology.

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## INTRODUCTION

As temperatures rise around the globe, organisms become metabolically active earlier in spring, potentially advancing major events such as emergence, migration and reproduction (Hughes 2000; Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006; Cleland *et al.* 2012). The earlier onset of photosynthesis in plants alters the nutritional and biophysical environment for animals, fungi and bacteria. In animals, the timing of development, foraging and mating influences opportunities for growth and reproduction, with direct consequences for life-history traits such as age and size at maturation, clutch size and life span (Forrest & Miller-Rushing 2010). At the community level, phenological advances can alter the strengths of ecological interactions if the activities of species advance asynchronously (Parmesan 2007; Forrest & Miller-Rushing 2010). For example, if prey become active earlier than predators, they may escape vulnerable stages of development (Visser *et al.* 2006). Although many aspects of phenological advances remain to be investigated, we know enough to conclude that climate warming will impact life histories through phenological shifts.

Phenological advances have diverse consequences because an earlier onset of activity does not necessarily imply a longer growing season. In fact, the growing season of a species can increase or decrease depending on the duration of activity, the life-history strategy and costs of reproduction (Steltzer & Post 2009; Sletvold & Ågren 2015). For example, light and nitrogen may limit the annual growth of arctic plants despite their earlier emergence (Ernakovich *et al.* 2014). Plants that produce leaves or flowers earlier in the year risk exposing these structures to frost damage (e.g. Inouye 2008). Experimental warming caused the leaves of one plant species to emerge

earlier, but did not advance later stages of the life history (Post *et al.* 2008); in this case, early growth was offset by delayed flowering. Similar complexities have been documented among mammals, where the energetic cost of a warmer winter can outweigh the energetic benefit of a warmer spring (Williams *et al.* 2015). Despite the potential for complex phenological responses to climate change, biologists have focused on events in spring at the expense of those in other seasons (Gallinat *et al.* 2015; Williams *et al.* 2015). Expanding the focus should enable biologists to predict how (or understand why) climate impacts phenology and phenotypes throughout the life cycle.

To address the problem of phenological shifts, we must consider opportunities for activity and production throughout the year and its impact on the life history of a species (Marra *et al.* 2015). Just because animals reproduce earlier and more often does not mean they will achieve greater fitness. The temporal distributions of opportunities for energy acquisition and reproduction jointly shape the potential for fitness. Warming might benefit an organism at one stage of the life cycle, but hurt an organism at another stage; for example, butterflies of *Boloria eunomia* respond negatively to warming during the larval stage, but positively to warming at other stages (Radchuk *et al.* 2013). Hence, the vulnerability of species depends on the sensitivity of every stage of the life cycle. To complicate matters further, warming creates opposing selective pressures on the timing of life-history transitions such as maturation and reproduction. Conflicts become most evident when considering how reproductive phenology affects the climatic extremes experienced by offspring. For instance, Pacific salmon (*Oncorhynchus* spp.) migrate to spawning sites earlier than they did in past climates, probably to avoid high temperatures that slow swimming and even higher temperatures that

cause mortality. However, earlier spawning exposes embryos to lethal temperatures (Crozier *et al.* 2008). Hence, climate warming creates a trade-off between behaviours that enhance survival at the beginning or end of the life cycle. The effective reproductive season lies at the intersection of time where adults and their offspring can thrive. As adults need time to accumulate resources and embryos need time to develop, this window of reproductive opportunity will be much narrower than the active season of an adult.

To better understand how phenological shifts relate to fitness, we modelled opportunities for activity, growth and reproduction in a group of North American lizards, the *Sceloporus undulatus* complex. Lizards have been a model organism for studying the relationships among climate, activity and life history (Dunham *et al.* 1989; Buckley 2008; Kearney 2013). On a geographical scale, warmer environments offer more opportunities for adults to forage and reproduce (Adolph & Porter 1993). Hence, populations that currently inhabit cold regions could benefit from a warmer environment (Fig. 1), which promotes earlier maturation and requires less allocation of resources per offspring because of a longer growing season (Angilletta *et al.* 2004, 2006). For populations that already experience warm conditions, however, further warming might restrict activity during the hottest periods (Sinervo *et al.* 2010), leading to bimodal patterns of activity and reproduction (Fig. 1). Moreover, warming raises the operative temperature of embryos in soil, leading to death of entire clutches of eggs (Levy *et al.* 2015b). The fitness consequence of a phenological shift depends on the intersection of three periods: the time when adults can gain energy to reproduce, the time when embryos can develop and the time when juveniles can grow. By including all life stages in an individual-based model, and

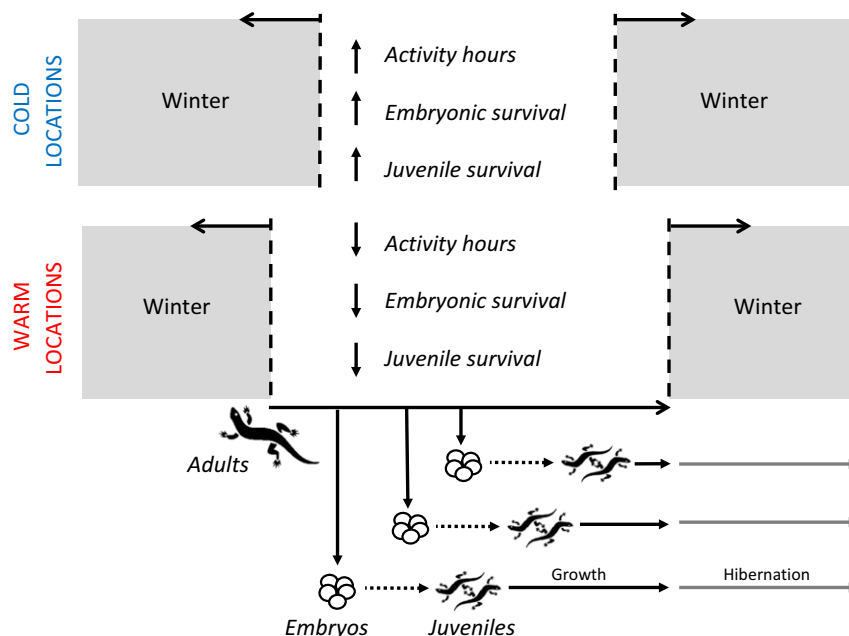
dissecting microclimates at an hourly resolution, we show how warming would reduce opportunities for activity and reproduction despite extending the activity and reproductive seasons.

## METHODS

Our analyses were based on a model of population dynamics for lizards of the *S. undulatus* complex, a clade of evolutionary species in the United States (Leache & Reeder 2002). The model, developed by Buckley (2008) and expanded by Levy and colleagues (Levy *et al.* 2015b), was used previously to explore the impacts of climate change on population growth. Here, we extend the model to analyse seasonal opportunities for activity, growth and reproduction in climates projected for the past and future. Parameterisation of the model followed our previous simulations (Buckley 2008; Levy *et al.* 2015b), except where noted below. See Tables S1 and S2 for initial values of parameters and Fig. S1 for locations and climates from which these values were derived.

### Activity season

We used a published set of hourly microclimates (Levy *et al.* 2015a) to calculate the operative temperatures of lizards (i.e. the steady-state temperature in a particular microclimate, Bakken 1992) on surfaces ranging from 0 to 100% shade. The microclimates represent the entire United States at a resolution of  $36 \times 36$  km for the past (1980–2000) and the future (2080–2100, assuming a radiative forcing of  $+8.5 \text{ W m}^{-2}$  at year 2100). We assumed that lizards could engage in activity whenever an operative temperature fell within the range of



**Figure 1** Warming affects annual cycles of growth and reproduction in different ways in warm vs. cold environments. Lizards become active when they can effectively thermoregulate in their environment. During this window activity, lizards have opportunities to grow and reproduce. These opportunities cease when the environment becomes too cold for behavioural thermoregulation. At this time, lizards hibernate until spring. In cold environments, warming widens the window for activity and increases opportunities for reproduction. In warm environments, warming widens the window for activity but also restricts activity during summer and limits opportunities for reproduction.

preferred temperatures (central 80% of field body temperatures; Table S2). Operative temperatures were calculated for a lizard of average size across the geographic range. See Supplementary Information for the values of parameters and additional information about calculating operative temperatures.

### Embryonic performance

We assumed that the first potential day of oviposition occurs after temperatures enable 30 days of activity (Tinkle & Ballinger 1972; Angilletta *et al.* 2001). For every day thereafter, we simulated development for clutches of eggs laid daily in a typical nest (6 cm depth and 50% shade, Angilletta *et al.* 2009). Clutches were not initiated on days when thermal conditions prevented activity by adult lizards.

We modelled the survivorship of embryos based on our previous experimental results (Levy *et al.* 2015b), assuming that embryos died if soil temperature exceeded 44 °C and that temperatures below 25 °C caused a graded increase in the chance of mortality (see algorithm in Fig. S2). Eggs that neither warmed to 44 °C nor cooled below 25 °C were assigned an 80% chance of hatching, based on the mean survivorship in experiments (Oufiero & Angilletta 2006). Based on embryonic survival to acute cooling (Levy *et al.* 2015b), eggs that dropped below 25 °C were assigned a chance of survival according to the lowest soil temperature during incubation:

$$\text{logit}(\text{survival}) = -2.19 + 0.14 \cdot T_{\text{soil, lowest}} \quad (1)$$

Surviving embryos developed at an hourly rate ( $D$ ,  $\text{dec}^{-1}$ ) described as

$$D = (0.00081 + 0.00067 \cdot T_{\text{soil}}) / 24, \quad (2)$$

where  $T_{\text{soil}}$  equals the temperature of soil (°C) at the shade and depth of the nest. We parameterised this function with rates of development recorded at constant temperatures (Angilletta *et al.* 2000) because the variance of temperature has little or no direct effect on developmental rates of *Sceloporus* embryos (Andrews *et al.* 2000).

### Juvenile performance

We used an energy balance model to calculate how the climate and the date of hatching interact to affect the risk of starvation during winter. Body temperatures were calculated as described above for adults.

To simulate winter survival, we modelled the accumulation of fat storage during the activity season and the loss of fat during winter hibernation (see algorithm in Fig. S3). At the end of each day, the model calculates the energetic balance between the amount of energy assimilated and the amount of energy consumed that day.

Upon hatching, juveniles are assumed to possess initial fat energy storage as:

$$J_{\text{fat}} = (0.1)(0.25) \cdot E_f \cdot M_b, \quad (3)$$

where  $M_b$  is the body mass (g), 0.1 approximates the decimal per cent of fat in a hatchling,  $E_f$  is the energetic content of fat and 0.25 is the proportion of body mass that is dry tissue.

Every day in the model, when energy intake exceeds energetic demands, the model stores excess energy as body fat:

$$J_{\text{fat}} = J_{\text{fat}} + J_{\text{excess}} \cdot 0.79, \quad (4)$$

where  $J_{\text{fat}}$  is the amount of energy stored as fat,  $J_{\text{excess}}$  is the amount of excess energy and 0.79 is the efficiency of converting a cricket to fat (see Table S2). When energetic intake failed to satisfy energy expenditure (e.g. during warm summer days or during cold winters), the model used energy stored as fat to complete energetic demands. We assumed no efficiency factor for converting fat storage into available energy. If fat storage was not sufficient to fulfil energetic demand, the model assumed juvenile starvation and death.

### Rates of population growth

Rates of population growth ( $r_0$ , lizards  $\text{y}^{-1}$ ) were computed according to Buckley (2008):

$$r_0 = m \cdot e_{\text{year}} - \mu, \quad (5)$$

where  $e_{\text{year}}$  equals the annual net energy gain by an adult ( $\text{J y}^{-1}$ ),  $\mu$  equals the daily rate of mortality and  $m$  equals the number of eggs produced per Joule multiplied by the probability of surviving to adulthood. For each location on the map, we calculated the survival to adulthood component of  $m$  as the product of the survivorship of embryos and the survivorship of juveniles (see above). We assumed that lizards can survive to maturity after successful overwintering, as we are interested in the thermal effects of climate change on phenology and growth rates. The annual net energy gain,  $e_{\text{year}}$ , was estimated by simulating feeding and digestion at predicted body temperatures (see algorithm in Fig. S4). See Supplementary Information for additional information about these calculations.

### Data analysis

We analysed spatial distributions of the activity season, reproductive season, reproductive success, winter survival of juveniles and rates of population growth. We used the first and last Julian days of activity to calculate the average length of the activity season, and the first and last days of successful reproduction (i.e. when embryonic survival exceeds 10%; see Table S3 for sensitivity analysis) to calculate the length of the reproductive season. To estimate effective days for reproduction, we counted the number of days for which reproduction was successful. Reproductive success was calculated for each Julian day based on the mean embryonic and juvenile survival rates of eggs laid that day. For each location, we defined the activity and reproductive seasons as either unimodal or bimodal. We declared locations as having a bimodal season when the predicted activity ( $\text{h d}^{-1}$ ) or survival (%) rates had two peaks across the year with at least 10% reduction in activity or survival between them. We smoothed the activity and survival data at each location across Julian days using a rolling mean with a window of 10 days.

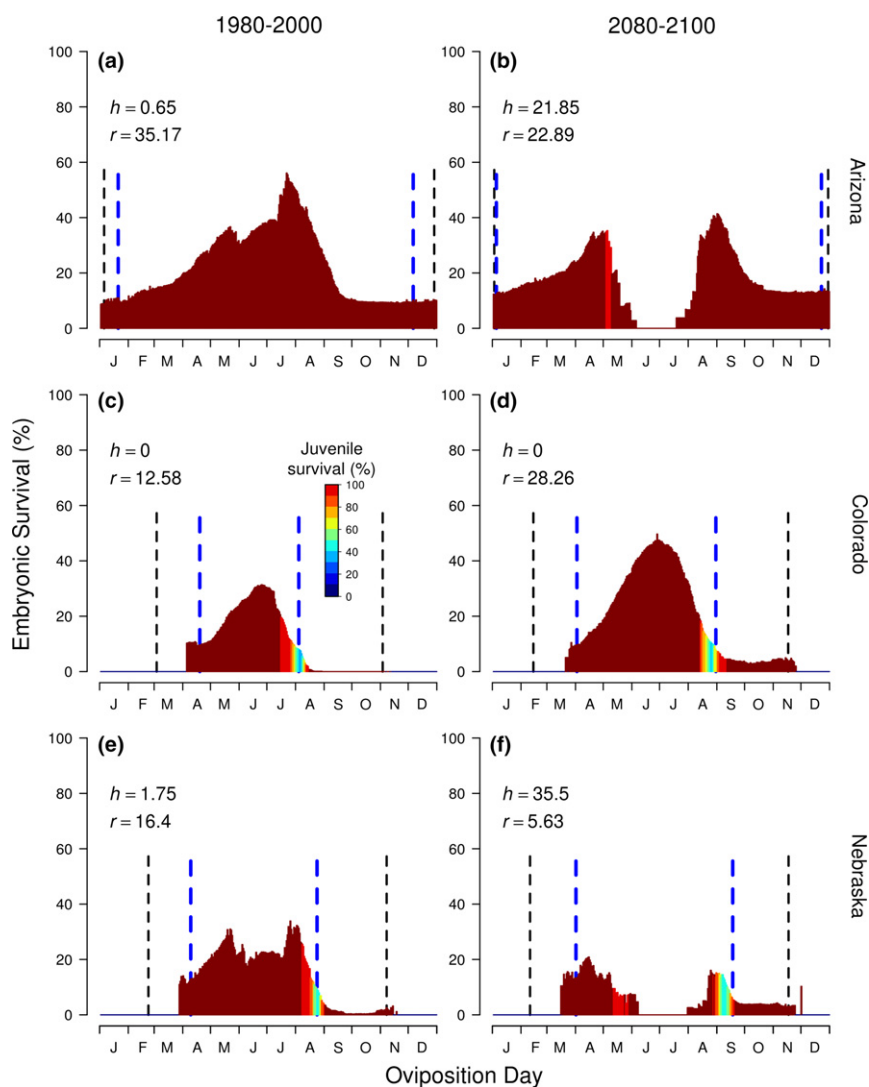
### Sensitivity analysis

To explore how the model's predictions depend on our assumptions, we altered the values of several parameters and

quantified the effect on dependent variables. Specifically, we quantified how activity season, reproductive opportunities and embryonic survival depended on the body size of adults, refractory period for reproduction and the sensitivity of embryos to cold and heat. As conditions during embryonic development can affect the performance after hatching (Niewiarowski & Angilletta 2008), we tested how juvenile survival in our model is sensitive to foraging success and rates of energetic assimilation. The amount of energetic allocation in each egg may also vary (Angilletta *et al.* 2006); hence we tested how the energy allocated per egg and the body size at hatching affects the survival of juveniles. For each parameter in our sensitivity analysis, we report the effect of increasing or decreasing its value on the predicted rate of population growth.

## RESULTS

By evaluating impacts of climate change on embryos and adults, we discovered the potential for complex phenological responses that differ among geographic regions. One can appreciate the range of outcomes by considering potential phenologies in 2080–2100 at a few locations (Fig. 2). In Arizona, where the current climate is warm, summers would become too warm for embryos to survive, resulting in a net decline in population growth. In Colorado, where the current climate is cooler, warming would extend the reproductive season, increasing embryonic survival and speeding population growth. Finally, in Nebraska, where summers are hot but winters are cold, further warming would enable earlier activity and reproduction; however, warming would reduce the



**Figure 2** Predicted phenological responses to climate change in three locations: Arizona (33.87°N –111.47°E), Colorado (37.70°N –104.85°E) and Nebraska (41.13°N –101.72°E). The frequency distribution depicts the outcome of laying eggs on a certain day of year (x-axis). The height of the distribution reflects the mean percentage of embryos that survive to hatching (y-axis). The colour of the distribution denotes the mean percentage of these hatchlings that survived their first winter. The dashed black and blue lines mark the boundaries for activity and reproduction, respectively; the reproductive season was defined as the period when embryonic survival exceeds 10%. For each population, we also report the number of lethal events for embryos per year,  $h$ , and the annual rate of population growth,  $r$ .

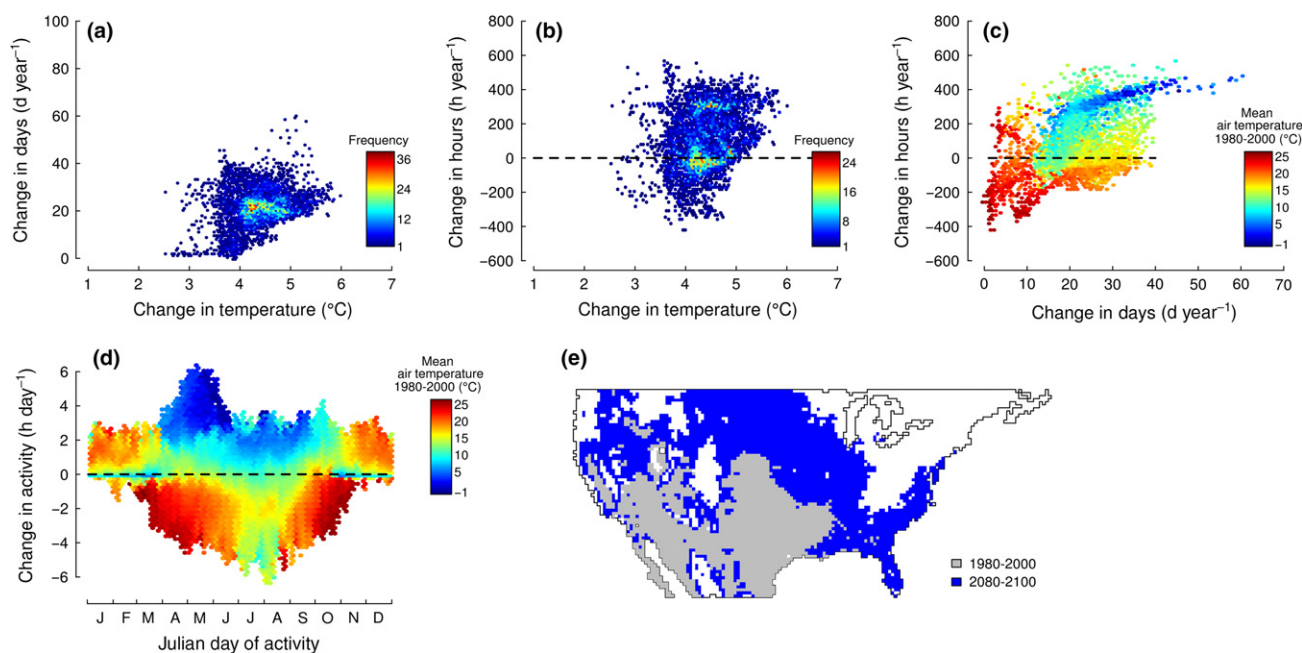


potential for reproduction by dramatically lowering embryonic survival in summer without sufficiently raising juvenile survival in winter. Each of these distinct scenarios occurs in some portion of the range, depending on the current climate and the anticipated change in climate.

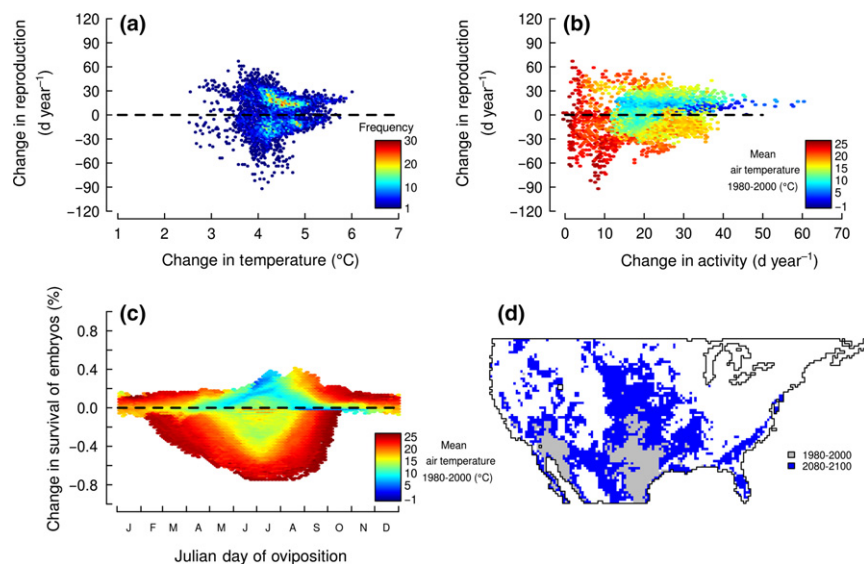
In some places, climate change would advance the onset of activity in spring and delay the onset of hibernation in winter, without creating more opportunity for activity throughout the year. We predict advances in the onset of activity in 96% of the locations between 1980 and 2080 (Fig. 3a). The average advance of  $12.5 (\pm 7.1 \text{ SD})$  days reflects a rate of 1.2 days per decade; however, this rate varies from 7.5 days per decade in cold regions to 0 days per decade in locations below  $30^\circ\text{N}$  (Fig. S5a–b). The distribution of predicted phenological advances includes the mean rate of advance observed among plants and animals in recent decades, which was 3 days per decade (Parmesan 2007; Poloczanska *et al.* 2013). We predict lizards will remain active later in 97% of the locations, adding an average of 0.9 days ( $\pm 0.5$  days) of activity per decade (Fig. S5c–d). Where current climates are cool, warming will extend the hours of activity as well as the days of activity per year (Fig. 3b, c). By contrast, warming in other locations would decrease the hours of activity despite increasing the days of activity. Thermal constraints on activity can occur as early as March and as late as November for the warmest locations, but will mostly occur during the summer months (Fig. 3d). The loss of activity would shift the pattern of activity on summer days from unimodal to bimodal (Fig. 3e). Our model predicted that 28% of the locations suffer from low activity hours during the

middle of the activity season (i.e. bimodal activity season, Fig. 3e) with an increase to 70% of the locations under future climate.

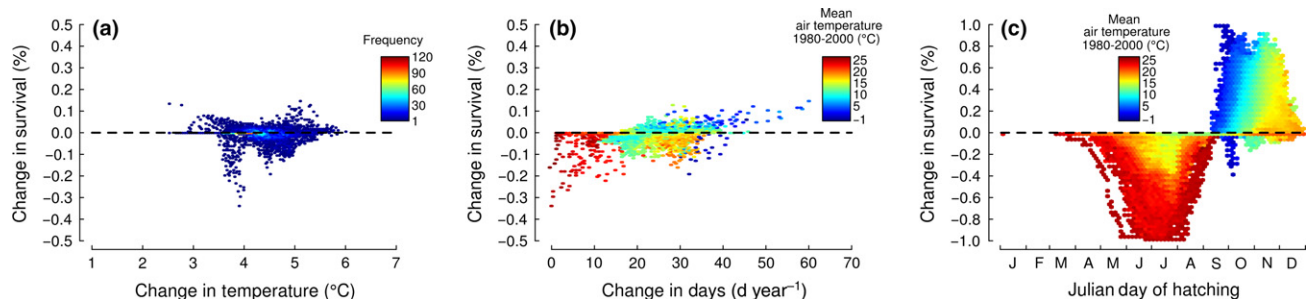
Warming can also decrease opportunities for reproduction despite enabling lizards to reproduce earlier or later each year. Since embryos cannot thermoregulate effectively, soil temperatures dictate the periods in which offspring could survive development and hatch with sufficient time to store energy before winter. In warmer regions, lizards have a wider span of days on which to lay eggs that would hatch successfully (Fig. S6). By 2080, this reproductive window begins 13 days earlier ( $\pm 9$  days) in 94% of the range (Fig. S6a–b) and ends 27 days later ( $\pm 12$  days) in 99% of the range (Fig. S6c–d). The effective reproductive season, however, would be shorter than this reproductive window because high temperatures would kill embryos. By 2080, embryos would overheat as early as February and as late as October in the warmest regions, but most overheating would occur during summer (Fig. 4). Even if offspring survive to hatching, they might starve during summer or winter if warming reduces opportunities for activity (Fig. 5); warming would reduce activity in summer from  $8.7 \text{ h day}^{-1} (\pm 1.3)$  to  $7.0 \text{ h day}^{-1} (\pm 1.7)$  at 28% of locations, while increasing activity in fall from  $3.5 \text{ h day}^{-1} (\pm 1.5)$  to  $4.5 \text{ h day}^{-1} (\pm 1.3)$  at 61% of locations. Poor survival of offspring during summer would favour lizards that avoid reproducing at this time, potentially leading to a bimodal pattern. Climate change would cause bimodal reproduction to spread from 9 to 39% of locations (Fig. 4d). At these locations, the annual reproductive window would drastically overestimate the days on which eggs can be laid



**Figure 3** Impacts of climate change on opportunities for activity. Climate change enables lizards to forage for more days per year (a) but not necessarily for more hours per year (b). The colour of the each point indicates the number of locations. The effect of warming on activity depends on the current temperature (c); lizards in currently cool locations will have more hours for activity, and lizards in currently warm locations will have fewer hours. The potential for activity will decline most in the spring and fall for currently warm locations and increase most in the spring for currently cool locations (d). In plots c and d, the colour of the each point indicates the mean air temperature at one or more locations (d). By 2080–2100, more locations will have climates that restrict lizards to a bimodal distribution of activity, peaking in spring and fall (e).



**Figure 4** Impacts of climate change on opportunities for reproduction. Climate change enables lizards to reproduce earlier in spring or later in fall, but could decrease reproduction during summer (a). Symbols denote the number of locations. The effect of warming on reproduction depends on the current temperature (b); lizards in currently cool locations will have more days for successful reproduction, but lizards in currently warm locations could have many more or fewer days. The effect of warming on embryonic survivorship depends on the current temperature and the date on which eggs are laid (c). In currently warm locations, survivorship will mostly decline for potential dates of nesting. In currently cool locations, survivorship will mostly increase for eggs laid during summer. In plots a and b, symbols denote the mean of air temperatures at one or more locations. By 2080–2100, more local climates will force lizards to reproduce bimodally (d).



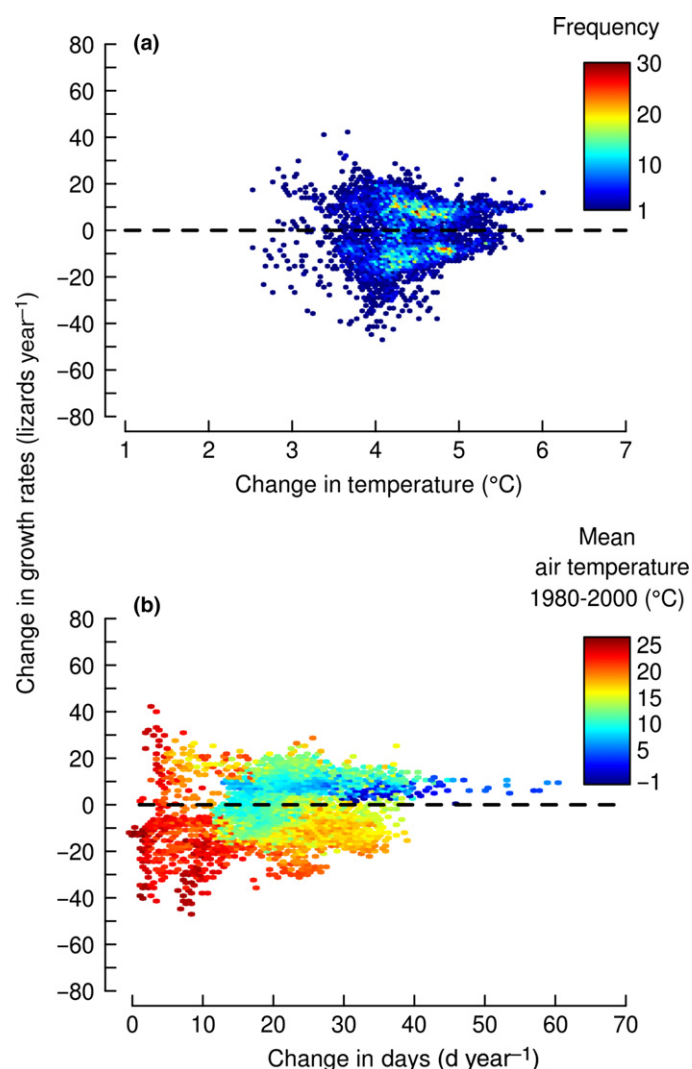
**Figure 5** Impacts of climate change on survivorship of juveniles. Survivorship of juveniles does not depend on the magnitude of warming (a) as much as it depends on opportunities for activity (b). The effect of warming on juvenile survivorship depends on the current temperature and the date on which a juvenile emerges from its egg. At cool locations, juveniles that hatch in fall will have more time for activity in future climate than in the past climate. At warm locations, however, juveniles that hatch during summer have less time for activity and face a greater risk of starvation in the future climate. Symbols represent either the number of locations (a) or the mean air temperature of the location between 1980 and 2000 (b and c). See Figs S15–S20 for plots based on our sensitivity analysis.

successfully (overestimates of  $190 \pm 40$  days and  $233 \pm 29$  days in past and future climates, respectively).

The fitness of lizards would suffer as warming diminishes the potential periods of activity and reproduction (Fig. 6). By summing opportunities for foraging and multiplying this quantity by the average survivorship of offspring throughout the year, we estimated rates of population growth ( $r$ ) at each location in past and future climates. When comparing populations in the current climate, we estimated that those from warmer environments have more time for activity and thus can achieve greater fitness ( $> r$ , Levy *et al.* 2015b). Yet this relationship between environmental temperature and population growth among locations has the potential to change over time. As climate warms, many populations will experience

more days of activity. Yet more days of activity will not generally yield greater fitness. In currently cold environments, warming will add many days to the activity season and support small-to-modest increases in population growth. In currently warm environments, however, further warming usually reduces rates of population growth despite adding days to the active season. A longer activity season fails to enhance fitness because performances of embryos, juveniles and adults interact to constrain phenology and dictate population growth.

When averaged over space, predicted impacts of climate change were robust to reasonable deviations in the values of parameters (Tables S3–S4). Potentials for activity, growth and reproduction were most sensitive at the margins of the temporal and spatial ranges (see Figs S7–S34), where extreme



**Figure 6** Impacts of climate change on population growth. Predicted change in population growth by 2080–2100 was unrelated to the magnitude of warming (a) or the increase in activity (b). Warming of cool locations would generally increase potential activity and population growth. However, further warming of warm locations would primarily decrease population growth, despite increasing the number of days for activity. Symbols represent either the number of locations (a) or the mean air temperature of the location between 1980 and 2000 (b). See Figs S21–S34 for plots based on our sensitivity analysis.

conditions were more likely to cross thermal thresholds for activity or survival. For example, changes in the length of the reproductive season (Fig. 4) and rate of population growth (Fig. 6) between past and future climates were unrelated to the degree of warming, regardless of the lethal temperature of embryos. However, when varying the lethal temperature between 42 ° and 46 °C, climate change was more likely to increase the number of reproductive days (Figs S11a and S12a) and the rate of population growth in warming environments (Figs S25a and S26a). Similarly, the change in the survivorship of juveniles was unrelated to the degree of warming, but positively related to the change in potential days for activity (Fig. 5). However, when varying the energy assimilation by juveniles by  $\pm 20\%$ , survivorship was more likely to

decrease in environments where climate change will create only a small increase in the activity season (compare Figs S19b and S20b).

## DISCUSSION

Ecologists expect global warming to advance the phenology of organisms, and meta-analyses established that activities have occurred earlier in spring with each passing decade (Parmesan & Yohe 2003; Root *et al.* 2003). The magnitude of advance varies dramatically among species (Parmesan 2007; Poloczanska *et al.* 2013), underscoring the need to identify factors that influence the response of each species. Moreover, the net impact on the life history involves more than events at the beginning of the activity season. Climates during summer and fall interact with the climate during the spring to influence periods of growth and reproduction (Gallinat *et al.* 2015). Advances in spring phenology could alter the structure of the active season in one of three ways: (1) if activity continues throughout summer but ends earlier in fall, the window for activity could remain the same or even contract; (2) if activity continues throughout summer and ends later in fall, the window for activity could expand or (3) if activity ceases in summer but resumes in fall, the window for activity could be divided. In our analysis, the window for activity expanded at every location, except those that currently permit activity 365 days a year (see Fig. 3a, and Fig. S5). At the same time, the activity season shifted from unimodal to bimodal in many locations (see Fig. 3e).

Biologists often infer impacts of climate change by substituting space for time in comparative analyses (McLean *et al.* 2005; Nooten *et al.* 2014; Heimonen *et al.* 2015). In our analysis, however, substituting space for time would mislead us about the impacts of climate change. Warmer locations permit more foraging and reproduction in current environments, but warming of an environment does not necessarily increase opportunities to forage and reproduce. Although warming would enable lizards to forage for more days per year, it can reduce the potential hours of foraging (Sinervo *et al.* 2010). In certain locations, the predicted loss of hours during summer offsets the predicted gains during spring and fall, leading to a bimodal distribution of activity throughout the year. Such bimodal distributions will become the rule rather than the exception if climates warm as projected (Figs 3, 4). Our predictions accord with those of previous models in which activity depends on access to preferred microclimates, which become rare or absent in the hottest conditions (Adolph & Porter 1993; Sinervo *et al.* 2010; Kearney 2013). On one hand, a daily hiatus due to heat stress could reduce opportunities for growth and reproduction. On the other hand, if animals feed early in the day, periods of inactivity at midday could permit digestion while lowering the risk of predation. The cost of inactivity, and thus the pressure to resume activity, depends on the microclimates below the surface relative to those above the surface, as evidence by experimental studies of lizards (Polo *et al.* 2005).

By focusing on the adult stage and ignoring the ecology of earlier stages, some models of species' distributions assume that a longer activity season implies a longer reproductive



season (e.g. see Buckley 2010); however, successful reproduction throughout the range depends on the thermal tolerances of embryos and larvae as well as that of adults (Kearney *et al.* 2009; Radchuk *et al.* 2013; Levy *et al.* 2015b). Three factors highlight why extending the activity season seldom expands the number of days when lizards can reproduce successfully. First, periodic cold snaps reduce the survival of embryos during spring and fall. Even if adults can forage and mate earlier in spring and later in fall, offspring may die during these periods as soil temperature falls below the lethal limit at night. Second, soil temperatures during summer can exceed the lethal limit of embryos, creating short and potentially unpredictable periods where offspring will survive. Moreover, our model suggests that even if mothers choose shaded or deeper nesting sites, juveniles that hatch during warm summers face a high risk of starvation. Individuals that reproduce in hot periods would be selected against, increasing the frequency of genotypes that reproduce later or less often. Finally, eggs laid too late in the summer would produce juveniles that cannot store enough energy in the fall to survive the winter. For all of these reasons, potential reproductive seasons were much narrower than activity seasons.

Since life-history phenotypes depend on opportunities for activity and reproduction (Dunham *et al.* 1989; Adolph & Porter 1993, 1996), changes in phenology will cause phenotypic plasticity or select novel strategies (Angilletta *et al.* 2004, 2006). Lizards that gain energy by extending activity can produce either larger eggs or more eggs (Adolph & Porter 1996). If the reproductive season increases by 4–6 weeks, females could produce an extra clutch of eggs (Tinkle & Ballinger 1972; Niewiarowski 1994). However, as summers become too harsh for offspring to survive, natural selection would favour genotypes that avoid unpredictable thermal stresses by producing either more, smaller clutches throughout the year (spreading risk) or fewer, larger clutches in a dependable period (avoiding risk). For example, birds in the Sonoran desert reproduce in spring and fall when prey are more abundant than they are in summer (Ohmart 1973). For lizards, our model predicts that bimodal reproduction would spread from a small region of the southwestern United States to other regions by 2080 (see Fig. 4d). By avoiding reproduction in summer, lizards prevent embryos from experiencing lethal soil temperatures. In the hottest locations, successful reproduction could occur only in fall because offspring produced during spring would have insufficient opportunities to forage during summer. Importantly, these projections assume that key biotic factors, such as densities of competitors, predators and prey remain stable.

In summary, temperatures that prevent development of embryos or growth of juveniles offset the reproductive benefits of phenological advances. Consequently, populations that will experience the same amount of climate warming, but experience different climates now, should diverge along two lines. Where warming increases opportunities for activity and opportunities for reproduction, species can use additional energy to reproduce (Kozłowski & Teriokhin 1999). Where opportunities for activity increase but opportunities for reproduction decrease, species must use additional energy to grow. These alternatives indirectly shape the evolution of life span because reproduction reduces future rates of survival and

fecundity (Shine & Schwarzkopf 1992; Niewiarowski & Dunham 1994; Stearns 2000). If the potential period for reproduction extends throughout the activity season, adults can allocate energy to offspring as they acquire energy from foraging (income breeding). By contrast, a restricted period for reproduction could favour adults that use their activity season to store the energy needed to produce offspring (capital breeding). These potential impacts of climate change emerge only by considering the integration of life stages as warming advances phenology. Our findings should prompt researchers to reformulate models that ignore thermal stresses on early life stages and to expand the focus on phenological impacts from spring activity to annual reproduction.

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## COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

## AUTHORSHIP

O.L., L.B.B., T.H.K. and M.J.A. conceived and designed the study; O.L. wrote the model and analysed the data; L.B.B., T.H.K. and M.J.A. contributed materials/analysis tools; O.L., L.B.B., T.H.K. and M.J.A. co-wrote this study.

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