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Divergent effects of climate change on the egg-laying opportunity of species in cold and warm regions

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Article Impact statement: We proposed a new metric for estimating the vulnerability of oviparous species and demonstrated its application in a widespread lizard.

Abstract

Climate warming can substantially impact embryonic development and juvenile growth in oviparous species. Estimating the overall impacts of climate warming on oviparous reproduction is difficult because egg-laying events happen throughout the reproductive season. Successful egg laying requires the completion of embryonic development as well as hatching timing conducive to offspring survival and energy accumulation. We propose a new metric—egg-laying opportunity (EO)—to estimate the annual hours during which a clutch of freshly laid eggs yields surviving offspring that store sufficient energy for overwintering. We estimated the EO within the distribution of a model species, _Sceloporus undulatus_, under recent climate condition and a climate-warming scenario by combining microclimate data, developmental functions, and biophysical models. We predicted that EO will decline as the climate warms at 74.8% of 11,407 sites. Decreasing hatching success and offspring energy accounted for more lost EO hours (72.6% and 72.9%) than the occurrence of offspring heat stress (59.9%). Nesting deeper (at a depth of 12 cm) may be a more effective behavioral adjustment for retaining EO than using shadier (50% shade) nests because the former fully mitigated the decline of EO under the considered warming scenario at more sites (66.1%) than the latter (28.3%). We advocate for the use of EO in predicting the impacts of climate warming on oviparous animals because it encapsulates the integrative impacts of climate warming on all stages of reproductive life history.

KEYWORDS
breeding, climate, energy, hatching success, heat stress, nesting, opportunity, oviparity

Efectos divergentes del cambio climático sobre la oportunidad de desove de las especies en regiones cálidas y frías

Resumen: El calentamiento global puede tener un impacto considerable sobre el desarrollo embrionario y el crecimiento juvenil de las especies ovíparas. Es complicado estimar el impacto general que tiene el calentamiento global sobre la reproducción ovípara ya que los eventos de desove suceden durante la época reproductiva. El desove exitoso requiere que se complete el desarrollo embrionario y que el momento de eclosión sea favorable para la supervivencia de las crías y la acumulación de energía. Proponemos una nueva medida—oportunidad de desove (OD)—para estimar las horas anuales durante las cuales una puesta de huevos recién desovados produce crías que sobreviven y almacenan suficiente energía para invernar. Estimamos la OD dentro de un modelo de distribución de la especie _Sceloporus undulatus_ bajo las recientes condiciones climáticas y bajo un escenario de calentamiento global mediante la combinación de datos microclimáticos, funciones del desarrollo y modelos biofísicos. Pronosticamos que la OD declinará conforme la temperatura aumente en 74.8% de los 11407 sitios. La disminución del éxito de eclosión y de la energía de las crías explicó más horas perdidas de OD (72.6% y 72.9%) que la presencia de estrés por calor en las crías (59.9%). Una anidación más profunda (a una profundidad de 12 cm) puede ser un ajuste conductual más efectivo para la retención de la OD que

los nidos con mayor sombreado (50% de sombra) porque el primero mitigó por completo la declinación de la OD bajo el escenario de calentamiento en más sitios (66.1%) que el segundo ajuste (28.3%). Defendemos el uso de la OD en el pronóstico del impacto del calentamiento global sobre los animales ovíparos porque encapsula los impactos integrales que tiene el calentamiento global sobre todas las etapas de la vida reproductiva. 气候变化在寒冷和温暖地区对物种产卵机会造成不同影响

PALABRAS CLAVE
anidación, clima, energía, estrés por calor, éxito de eclosión, oportunidad, oviparidad, reproducción

气候变化在寒冷和温暖地区对物种产卵机会造成不同影响 摘要

气候变暖可能严重影响卵生物种的胚胎发育和幼体生长。由于产卵事件先后发生在整个繁殖季节，评估气候变暖对卵生物种繁殖的总体影响十分困难。一次成功的产卵除了让胚胎能够完成发育外，还需要让卵在有利于后代生存和能量积累的时机孵化。我们提出了一个新的指标——产卵机会(EO)——用来估计一年中一窝新产卵能够产生成功越冬后代的时间。结合微气候数据、胚胎发育数据和生物物理模型，我们估算了模式物种东部强棱蜥(*Sceloporus undulatus*)在当前气候条件和气候变暖情景下，其分布范围内的EO。我们预测，在东部强棱蜥分布区内的11407个位点中，74.8%的位点的EO将随着气候变暖而缩短。由孵化成功率降低和后代能量积累减少所造成的EO损失(72.6%和72.9%)大于由新生幼体热压力所造成的EO损失(59.9%)。在气候变暖情景下，增加产卵巢穴深度(12 cm)可能比更郁闭的巢穴中产卵(50%郁闭)更有效地减缓EO损失，因为在东部强棱蜥的例子中前者(66.1%)比后者(28.3%)在更多的地点避免了EO的损失。我们提倡使用EO来预测气候变暖对卵生动物的影响，因为它概括了气候变暖对繁殖生活史各个阶段的综合影响。

人造生境:
卵生, 繁殖, 孵化成功率, 热压力, 能量, 气候, 巢址选择, 机会

INTRODUCTION

Oviparous species lay eggs in nests exposed to temperature variation, which affects embryonic development and induces fitness consequences (Bonebrake et al., 2010; Du & Shine, 2015; Sun et al., 2018). Climate warming may preclude the embryonic development of oviparous species, which can induce population decline (Carlo et al., 2018; Ye et al., 2019). Therefore, estimating how climate warming affects embryonic development is crucial for assessing the vulnerability of species. However, egg-laying events happen throughout the reproductive season due to multiclutch reproduction, variable maternal condition (Bêty et al., 2003), heritable individual variation (Ikeno et al., 2010), and abiotic (e.g., precipitation [Papaj et al., 2007], temperature [Visser et al., 2009]) and biotic environmental factors (prey abundance [Evans, 1982], joint breeding [Eggert & Müller, 2000]). Because it is difficult to predict when each clutch of eggs begins to develop for a given population, shifting perspective from the particular clutch of eggs to the environments where eggs are incubated and juveniles are growing may clarify the problem. At an egg-laying event, the mother bets that the soil temperatures (incubation temperatures during embryonic development) and climate conditions (for juvenile growth [Du & Shine, 2015; Du et al., 2019]) will support her clutch of eggs. Sometimes she wins in that a brood of hatched offspring survive and accumulate enough energy for overwintering. Sometimes she loses and the maternal energetic investment is wasted (Chmura et al., 2018; Olsson & Shine, 1997; Shine, 2004). The hours in a year that allow for success in egg laying (i.e., egg-laying opportunity [EO]) are, therefore, crucial to population recruitment.

Egg-laying opportunity relies on developmental success and hatching timing. Developmental success is the most direct consequence of egg laying and is affected by the incubation temperatures during the period between egg laying and hatching (Du & Shine, 2015; Jarošík et al., 2004). Developmental success determines the number of hatched offspring and has a direct impact on population recruitment (Croxall et al., 1990; While et al., 2015). Incubation temperatures (at the nesting site) following the egg-laying event determine the developmental rate and, therefore, the hatching timing, which has a series of cascading consequences for posthatching life-history stages. Hatching timing subsequently determines available activity time for juvenile energy accumulation before overwintering (Kearney, 2013; Levy et al., 2016c), which is crucial for their overwintering survival and future reproductive success (Warner & Shine, 2007; Warner et al., 2008). Hatching timing also determines heat stress encountered by juveniles and has implications for survival (Rukke et al., 2018). Any detriments to developmental success or post-hatching conditions (e.g., heat stress or deficient stored energy) ("limiting effects" below) result in unsuccessful

egg laying. Therefore, the EO can be determined based on the collective limiting effects.

We propose that the change in the amount of EO can be used as a metric for estimating climate warming impacts on oviparous populations because this metric accounts for the effects of climate warming on embryonic development and juvenile growth throughout a year. We used the eastern fence lizard (*Sceloporus undulatus*) as a model system to identify geographic variation in EO and the impact of climate warming on EO. This species has conservative thermal tolerances at embryonic and individual stages throughout its distribution range (Angilletta et al., 2013; Crowley, 1985). By combining microclimate data, embryonic developmental functions, and biophysical models, we sought to determine the EO in an average year for all sites within the distribution range of *S. undulatus* under recent climate condition and a climate warming scenario. We aimed to address the following four questions: how does EO vary geographically, how do climate warming impacts on EO vary geographically, what limiting effects are most responsible for lost and gained EO under climate warming, and can maternal behavior buffer the climate warming impact on EO? The developmental rate and success of embryos and the growth and survival of juveniles are highly dependent on temperature in lizards (Du & Shine, 2015; Huey & Kingsolver, 1989; Pike et al., 2008). Lizards in warm regions have a longer reproductive season with more suitable temperatures for embryonic development and offspring growth than their counterparts in cold regions (Levy et al., 2016c; Mesquita et al., 2016). Accordingly, we predicted that the EO of warm sites would tend to be longer than those of cold sites.

Climate warming may create a longer period during which temperatures are suitable for embryonic development and juvenile growth in cold regions, but it may reduce the thermal quality of habitats in warm regions (Kingsolver et al., 2013; Levy et al., 2015). Therefore, we predicted that the EO would be longer at cold sites and shorter at warm sites under climate warming.

Climate warming may change the hatching success of eggs (Sun et al., 2021) the energy budget (Levy et al., 2016c) and the heat stress (Ma et al., 2018b) of hatched individuals. We predicted the limiting effects associated with loss and gain in EO under climate warming would vary among populations.

The nesting behavior of oviparous mothers determines the development environment of their embryos (Angilletta et al., 2009; Du & Shine, 2022). Gravid females may adjust the shade and depth of their nesting sites to buffer potential negative effects induced by warming temperatures (Telemeco et al., 2017). We thus predicted that maternal adjustments in the shade at and depth of a nesting site would mitigate some EO loss associated with climate warming.

METHODS

Microclimate data, model species, and modeling framework

All analyses were based on hourly estimates of microclimates. We downloaded hourly microclimate data for recent (1980– 2000) and future (2080–2100, RCP8.5) climate conditions. These microclimate data (hourly climate variables at various heights and depths and various shade intensities) were generated to represent typical microclimate conditions in 36 × 36 km grids covering North America by dynamically downscaling climate data (Levy et al., 2016a, b). Compared with statistical downscaling, dynamic downscaling captures processes relevant to organisms, such as extreme weather, surface–atmosphere interactions, vegetation cover, and land use (Fowler et al., 2007; Stefanova et al., 2012), and, therefore, yields a more realistic forecast of climate in most cases (Fowler et al., 2007). The model species we used, *S. undulatus*, is widely distributed in North America. We downloaded a polygon indicating the distribution range of *S. undulatus* from the International Union for the Conservation of Nature Red List (Hammerson et al., 2007) and restricted our calculations and statistical analyses to grid cells in this polygon. We collected biophysical and physiological traits of *S. undulatus* from the literature (Appendix S2) for parameterizing the models. For traits that had not been measured for *S. undulatus* (i.e., radiation absorptivity, thermal preferences for gravid females and juveniles, energy conversion efficiency, and juvenile maximal velocity), we used data for other species from the *Sceloporus* genus or other lizard groups.

We estimated whether each hour of the year is viable for egg laying to estimate EO. Therefore, our estimates (Figure 1) are based on the assumption that a clutch of eggs is laid into a nest in an open area at a depth of 6 cm (Angilletta et al., 2009) each hour. The cascading developmental success, offspring heat stress, and offspring stored energy were then calculated using developmental functions and biophysical models. We determined whether a clutch of eggs laid in each hour of year would result in a probability of developmental success >0.6; no heat stress experienced by offspring within 2 weeks after hatching; and sufficient energy accumulation by offspring by the end of the year. To facilitate the application of our methods, detailed methods are provided in Appendix S1 and with the relevant R code is embedded into the corresponding sections. The full R code is available from Github (https://github.com/mayinsitan1/Egg-laying-opportunity).

Developmental success

For each hour in a year, we assumed a clutch of eggs was laid into the nest. Hourly developmental rates were calculated using an established equation (Equation 1 in Appendix S1 [Telemeco et al., 2017]) of developmental temperatures, which are assumed to be soil temperature at 6-cm depth in 0% shade for *Sceloporus* lizards (Angilletta et al., 2009). Subsequently, we calculated the developmental period and determined the corresponding hatching hour by accumulating developmental rates (percentage of development per hour) until 100% development (cal.Devtime in code). The probability of developmental success was then calculated as a function (for *Sceloporus* lizards) of the daily maximum and minimum developmental temperatures during this developmental period (Equation 2 in Appendix S1 [Telemeco et al., 2017]). We assumed that developmental success was 0 when the
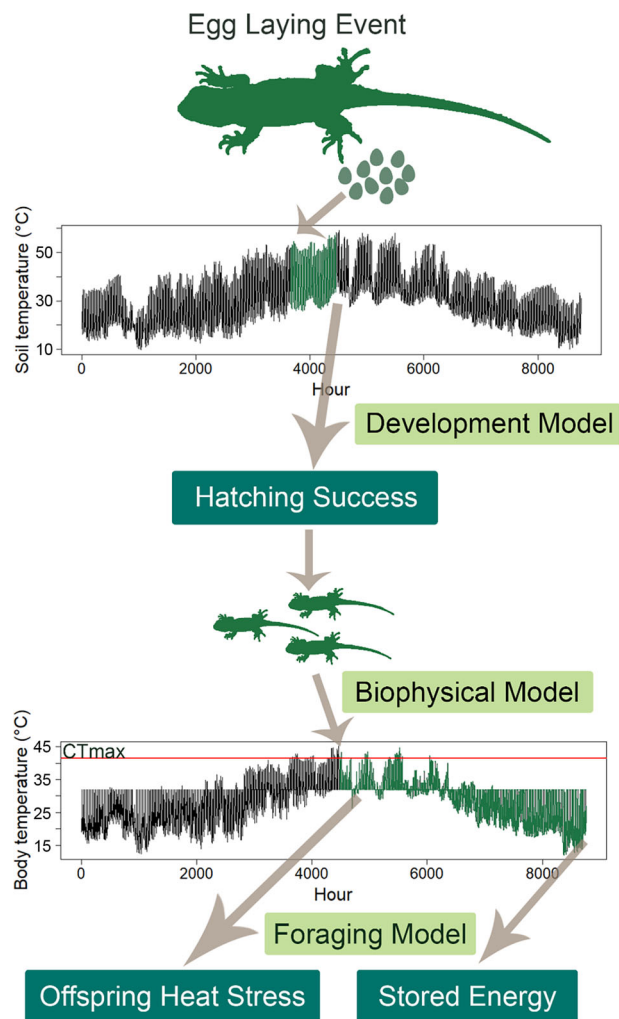
FIGURE 1 A framework for evaluating whether an hour in a year represents an egg-laying opportunity (i.e., the probability of developmental success >0.6, no hatchling heat stress for 2 weeks, and sufficient energy accumulated by offspring [1.2 kJ] by the end of the year) for oviparous lizards.

Levy et al., 2016c) (see Appendix S2 for parameters used). Second, we predicted the body temperatures of individual juveniles by allowing them to achieve body temperatures as close as possible to their body temperatures (Appendix S2) achieved via thermoregulation during the day and to conform to burrow temperatures (soil temperatures at 6-cm depth with 100% shade) at night (Buckley, 2008; Ma et al., 2018a). For thermoregulation, juveniles can shift among four potential temperatures: operative temperatures on the ground in 0% and 100% shade and temperatures of burrow (soil temperatures at 6-cm depth) in 0% and 100% shade (detailed methods in Appendix S1).

Lizard offspring incur the highest death rates shortly after hatching (Andrews et al., 2000). When body temperature reaches thermal tolerance, individuals become immobile (no foraging or escaping) (Camacho & Rusch, 2017), and their metabolic rate surges (Huey & Kingsolver, 1989), greatly increasing their chances of dying from predation and starvation, especially juveniles. We, therefore, compared juvenile body temperatures during the 2 weeks following the hatching hour with their critical thermal maxima (Appendix S2) and used no heat stress experienced by juveniles (i.e., body temperature <critical thermal maxima) during this period as one of the conditions to determine whether an hour contributed to EO.

Offspring stored energy

We calculated energy budgets from the hatching hour to the end of the year. We assumed that juveniles were able to forage during thermal opportunity hours (when body temperatures were 29.3–36.3°C), which allowed them to feed and digest rapidly (Angilletta, 2001; Levy et al., 2016c). However, juveniles were only predicted to forage when their gut content was less than the maximal gut space (Appendix S2). The maximal amount of ingested energy was calculated using an established foraging energetic model (Equation 3 in Appendix S1), whereas the actual ingested energy was contingent on gut space, which was updated hourly. We calculated maximal daily digestion as a function of thermal opportunity hours (Equation 4 in Appendix S1). Actual daily digestion depended on gut content. After digestion, the gut space and gut content were updated accordingly. We calculated the resting metabolic rate (RMR) for each hour as a function of body temperature (Equation 5 in Appendix S1). The metabolic rate during digestion (no foraging occurred) was calculated by multiplying the RMR by 1.5 (Roe et al., 2005), and the metabolic rate during foraging was calculated by multiplying the RMR by 2 (Bennett, 1982). The hourly energy budget was calculated by subtracting metabolic consumption from digested energy. A negative hourly energy budget was regarded as hourly energy loss. We calculated hourly energy gain by multiplying positive energy budgets by 0.79 (conversion efficiency) (Appendix S2) because juveniles stored gained energy as fat. We calculated the offspring accumulated energy by adding up hourly energy loss or gain (details in Appendix S1).

A demographic study suggested that the latest hatchlings (appearing during the first week of October) for a population

projected developmental period was over 100 days (developmental times at least this long are rare in the literature [Andrews et al., 1999; Tinkle & Gibbons, 1977]) or the eggs failed to accumulate 100% of development before the end of the year (details in Appendix S1). We analyzed hatching success data for 82 oviparous reptile species from the RepDevo database (Noble et al., 2018) and found that most (>70%) hatching success measurements had probabilities >0.6. We, therefore, used probability of developmental success >0.6 as one of the conditions to determine whether an hour contributed to EO.

Offspring heat stress

From the hatching date to the end of the year, we modeled juveniles' thermoregulation and calculated their body temperatures. First, we translated microclimates to operative temperatures of juveniles in habitats with 0% shade and 100% shade, respectively, with an established biophysical model (Buckley, 2008;

at the northern edge of *S. undulatus*' distribution range have an average snout-vent length of 33 mm when they first appear the next spring (April) (Tinkle & Ballinger, 1972). We converted the snout-vent length to stored energy (1.2 kJ) with an established function (Levy et al., 2016c). We, therefore, assumed that juveniles must store at least 1.2 kJ (energy content of hatchling plus accumulated energy) by the end of the year as one of the conditions to determine whether an hour contributed to EO.

Integrating the three conditions for oviposition success

In nature low developmental success, encountering heat stress, or deficient offspring stored energy risks a failure of oviposition. Therefore, we required all three conditions to be fulfilled (developmental success >0.6, no heat stress experienced by juveniles, juvenile stored energy at year end >1.2 kJ) for an hour to contribute to EO. We used these three conditions to define EO. To explore how climate-warming impacts vary geographically and with local climates, we calculated the mean value and interquartile range (IQR) of hourly soil temperature (representing the average condition and variability of climate, respectively) in an average year under recent climate (1980–2000).

We estimated the contribution of the three conditions to the changes in EO. For each site within the species' distribution range, we identified the lost and gained EO under the climate warming scenario. We first estimated the lost and gained EO under climate warming for each site considering all three conditions. We then calculated percentages of the lost or gained EO that were also predicted to be lost or gained if the EO was determined by only one of the three conditions instead of all three. We refer to these percentages as *contributions* of each of the three conditions to the loss or gain of EO hours (the contribution of each condition ranges from 0% to 100% and is not dependent on the contributions of other conditions [i.e., does not sum to 100%]).

Potential mitigating effects of nesting behaviors

To examine how maternal nesting behavior might mitigate declining EO under the climate warming scenario, we reran the above analysis with shadier (change 0% shade to 50% shade) and deeper (change 6–12 cm) nesting sites. The mitigating effect was calculated by subtracting the new EO change from the previous EO change and dividing the result by the previous EO change.

Model validation

To test the performance of our models, we conducted three model validations. First, we compared nest temperatures derived from the microclimate data set with observed nest temperatures in Burlington, New Jersey (USA) (Appendix S3). Second, we compared incubation periods predicted by

our models with laboratory measurements at the same series of incubation temperatures (Appendix S3). Finally, we compared hatchling growth predicted by our models with hatchling growth data collected in the field (Appendix S3). The model validations suggested the good performance of our models (details in Appendix S3).

RESULTS

Geographic variation in EO

The estimated EO varied from 0 to over 4000 h (average 1285.3 h) across the species' distribution range (Figure 2). Sites with relatively high EO were in the southeastern parts of the distribution range, where the soil temperatures are high and stable. Temporally, EO was continuous for some sites (Figure 2c,d) but discrete for others (Figure 2e). The three conditions for determining EO hours were fulfilled at different periods.

Change in EO under climate warming

Our model predicted that *S. undulatus* will lose EO under climate warming at most sites (74.8%, Figure 3). Sites with relatively large predicted decreases in EO were in the southeastern part of the distribution range. These sites have high mean soil temperatures. Our model predicted that *S. undulatus* will gain EO under climate warming at only 24.8% of sites. Sites predicted to gain substantial EO were either close to the southwestern border of the distribution range or at the northeastern part of the distribution range. These sites had either low means or variabilities (IQR) in soil temperatures.

Contribution of the three conditions to the loss and gain of EO

Under the climate warming scenario, the contributions to the three conditions to changes in EO varied throughout *S. undulatus*' distribution (Figure 4). For lost EO hours, decreasing hatching success (72.6% of lost EO hours on average) and decreasing juvenile energy (72.9% of lost EO hours in average) generally contributed more than the appearance of juvenile heat stress (59.9% of lost EO hours on average). Specifically, in the western part of the distribution, both decreasing hatching success and decreasing juvenile energy contributed to nearly all the lost EO hours (Figure 4a,e & Appendix S3). In contrast, in the northeastern part of the distribution, the appearance of juvenile heat stress contributed to nearly all the lost EO hours (Figure 4c & Appendix S3). In other regions, the violation of each condition contributed to some but not all of the lost EO hours.

For the gained EO hours, increasing hatching success (95.9% of gained EO hours on average) generally contributed more
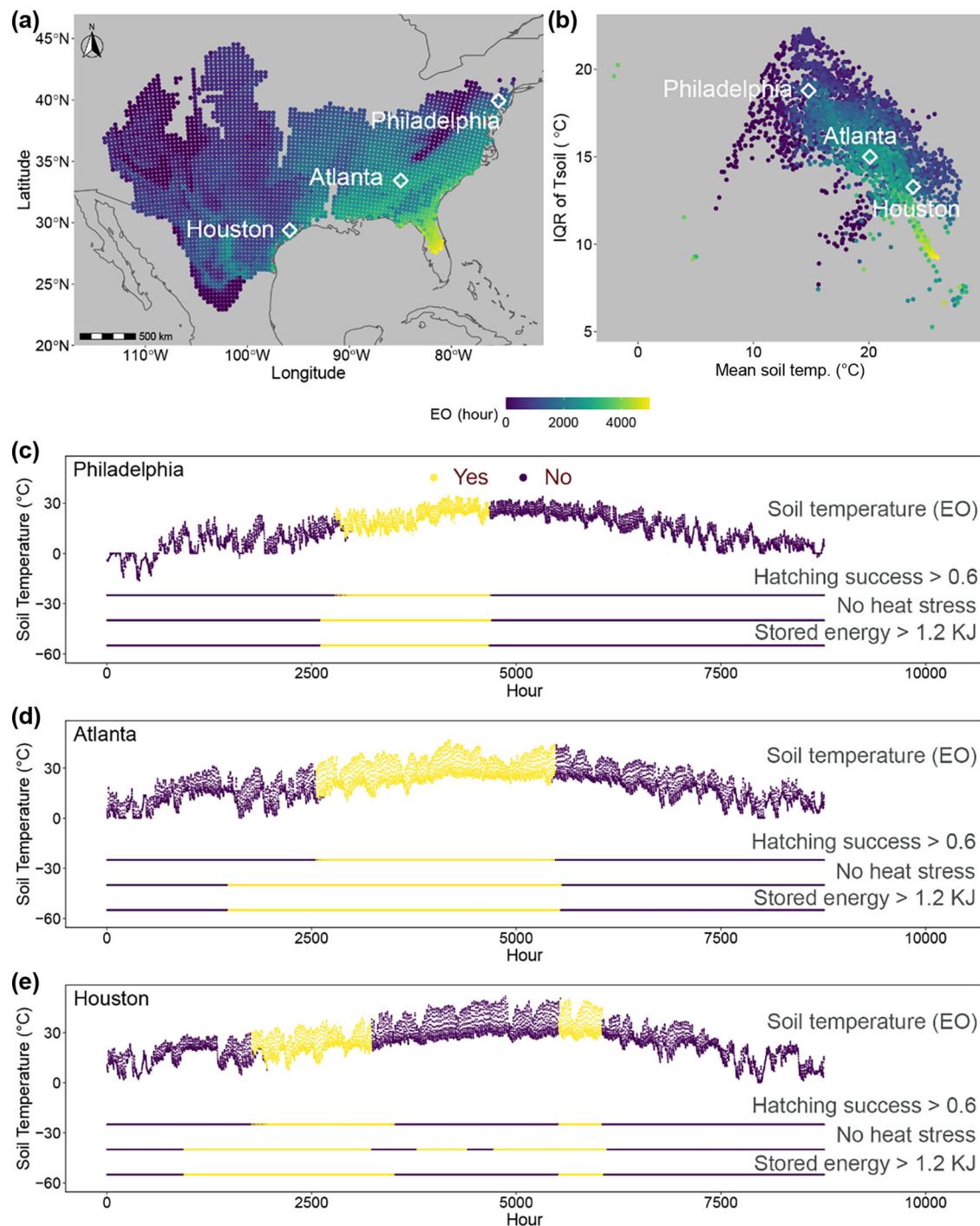
FIGURE 2 Egg-laying opportunity (EO) in (a) an average year in the distribution range of *Sceloporus undulatus* under recent climate (1980–2000), (b) data points from (a) relative to annual mean soil temperature and the interquartile range (IQR) of annual soil temperature in an average year under recent climate, (c–e) hourly soil temperature of three sample sites in an average year under the recent climate. The color of the soil temperature curve indicates EO hours. The colors of the lines below the soil temperature curve indicate whether the three conditions used to determine EO hours (hatching success >0.6, no heat stress, and stored energy >1.2 kJ) were met.

than increasing juvenile energy (62.8% of gained EO hours on average) and alleviation of juvenile heat stress (60.1% of gained EO hours in average). Specifically, throughout the distribution, increasing hatching success (beyond the 0.6 threshold) contributed to nearly all the gained EO hours (Figure 4b & Appendix S3), whereas the other two conditions contributed to some but not all of the gained EO hours (Figure 4d,f & Appendix S3).
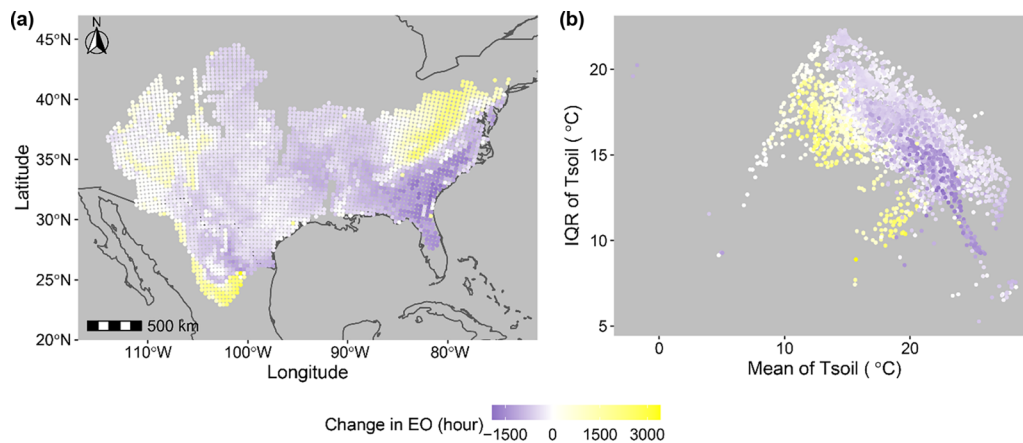
FIGURE 3 (a) Change in egg-laying opportunity (EO) hours in the distribution range of *Sceloporus undulatus* from recent time (1980–2000) to the end of the century (2080–2100) under a climate warming scenario and (b) data points in (a) relative to annual mean soil temperature and the interquartile range (IQR) of annual soil temperature in an average year under recent climate (1980–2000).

Potential mitigating effects of nesting behavior

For sites predicted to have fewer EO hours under the climate warming scenario, nests at a depth of 12 cm (deeper than the default 6 cm) better mitigated the decline of EO than nests with 50% shade (shadier than the default 0% shade) (Figure 5). Specifically, shadier nests fully mitigated the decline of EO at only 28.3% of sites (Figure 5a), whereas deeper nests fully mitigated the decline of EO at 66.1% of sites (Figure 5b). The mitigation effects of both strategies diminished toward the east. Shadier nests mitigated over 50% of the EO decline at fewer sites (28.6%) than deeper nests (32.2% of sites). In contrast, shadier nests induced larger declines of EO under the climate warming scenario than the default (nests with 0% shade and 6-cm depth) at 1.2% of sites, whereas larger declines were not predicted for deeper nests.

DISCUSSION

Our new EO concept tested well in our set of mechanistic models based on empirical data (Appendix S3) that estimated the overall impacts of climate warming on EO. By integrating microclimate data, developmental functions, and biophysical models, we found that sites with warm and stable thermal environments had higher EO; EO declined at most sites in the species' distribution under climate warming, especially at sites with high temperatures; loss of EO hours was mainly induced by decreases in hatching success and juvenile energy, whereas gain of EO hours was mainly induced by increases in hatching success; and deeper nests better mitigated declines in EO than increased shade. These results suggested that EO can be used to evaluate the impact of climate warming on reproduction in oviparous lizards and could be applied to other species and taxonomic groups as well. Moreover, our model can be used to predict the vulnerability of oviparous species and, therefore, inform conservation.

Previous studies show that the length of the breeding season varies geographically; usually, it is longer in warmer regions (Mi et al., 2022; Morrison & Hero, 2003). This is thought to be related to the behavioral and physiological restriction induced by the thermal environment (Jarošík et al., 2004; Visser et al., 2009). However, how embryonic development and offspring survival constrains the breeding season is less explored. We found that EO was longer in warmer regions, which is consistent with the trend of geographic variation in the breeding season. However, we also found that EO was lower in regions with large temperature fluctuations. Because extreme temperatures limit the development of embryos and the growth of offspring in these regions, parts of the breeding season may become unsuitable for reproduction even if adults can move and mate. This highlights the importance of considering EO in quantifying the thermal quality of habitat for reproduction.

Unfortunately, our model predicted that EO will decrease in most areas in the species' range under a climate warming scenario. Areas facing declines tended to have high or variable recent temperatures. Because climate warming will further increase average temperatures and temperature fluctuations, it may reduce hatching success, increase heat stress experienced by juveniles, and shorten the time available for juvenile energy accumulation. This suggests that the focus should be on the conservation of oviparous species in these habitats. Our results predicted that EO will remain unchanged or even increase under climate warming at some sites. These sites were usually located in cooler and less thermally variable areas. Individuals in these regions had less EO under the recent climate, and warming may improve hatching success, which is the main driver of EO increases at these sites (Figure 4b). Climate warming will also alter the thermal environment experienced by juveniles, which may increase juvenile energy stores at some sites. Climate warming may also alter hatching time, which may allow juveniles to avoid the extreme heat they would have experienced in the recent climate. By analyzing how the three factors contribute to EO changes, we discovered how multiple life-history stages
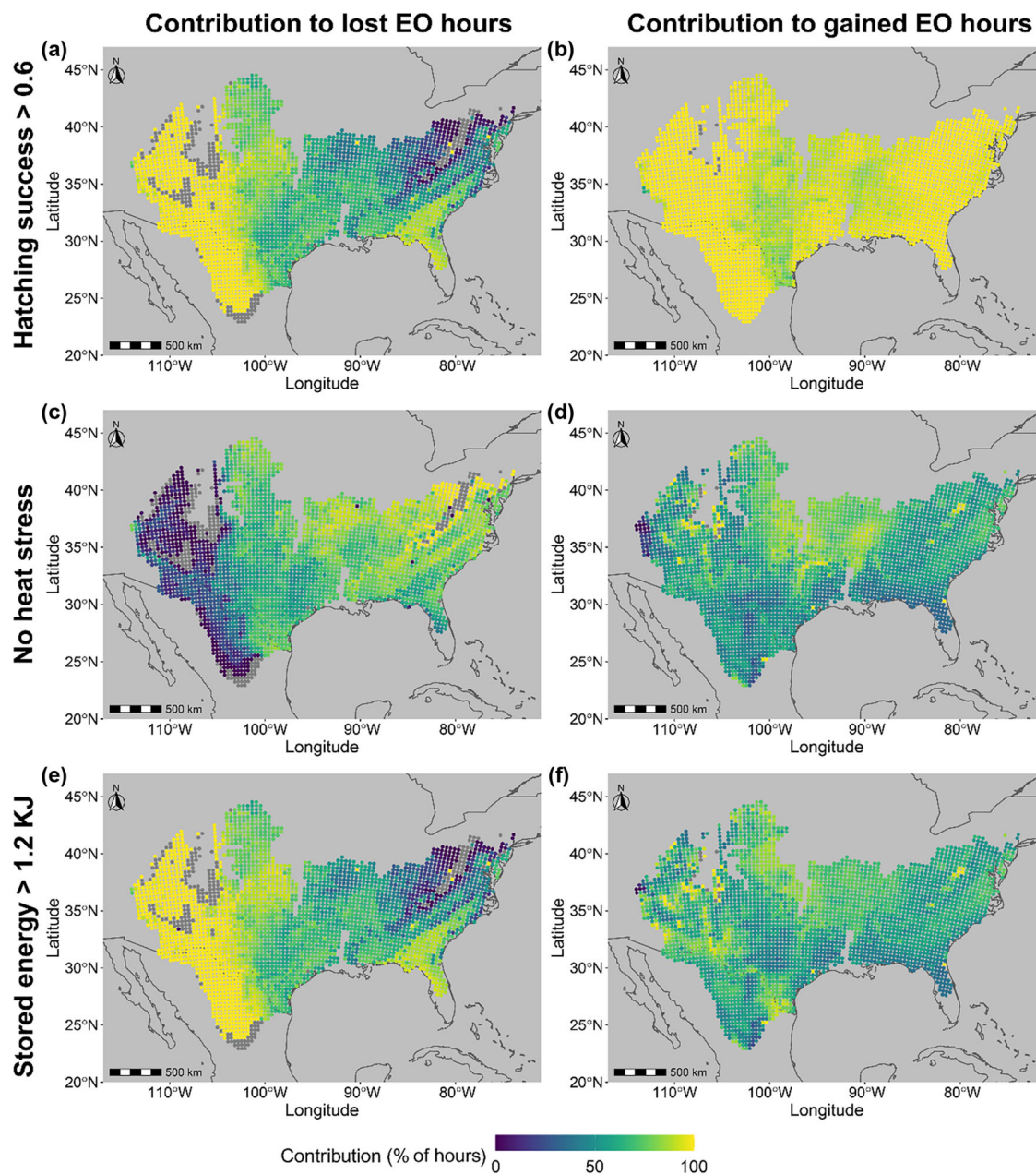
FIGURE 4 Percentage of cases (lost or gained hours) that each of the three requirements (hatching success >0.6, no heat stress, and stored energy >1.2 kJ) for successful oviposition contributed to the (a, c, e) loss and (b, d, f) gain of egg-laying opportunity (EO).

contribute to reproductive success. Future studies might explore how divergent changes in EO within ranges of species affect their persistence, which would be useful in evaluating species' vulnerability under climate change.

Our results suggest that species can buffer the effects of climate warming on EO by changing the shade on and depth of nest sites. In particular, we found that the negative impacts of climate warming on EO could be completely offset in most areas where EO was reduced, simply by laying eggs 6 cm deeper than before. This new nest depth, although deeper than the mean value suggested for *S. undulatus* (Angilletta et al., 2009), is within the range of nesting depth observed in other *Sceloporus* lizards (Telemeco et al., 2017). An experimental study of *Sceloporus* lizards shows that pregnant mothers fail to adjust

nesting behavior as needed to buffer populations from warming temperatures (Telemeco et al., 2017). However, studies on other lizards show that maternal nesting behavior can mitigate the effects of climate warming. For example, females select more open nest sites in cooler locations to compensate for climatic differences along the latitudinal cline in the Australian water dragon (*Physignathus lesueurii*) (Doody et al., 2006). Nesting lizards (*Bassiana duperreyi*) partly mitigate climate warming impacts by laying eggs earlier in the season and placing eggs in deeper nests (Telemeco et al., 2009). Although we found that nests of a depth of 12 cm better mitigated the decline of EO than nests with 50% shade, it was still difficult to conclude the relative usefulness of the two strategies because they depend on the availability of deeper and shadier nesting sites
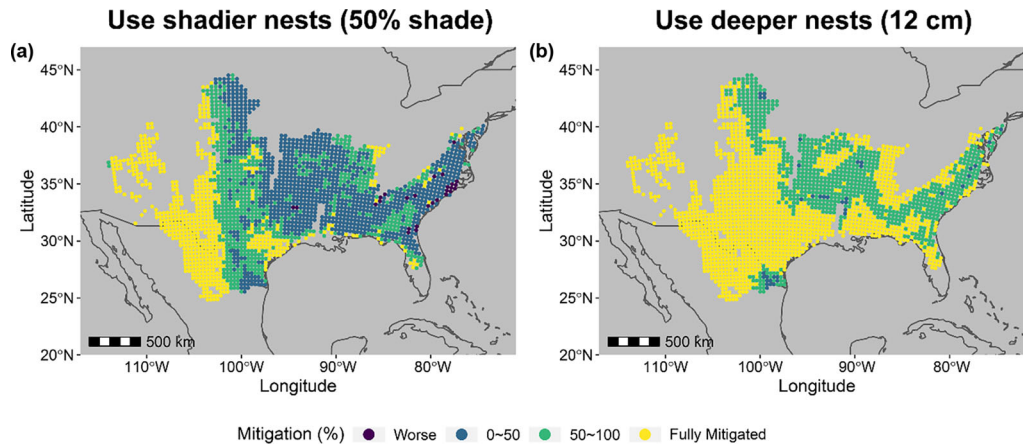
Use shadier nests (50% shade) Use deeper nests (12 cm)

FIGURE 5 Proportion of lost egg-laying opportunity (EO) hours regained through nesting behavioral adjustments of (a) nesting in 50% shade and (b) using nests 12 cm deep for sites that were predicted to experience EO loss to the end of the century (2080–2100) under the climate warming scenario. Mitigation was calculated by subtracting the EO loss associated with behavioral adjustment from the initial EO loss and dividing this amount by the initial EO loss.

and there are costs associated with using deeper and shadier nests.

Although model validations suggested that our models used a realistic nesting temperature and predicted developmental rate and hatchling growth well, future studies could use more empirical data to further validate and fine-tune the models. First, a combination of controlled experiments and field recapture could be used to determine the thresholds of hatching success (minimum value), offspring heat stress (period of sensitivity to temperature extremes), and offspring stored energy (minimum value) that would allow population persistence. Second, long-term survey data could be used to test the attribution of EO in determining population dynamics. For example, researchers could either compare population sizes at a single site through multiple years with corresponding EOs or compare population sizes in a single year at multiple sites with corresponding EOs. Finally, it would be interesting to look at the overlap between periods in a year when gravid females actually lay eggs and the EO. The timing of egg-laying events can be affected by the timing of fertilization, female body condition, and environmental conditions (Olsson & Shine, 1997). The mismatch between the egg-laying events and EO limits the number of viable offspring. Under a changing climate, how this mismatch (or matched period) changes is crucial to population persistence.

Our results demonstrate that climate warming decreases EO in warm and thermally variable regions, largely due to decreased hatching success. Such areas may require increased conservation attention for egg-laying species. More generally, we advocate for the use of EO in predicting the impacts of climate warming on oviparous animals. Contingent on the increasing availability of species traits (e.g., Noble et al., 2018), researchers could calculate the EO of other reptile species with our models by replacing species-specific traits in Appendix S2 and parameters of Equations (1–5) in Appendix S1 with values for the species of interest. Adjusting available microclimates for thermoregulation may be necessary for species with different nesting (e.g.,

depth and shade) and thermoregulating behavior (e.g., diurnal or nocturnal, can or cannot climb).

The increasing availability of hourly climate data (e.g., ERA5; Hersbach et al., 2018) and microclimate models (e.g., NicheMapR; Kearney, 2022) also enables researchers to apply our methods to species with distributions outside North America. Our model can also be applied, with minor modifications, to species with more specific life histories, including oviparous species other than reptiles. Potential modifications include the assumptions about microclimates that the embryos and juveniles were exposed to and sensitive to. For example, eggs exposed to air (insects) and water (fish) may have a different thermal environment than eggs in the soil. The incubating behavior of birds may fundamentally alter the dependence of embryonic development on ambient temperature (eggs are incubated at the mother's body temperature instead). Juveniles of altricial birds may be more exposed to heat stress induced by climate warming because of a lack of behavioral thermoregulation (Rodríguez & Barba, 2016). The diapause phase in insect life history, which is characterized by arrested development and suspended development, should be modeled as a period with increased resistance to environmental extremes (Tougeron et al., 2020).

Modifications to the model could also include the assumptions about factors and thresholds that determine whether an hour in a year belongs to EO. For example, egg-laying events resulting in seriously biased offspring sex ratio should be excluded from EO for species with temperature-dependent sex determination (Mitchell et al., 2008, 2010). Besides the effects of temperature, the water loss of eggs and hatchlings may also affect survival, especially for species in arid areas (Albright et al., 2017; Tracy et al., 1978). Natural events, such as snow cover, predator activity, and pulses of food availability, may reduce juvenile activity time or the energy gained during the activity time (Kearney, 2020; Paterson & Blouin-Demers, 2018; Stephen et al., 2019). All the above factors can be captured with modern biophysical models and a range of energy budget models

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.