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Variable impacts on reproductive energetics may render oviparous squamates more vulnerable to climate warming than viviparous species

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Squamate reptiles exhibit two reproductive modes: oviparity and viviparity. Existing large-scale studies suggest that viviparous species are more vulnerable to climate warming based on viviparous species occupying relatively colder environments, which are predicted to decline in availability under climate warming. However, oviparous and viviparous squamates are geographically widespread and their distributions often overlap. Are oviparous or viviparous squamates more vulnerable to climate warming when they inhabit similar thermal environments? We used *Sceloporus* lizards in North America as a model system to predict the impact of climate warming on oviparous and viviparous species in sympatric zones. We used mechanistic models to quantify the changes in maternal energy balance (MEB) and offspring energy balance (OEB) under a climate warming scenario. We then projected the fitness impacts of future climate warming based on estimates of MEB and OEB. Under a climate warming scenario (RCP8.5), oviparous females are predicted to increase reproductive frequency more than viviparous females, which restricts time for postpartum energy accumulation before the end of the season and decreases MEB. Under climate warming, OEB of oviparous species increased more than viviparous species, but the increases were less geographically widespread. Interestingly, the developmental success and OEB of oviparous species are predicted to decline at some sites under climate warming, which is not predicted to happen for viviparous species. Our results highlight that oviparous species will respond more variably to climate warming than viviparous species. More specifically, oviparous species in hot areas with high temperature variation may be especially vulnerable under climate warming compared to sympatric viviparous species.

Keywords: climate change, energy balance, life-history model, mechanistic model, oviparity, viviparity

Introduction

Identifying organisms that are vulnerable to ongoing climate warming is a challenging but critical task for ecologists. As ectotherms, squamate species are highly dependent on environmental temperature and thus particularly sensitive to climate warming (Huey et al. 2012, Böhm et al. 2016). Previous studies have suggested species with oviparous (egg-laying) and viviparous (live-bearing) reproductive modes differ in vulnerability to climate warming due to differences in physiology and distributions (Sinervo et al. 2010, Wang et al. 2017, Jara et al. 2019). Contrasting oviparous versus viviparous life history addresses the mechanisms of responses to climate warming and can help inform future conservation and management decisions.

A species' vulnerability to climate warming depends on its environmental exposure, organismal sensitivity, resilience and capacity for adaptation (Williams et al. 2008, Huey et al. 2012). Exposure to climate warming varies geographically (Deutsch et al. 2008). Viviparous species may be more vulnerable to climate warming due to their being confined to relatively higher altitudes and adapted to colder environments (Sinervo et al. 2010, Jara et al. 2019). These studies support the 'cul-de-sac' hypothesis which predicts that the cold-adapted viviparous species will be trapped in shrinking cold habitats, while more oviparous species are predicted to move into habitats that have warmed from climate change (Pincheira-Donoso et al. 2013). However, viviparous species are not restricted to cold climates. For example, some viviparous *Sceloporus* species inhabit warm environments (Lambert and Wiens 2013). In general, oviparous and viviparous squamates are geographically widespread and their distributions often overlap (Blackburn 2006, Meiri et al. 2020).

For those sympatric oviparous and viviparous squamates, their vulnerability is likely determined by the sensitivity, resilience and adaptation of species to climate warming. Sympatric oviparous and viviparous species may have divergent thermal niches shaped by their morphological, behavioral and physiological traits, which can affect their sensitivity to climate warming (Kearney and Porter 2009, Huey et al. 2012). First, oviparous and viviparous species may use microhabitats (e.g. terrestrial versus arboreal) that differ in thermal opportunity (Meiri 2018). Second, viviparous species may select lower body temperatures than oviparous ones (Yuan et al. 2016). Third, a global comparative study found that viviparous squamates have a lower heat tolerance than do oviparous species (Clusella-Trullas et al. 2011). Accordingly, viviparous species is hypothesized to be less resilient to climate change than their oviparous congeners because they have evolved relative low body temperature and heat tolerance as a result of invasion to cold climate regions at high latitudes and elevations (Sinervo et al. 2010, Wang et al. 2017). However, many studies have argued the exact opposite – that tropical species (most are oviparous) are more vulnerable to climate warming because they operate near their thermal maxima already, whereas subtropical and temperate species (including a higher proportion of viviparous species) have a greater thermal buffer (Deutsch et al. 2008, Tewksbury et al. 2008). Surprisingly, we still know little about how the most fundamental difference – reproductive mode itself – affects the vulnerability of oviparous and viviparous species to climate warming.

Differences in parity mode correspond to differences in reproductive life-history (Shine and Bull 1979). Most oviparous females carry the embryos for one-third of their development (Andrews and Mathies 2000), rather than carrying them until birth (viviparity). Therefore, oviparous females have less time than viviparous females to actively select optimal temperatures (that differ from nest temperatures), which may lead to a divergence in the rate and success of embryonic development (Shine 2004, Ma et al. 2018a). Oviparous species in warm areas often have multiple clutches per year, whereas viviparous females generally produce a single litter annually with very few exceptions (Shine 1995, Meiri et al. 2012, Mesquita et al. 2016a). Given that brood size (number of hatchlings/neonates per brood) and hatchling/neonate size in reptiles does not differ between parity modes (Meiri et al. 2020), the greater reproductive frequency may result in a larger reproductive investment for oviparous species compared to viviparous species. This can also result in a larger number of offspring per year for oviparous species, contingent on developmental success and juvenile growth (i.e. larger juveniles have higher winter survival rates; Civantos et al. 1999, Miles 2004, Iraeta et al. 2008). Although viviparous females devote less energy to producing multiple broods, they spend more energy on prolonged gestation because of the considerable metabolic cost of carrying large embryos (Beuchat and Vleck 1990, Munns and Daniels 2007). In addition, viviparous females may suffer a longer period of decreased food consumption induced by gestation (Ortiz et al. 2001, Weiss 2001). However, whether pregnant females reduce their food consumption varies between species (Shine 1980). These life-history differences between oviparous and viviparous species may affect the energetic consequences of climate warming, with implications for survival and reproductive potential (Iraeta et al. 2008).

To compare oviparous and viviparous species' vulnerability under climate warming from an energetic perspective, we need an integrative model incorporating reproductive timing and energy balance of the mother, as well as developmental processes (rate and success) and energy balance of each brood of offspring. In this study, we used *Sceloporus* lizards as a model system to predict the impact of climate warming on widespread oviparous and viviparous squamates in sympatric zones. The *Sceloporus* genus includes species of both parity modes (Supporting information), and the physiology and life-history traits of these species are available. We incorporated a biophysical model that translated microclimates into energy budgets, with a life-history model that predicted reproductive phenology. We then estimated maternal energy balance (MEB) by subtracting yearly metabolic consumption and reproductive investment of females from their digested energy. We also estimated the offspring energy balance (OEB; total energy of surviving hatchlings/neonates) by summing the

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combined energy content of all broods that survived to the end of the year. Our analyses were conducted using recent and future estimates of microclimates from Levy et al. (2016a). We then calculated the changes in MEB and OEB to assess whether oviparous and viviparous species will experience a fitness decline or increase under a climate warming scenario. In addition, we explore geographic variation in the impacts of climate warming, as well as their relationship to local climates.

Material and methods

Identifying the sympatric zones

We downloaded range maps for 84 *Sceloporus* species from IUCN Red List (see Supporting information for species-specific reference) and subset them to grid cells within the reported elevational range (including a 100 m buffer; IUCN 2020). We extracted parity mode from a squamate dataset (Pyron and Burbrink 2014). We restricted our analyses to the 'sympatric zones' where oviparous and viviparous *Sceloporus* species coexist. The sympatric zones include 28 oviparous and 23 viviparous *Sceloporus* species (Supporting information). We assumed static sympatric zones through our analysis given the short dispersal distances of *Sceloporus* lizards (< 150 m per year; Massot et al. 2003, Middendorf et al. 2005).

Microclimate data and biophysical model

We extracted both the recent (1980–2000) and future (2080–2100; under the 'business-as-usual' scenario: RCP8.5 (Schwalm et al. 2020)) hourly microclimate data from a dynamically downscaled dataset (see Supporting information for maps for the mean air temperature and the interquartile range of air temperature), which covered North America at a 36×36 km resolution (Levy et al. 2016a). Microclimate data for these time periods capture the effect of climate change from the near-past to the future. We then used a widely employed biophysical model (Buckley 2008, Levy et al. 2016b, Ma et al. 2018a) to translate microclimates into body temperatures, activity and energy budgets for both adults and juveniles (see Supporting information for detailed description). The aim of this study is to explore how life-history differences between sympatric oviparous and viviparous species may affect their energetic shifts under climate warming. We used one set of biophysical and physiological parameters for both oviparous and viviparous species to isolate differences associated with parity mode (Supporting information). For parameters that are widely available for the species considered in this study (Supporting information), we used the values for *S. undulatus*, because these values are representative of other species (Supporting information) and *S. undulatus* has been widely used as a model species in studies of thermal and biophysical ecology (Buckley 2008, Levy et al. 2016b, Ma et al. 2018a). We also used phylogenetic generalized linear models (using 'caper' package – Orme et al. 2018; phylogenetic tree – Tonini et al. 2016) to compare model parameters (Supporting information) between oviparous and viviparous species considered in this study and found no significant differences (all p > 0.05; Supporting information). To explore how climate-change impacts vary among local climates, we calculated mean values and interquartile ranges of air temperatures across grid cells within the sympatric zones.

Life history model

As brood size and offspring body size do not differ between parity modes either in all reptiles (Meiri et al. 2020) or in *Sceloporus* lizards considered in this study, we assumed that oviparous and viviparous mothers invest the same amount of energy into each brood, which is equal to the energy content of a clutch of eggs (Supporting information). However, the total energy cost of producing a brood is larger in viviparous species because of a longer period of feeding reduction and the metabolic cost of prolonged gestation (Supporting information). Because females must rebuild their energy reserves following reproduction (Doughty and Shine 1998, Sperry and Weatherhead 2009) and squamate species keep growing after maturation although the growth rate is quite reduced (Shine and Charnov 1992), we assumed that 1) a postpartum female has to recover to the energy balance she was in when she initialized her first brood to start producing a new brood, and that 2) the maternal energy cost for producing all broods can never reach or surpass the yearly energy gain. Oviparous species are characterized by spring reproduction (Méndez de la Cruz and Manríquez Morán 2014), while most viviparous species breed in the fall followed by a period of embryonic diapause (most parturitions occurs after April of the second year; see Supporting information for breeding phenology of viviparous *Sceloporus* species). Therefore, we initiate possible embryonic development of the first brood for oviparous and viviparous species on 1st March and 1st January respectively. We assume oviparous females can potentially breed until the end of the year if the thermal environment allows (Méndez de la Cruz and Manríquez Morán 2014), while viviparous females must give birth to their last brood of neonates before 1st September, to allow time for ovulation and fertilization before overwintering (Supporting information). We simulated the reproductive phenology and developmental success of each brood of offspring in a year by incorporating maternal energy budgets and equations for developmental rate and success in a life-history model (see Supporting information for detailed description for the life history model).

Maternal energy balance (MEB)

We estimated maternal energy balance (MEB) by subtracting the yearly maternal metabolic consumption and reproductive investment (all broods) from their digested energy using the following equation:

$$MEB = E_m - \sum_{i=1}^{n} E_e \tag{1}$$

where n is the reproductive frequency (number of broods) through a year, E_m is the yearly energy gain (digestion minus metabolic consumption) and E_e is the energy content of a clutch of fresh eggs (Supporting information). It is worth noting that the calculation of E_m incorporates reduced feeding during pregnancy (for both oviparity and viviparity) and the metabolic cost of prolonged gestation (viviparity) (Supporting information).

Hatchling/neonate energy balance and offspring energy balance (OEB)

We calculated the energy gain of individual hatchlings/neonates from hatching/birth to the end of the calendar year by summing up hourly energy budgets (digestion minus metabolic consumption). Assuming all hatchlings/neonates contained the same amount of energy at hatching/birth (Supporting information), we calculated total energy content of a brood of hatchlings/neonates at the end of the calendar year by adding initial energy content of a hatchling/neonate to the hatchling/neonate energy balance, and then multiplying the result with brood size (Supporting information) and developmental success. When the sum of initial energy content and energy balance is negative, the brood of hatchlings/neonates will starve to death. As early and later broods (brood sequence in a given year) of hatchlings/neonates experience different thermal environment and have different amount of time for growth, their energy balance was calculated separately. Finally, we calculated the offspring energy balance (OEB) by summing up the energy content from all surviving (through embryonic development and hatchling/neonate growth) broods at the end of year using the following equation:

$$\text{OEB} = \sum_{i=1}^{n} \begin{cases} \text{bro\_size} \times \text{success} \times (E_{j0} + \text{NEG}_j)\left(E_{j0} > -\text{NEG}_j\right) \\ 0\left(E_{j0} \le -\text{NEG}_j\right) \end{cases} \quad (2)$$

where n is the reproductive frequency for a year, 'bro_size' is the brood size, success is developmental success, E_{j0} is the initial energy content of a hatchling/neonate and NEG_j is the energy balance of individual hatchlings/neonates from hatching/birth to the end of the calendar year.

Data analysis

We averaged all results across 1980–2000 and 2080–2100 representing the recent climates and a climate warming scenario ('business-as-usual' scenario: RCP8.5), respectively, and subtracted the average results for 1980–2000 from the average results for 2080–2100 to estimate changes under a climate warming scenario. All models and analyses were generated with R ver. 4.0.3 (<www.r-project.org>).

Model validation

To test the accuracy of our model prediction, we compared the reproductive frequency (1980–2000) predicted by our model with records in the literature (Supporting

information). We obtained the values for reproductive frequency of *Sceloporus* species (populations) from a global dataset of lizard life-history (Mesquita et al. 2016a, b) and individual papers (Supporting information). Only records with accurate description of location and reproductive frequency were used (e.g. not descriptions like 'more than one clutch'). We spatially matched literature records to a prediction within a 36 km grid cell. Using a Pearson's correlation test, we found a strong correlation between the reproductive frequency predicted by our model and the literature records for oviparous species [r(12) = 0.781, p = 0.0009], although our model predictions are on average 0.7 brood less than the literature records (Supporting information). Based on limited number of references (Supporting information), we did not find literature records for viviparous *Sceloporus* lizards producing more than one brood in our study area, which was in accordance with our model predictions (Supporting information).

Sensitivity analysis

Squamate species exhibit interspecific variation in food intake reduction during pregnancy (for both oviparity and viviparity; Shine 1980) and the metabolic cost of prolonged gestation (only for viviparity; Beuchat and Vleck 1990, Munns and Daniels 2007), we therefore conducted sensitivity analyses by scaling up and down these two parameters by 50% and rerunning the models (Supporting information). *Sceloporus* lizards are known to show both interspecific and intraspecific variation in solar absorptance (Hutchinson and Larimer 1960, González-Morales et al. 2020) and field body temperature (Andrews 1998), we therefore conducted sensitivity analyses for solar absorptance and selected body temperature accordingly based on known variations. We also adjust the voluntary temperature range limits (the minimum and maximum body temperatures that allow for feeding and fast digestion) isometrically according to the selected body temperature we use in the sensitivity analyses (Supporting information). These values reflect extreme solar absorptances and body temperatures of *Sceloporus* lizards that are recorded in literature. Oviparous and viviparous species may use different microhabitats (e.g. terrestrial, arboreal, saxicolous), which may differ in available thermal opportunity. We therefore did a sensitivity analysis using a narrower and wider (by 2°C) voluntary temperature range for activity (Supporting information). We found that the overall patterns (comparisons between oviparous and viviparous species) of our predictions are not sensitive to the variation of these parameters.

Results

Changes in reproductive frequency and maternal energy balance (MEB)

Under a climate warming scenario, our model predicts that both oviparous and viviparous species will reproduce more frequently, while oviparous species will exhibit a larger

increase (1.014 ± 0.374 broods) in reproductive frequency than viviparous species (0.009 ± 0.065 broods) (Fig. 1). For oviparous species, the increases in reproductive frequency are largest (up to two more broods) at sites with moderate mean air temperatures (~20°C, for climate in 1980–2000; Fig. 1c), which are within or close to the transvolcanic region of southern Mexico. For viviparous species, the predicted increase of reproductive frequency is between zero to one brood (non-integer increase at some sites is because we are averaging simulation results for multiple years [1980–2000 and 2080–2100]).

Correspondingly, oviparous species exhibited decreased MEB (−10.71 ± 8.02 kJ) at most sites (83.9% sites), while viviparous species exhibited increased MEB (20.49 ± 11.21 kJ) at most sites (99.1% sites) (Fig. 2). For oviparous species, the decreases of MEB are larger for sites with large increases in reproductive frequency (Fig. 2c). For viviparous species, the greatest increases of MEB are at sites in central and southern Mexico (Fig. 2b). There are no sites for which we predict negative MEB either in recent climates or under a climate warming scenario.

Changes on average developmental success, hatchling/neonate energy balance and offspring energy balance (OEB)

For both parity modes, our analyses show that sites with no developmental success in recent climates will become suitable for development with up to 50% success rate under a climate warming future (Fig. 3). These 50% increases in developmental success will occur in more sites for oviparous species (20.0% sites) than for viviparous species (3.5% sites). Our model predicts a decrease of average developmental success (−17.05 ± 9.19 % success rate) at many sites (23.6% sites) with high mean air temperatures (22.73 ± 1.50°C) for oviparous species, but at no sites for viviparous species.

In general, hatchling/neonate energy balance decreases with hatching/birth date, and correspondingly, with brood sequence (Fig. 4). Under a climate warming scenario, as the activity season gets longer and winters shorter, hatchlings/neonates from existing broods will have more time to assimilate energy before winter and therefore have greater hatchling/neonate energy balances. Another consequence of prolonged activity season is that females will have more time for reproduction and may produce additional broods, which contribute relatively smaller amounts of hatchling/neonate energy balance to total OEB.

Our modeling predicts that, under a climate warming scenario, the OEB of oviparous species will increase at 92.2% sites with an average magnitude of 50.47 ± 27.15 kJ, while the OEB of viviparous species will increase at all sites with a smaller average magnitude (19.58 ± 6.78 kJ) (Fig. 5). Increases in OEB are larger at warmer sites for both parity modes (Fig. 5c, d), while increases are canceled out at sites with decreased average developmental success for oviparous species. More interestingly, because of large decreases in average developmental success under the climate warming scenario, the OEB of oviparous species is predicted to decline at 3.8% sites with an average magnitude of −18.64 ± 19.45 kJ.

Integrating the changes in MEB and OEB

Under a climate warming scenario, we project oviparous species will experience decreases in both MEB and OEB in 2.2% of sites, a scenario which is not predicted to occur for viviparous species (Fig. 6), especially in hot areas with large variations in temperature (mean air temperatures > 21°C and interquartile range of air temperature > 11°C) (Fig. 6c). Increases in MEB but decreases in OEB will occur exclusively for oviparous species (1.5% sites) in hot areas with pronounced temperature variation (mean air temperatures > 23°C and interquartile range of air temperature > 12°C).

Oviparous species are predicted to have fewer sites (14.5% sites) with increases in both MEB and OEB than viviparous species (99.1% sites). For oviparous species, these sites are concentrated in either cold areas with small temperature variations or warm areas with large temperature variations. For viviparous species, such sites are widely spread. Declining MEB but increasing OEB is the most common scenario for oviparous (81.7% sites), which rarely occurs for viviparous species (0.9% sites).

Discussion

The reproductive life-history traits of the two parity modes have been assumed to directly translate to when and how gravid females and developing embryos are affected by environmental changes (Andrews and Mathies 2000, Shine 2004). In this study, we used biophysical and life-history modeling to link recent and future microclimates to energy budgets and reproductive phenology. Our results highlight that vulnerability to climate warming is variable for oviparous species and depends on the environmental context.

Changes in reproductive frequency and maternal energy balance (MEB) under climate warming

Our models predict that oviparous species will have a larger increase in reproductive frequency than viviparous species under a climate warming scenario (Fig. 1), especially in southern parts of the sympatric zones. These areas of Mexico have a moderate climate conditions with mean air temperatures around 20°C. Empirical studies have demonstrated that experimental warming can increase reproductive frequency in oviparous squamates for 2–3 clutches (Du et al. 2005b, Lu et al. 2018), which also appear in some sites according to our prediction. However, reproductive frequency in viviparous species has not been shown to increase under experimental warming (Ma et al. 2018b), although some viviparous species (not including *Sceloporus* lizards) in warmer regions tend to have a larger probability of producing two litters (or more in very few cases) rather than one per year (Mesquita et al. 2016a, Schwarzkopf et al. 2016).
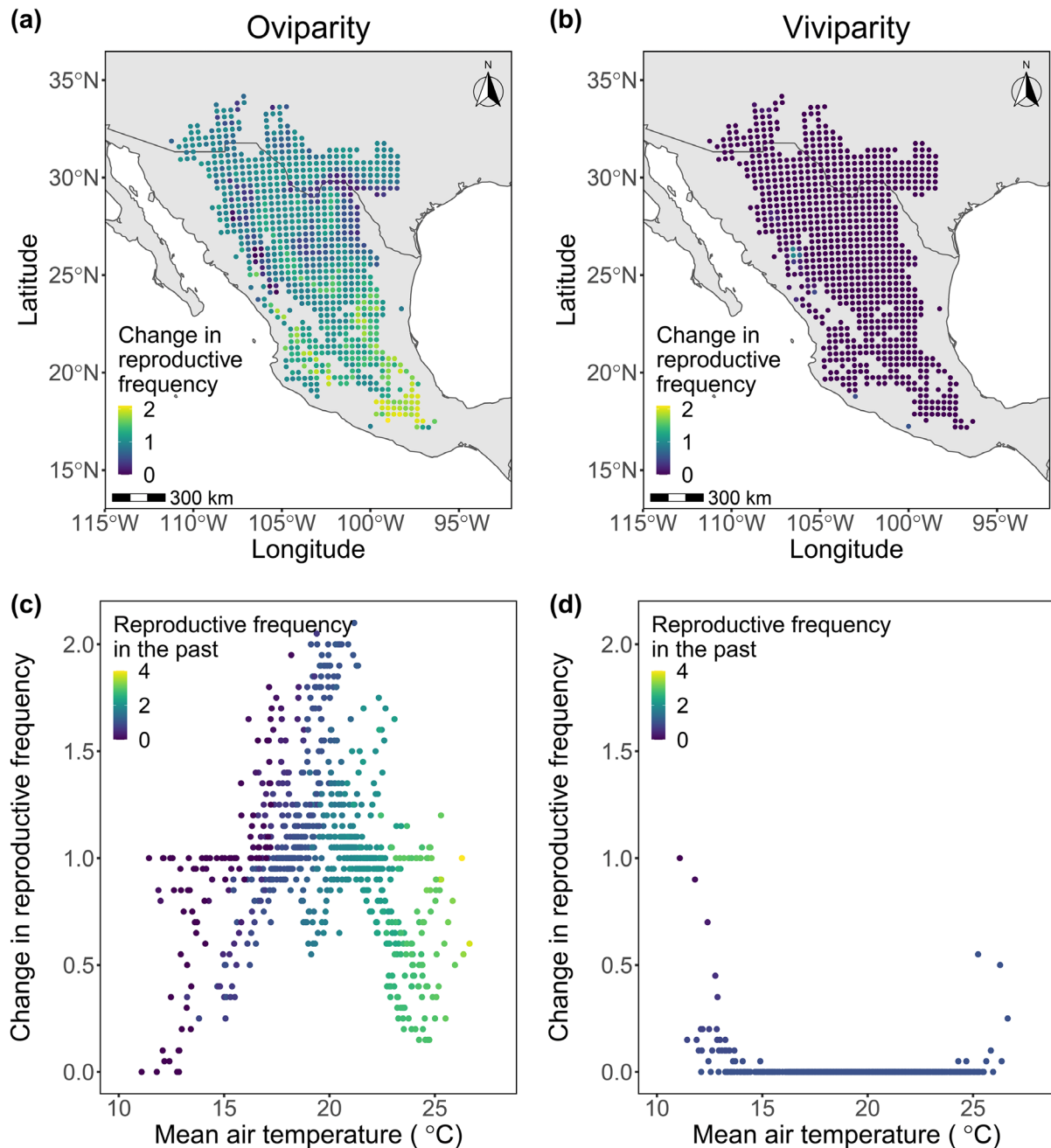
Figure 1. Changes in reproductive frequency for oviparous and viviparous species in sympatric zones under climate warming. (a), (b) Heatmaps showing the changes (2080–2100 minus 1980–2000) in the reproductive frequency (i.e. number of broods produced in a year) for oviparous (a) and viviparous (b) *Sceloporus* species at the locations (points) within their sympatric zones under climate warming. (c), (d) X–Y plots corresponding to (a) and (b), respectively, showing the relationship between the changes in reproductive frequency and mean air temperatures (1980–2000). The colors of the points in (c) and (d) represent the corresponding values of reproductive frequency in recent climates (1980–2000).

Under climate change, the reproductive frequency of viviparous species will increase at few sites (4.49% sites) only, where gravid females were estimated to not reproduce every year in recent climates (Fig. 1). This reflects a more constrained reproductive frequency in viviparous species, which is a consequence of the reproductive mode including thermoregulation strategies (maternal control of developmental temperature) and time opportunities (longer gestation time and recovering time; Supporting information). Moreover, the flexibility of reproductive frequency in viviparous species may be further constrained if their reproduction is initiated at a relatively higher body condition compared to oviparous species (see Naulleau and Bonnet 1996 for an example in viviparous snakes).
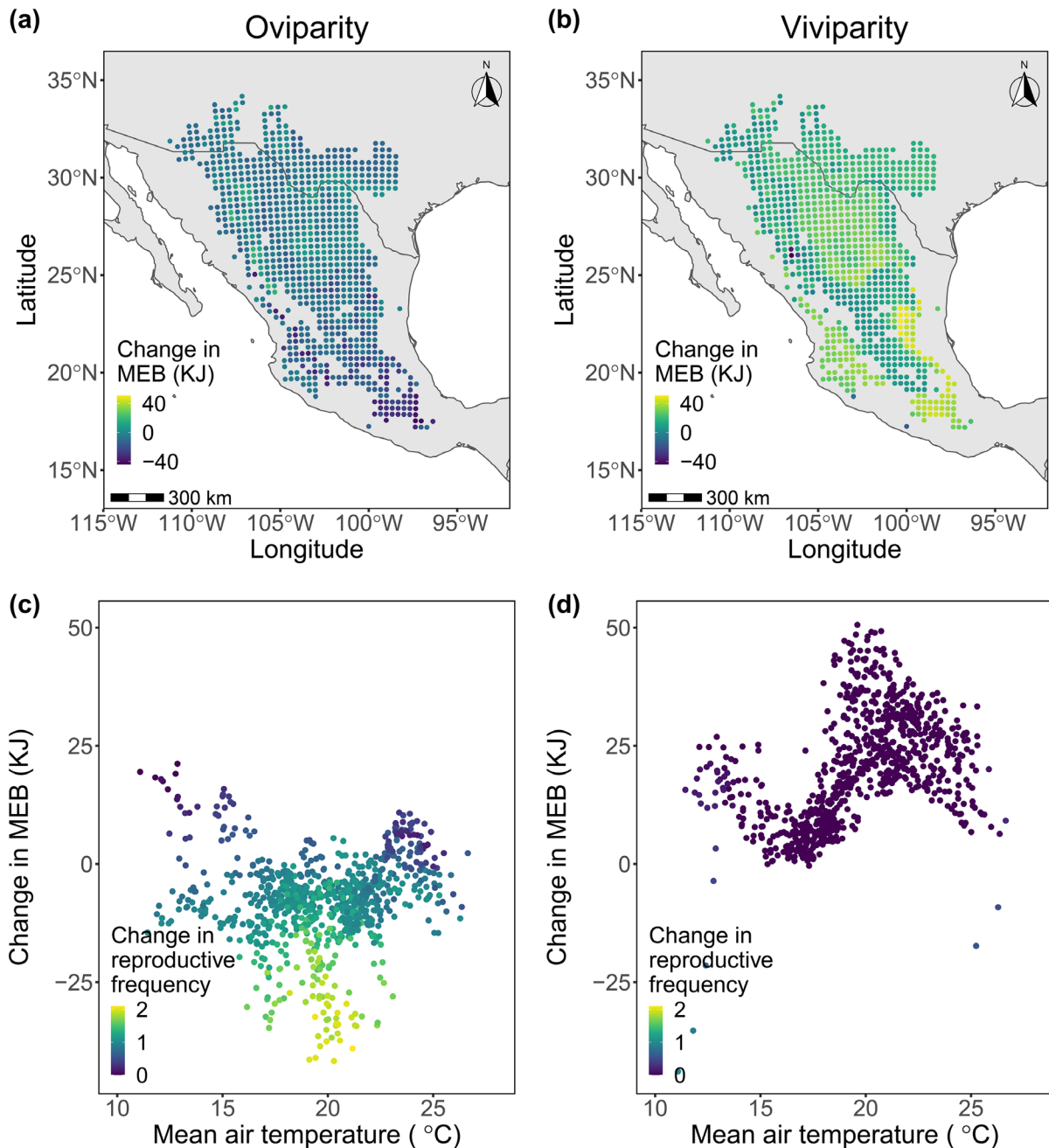
Figure 2. Changes in the maternal energy balance (MEB) for oviparous and viviparous species in sympatric zones under climate warming. (a), (b) Heatmaps showing the changes (2080–2100 minus 1980–2000) in maternal energy balance throughout a year (MEB = digestion minus metabolic consumption minus reproductive investment) for oviparous (a) and viviparous (b) *Sceloporus* species at the locations (points) within their sympatric zones under climate warming. (c), (d) X–Y plots corresponding to (a) and (b), respectively, showing the relationship between the changes in MEB and mean air temperatures (1980–2000). The colors of the points in (c) and (d) represent the changes in reproductive frequency under climate warming.

Increases in reproductive frequency result in reductions in MEB, which over-canceled the benefits brought by longer thermal opportunity (Supporting information) because more broods result in less time for postpartum energy accumulation (after the last brood) before the end of the season. This also explains why our model predicts the greatest increases of MEB for viviparous species and the greatest decreases of

MEB for oviparous species in the same areas (southern parts of the sympatric zones). A basic assumption of our models is that reproductive females allocate all of their additional energy gain (digestion minus metabolic consumption) into producing more broods (with fixed brood size, egg size and offspring size), contingent on additional broods of embryos being able to complete their development. The allocation
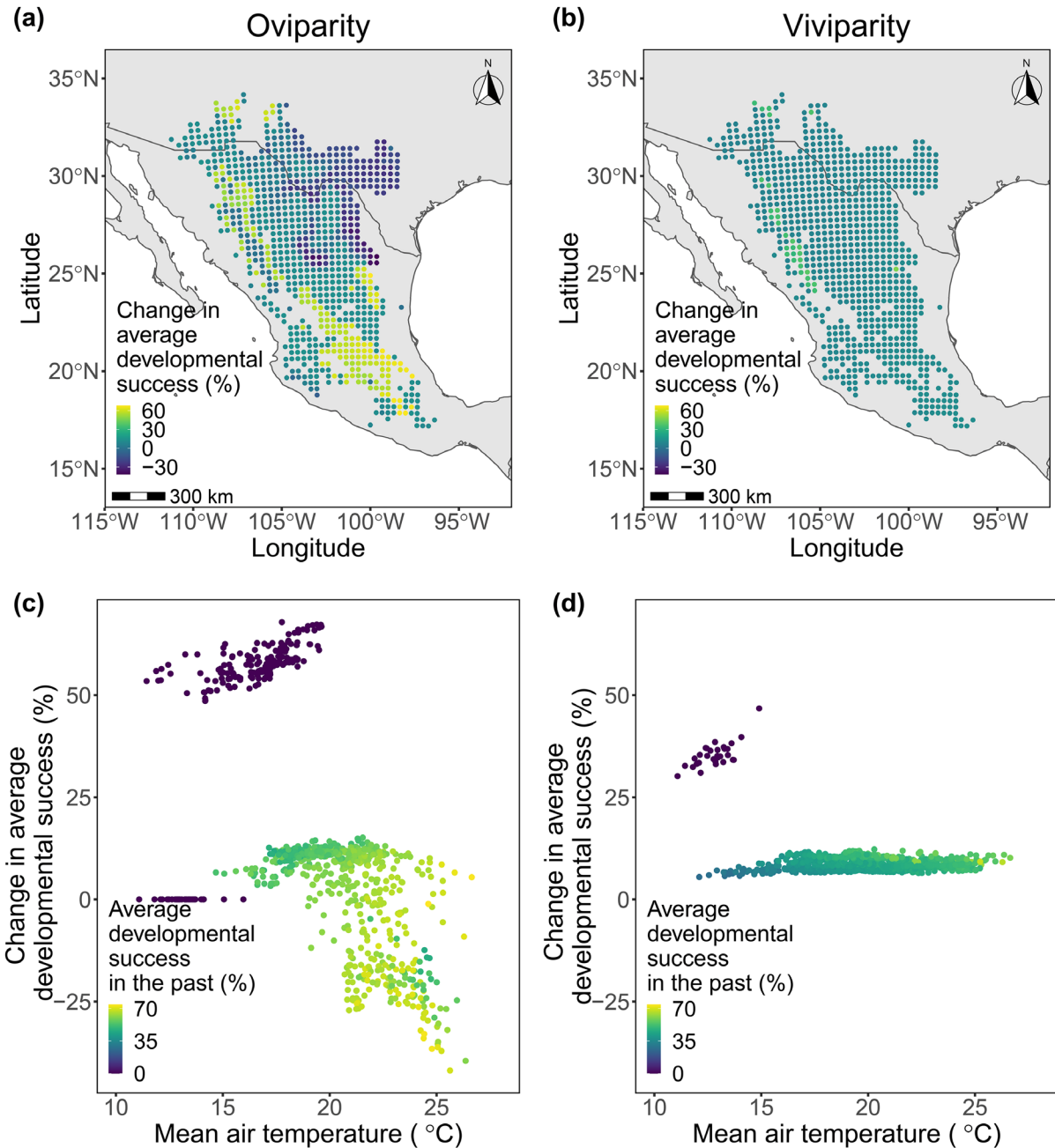
Figure 3. Changes on average developmental success for oviparous and viviparous species in sympatric zones under climate warming. (a), (b) Heatmaps showing the changes (2080–2100 minus 1980–2000) on average developmental success (average developmental success of broods in a year) for oviparous (a) and viviparous (b) *Sceloporus* species at the locations (points) within their sympatric zones under climate warming. (c), (d) corresponding to (a) and (b), respectively, showing the relationship between the changes on average developmental success and mean air temperatures (1980–2000). The colors of the points in (c) and (d) represent the corresponding average developmental success in recent climates (1980–2000).

of additional energy gain into reproduction is supported by empirical evidence showing that energy stores can affect reproductive investment but not growth rates of reproductive females (Smyth 1974, Dial and Fitzpatrick 1981, Doughty and Shine 1998). Egg sizes (or offspring sizes for viviparity) and brood sizes were also found to depend on available maternal energy reserves in some squamate species (Doughty and Shine 1998, Kubička and Kratochvíl

2009, but see Du 2006), and to vary seasonally or annually in *Sceloporus* lizards (DeMarco 1989, Smith et al. 1995). Nevertheless, the additional energy available for allocation to existing broods is constrained by the physical limits of the maternal body (Sinervo and Licht 1991, Du et al. 2005a), and the short window of time for energy allocation (vitellogenesis) (Andrews and Mathies 2000). Females may also incur trade-offs and store their additional energy gain for
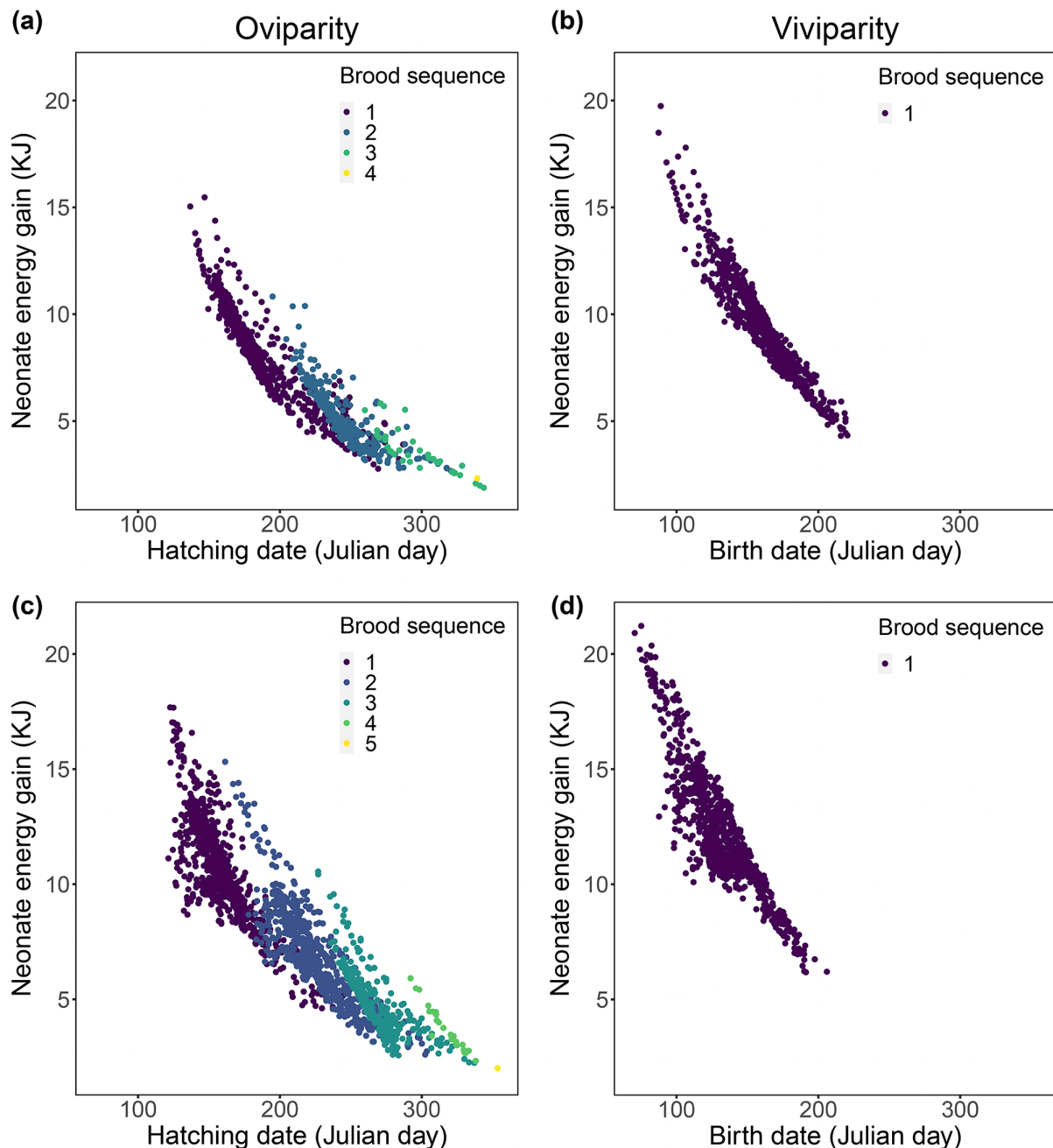
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Figure 4. Hatchling/neonate energy balance from broods of oviparous and viviparous species in sympatric zones under recent and future climate scenarios. (a), (c) Hatchling energy balance (accumulated energy from the hour of hatching to the end of the year) of individual oviparous offspring from each clutch. (b), (d) Neonate energy balance (accumulated energy from the hour of birth to the end of the year) of individual viviparous offspring from each litter. The values are averaged across years in 1980–2000 (a), (b) and 2080–2100 (c), (d) respectively. The colors of the points represent the corresponding brood sequence (i.e. first, second, third brood etc.).

future reproduction (Cox et al. 2010), which may cancel out the advantage or disadvantage induced by a large increase in reproductive frequency. By considering and synthesizing all possible shifts in reproductive output (e.g. reproductive frequency, brood size, egg size, offspring size) and corresponding constraints, future studies can further remove assumptions from our models and make predictions for specific species and populations.

Changes in average developmental success, hatchling/neonate energy balance and offspring energy balance (OEB) under climate warming

Large increases (around 50%) in developmental success are predicted to occur in more sites for oviparous species than for viviparous species (Fig. 3). In a warmer climate, oviparous species are predicted to shift to annual reproduction at more sites
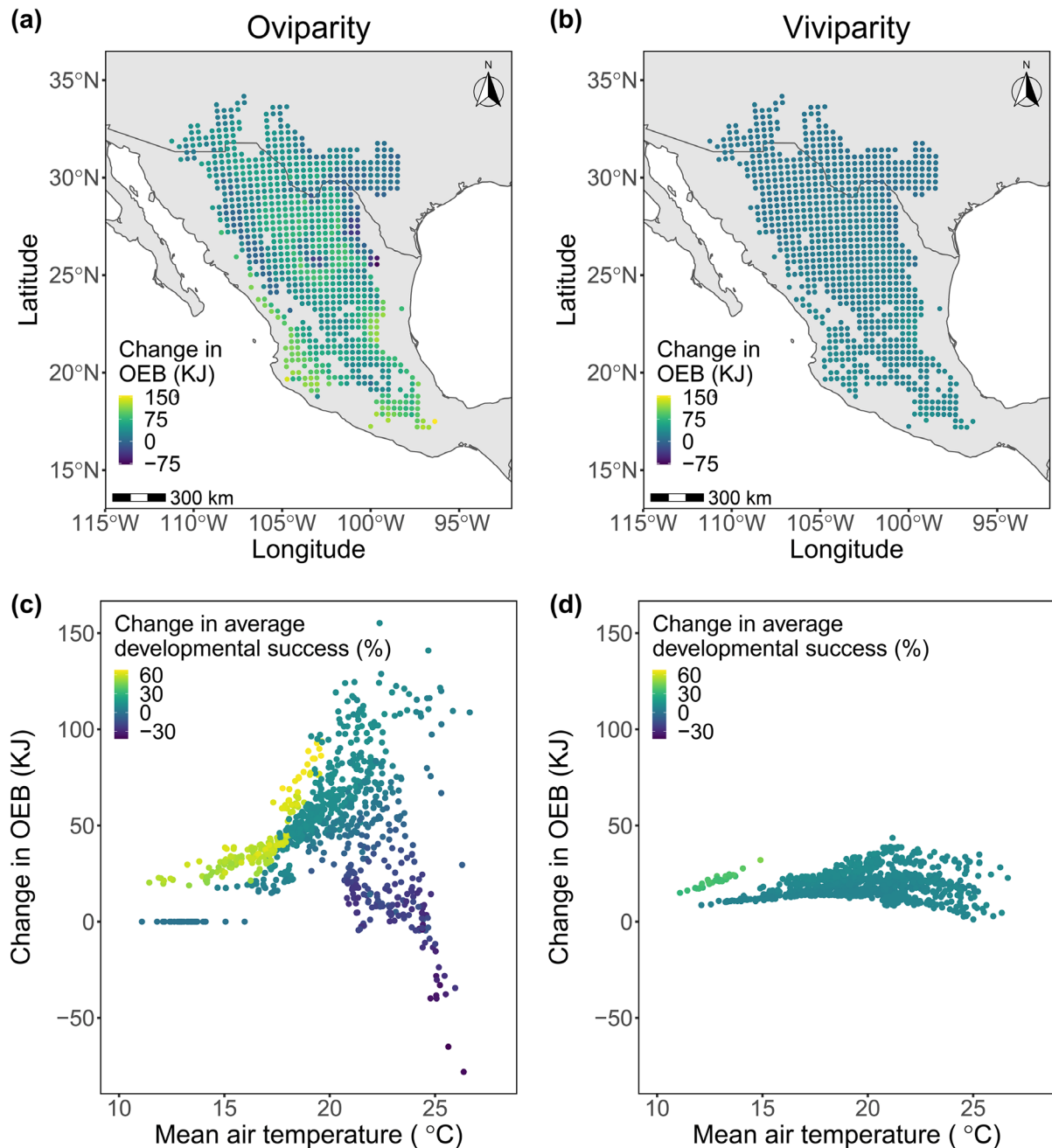
Figure 5. Changes in offspring energy balance (OEB) for oviparous and viviparous species in sympatric zones under climate warming. (a), (b) Heatmaps showing the changes (2080–2100 minus 1980–2000) in mean annual OEB for oviparous (a) and viviparous (b) *Sceloporus* species at the locations (points) within their sympatric zones under climate warming. (c), (d) Corresponding to (a) and (b), respectively, showing the relationship between the changes in mean annual OEB and mean air temperatures (1980–2000). The colors of the points in (c) and (d) represent the changes on average developmental success under climate warming.

relative to viviparous species (Fig. 1c, d), which caused a relatively large increase in average developmental success at these sites (Fig. 3c, d). For those sites with non-zero developmental success in recent climates, a decline on average developmental success will occur under climate warming for oviparous species (most of the pattern is driven by the north-eastern part of the sympatric zones), but not for viviparous species. This

highlights the importance of viviparous mothers being able to protect their developing embryos to a degree, by selecting thermal microhabitats to ensure their body temperature is within a range of values favoring embryonic development (Tinkle and Gibbons 1977, Shine and Bull 1979, Ma et al. 2018a).

Compared with viviparous species, oviparous species are predicted to have more broods and an increase in brood
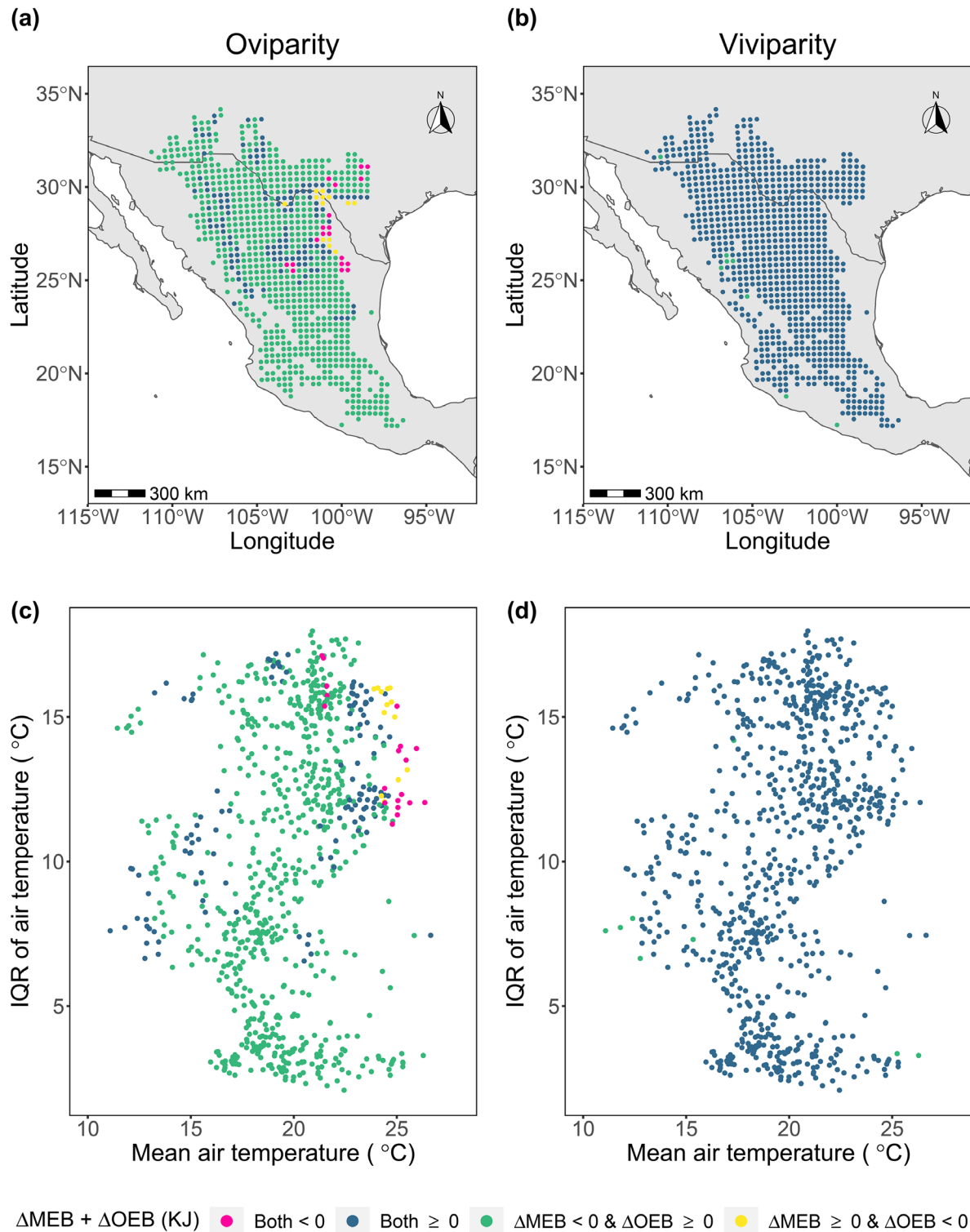
Figure 6. Impacts of climate warming on maternal energy balance (MEB) and offspring energy balance (OEB) for oviparous and viviparous species in sympatric zones. (a), (b) Heatmaps showing four scenarios in which MEB and OEB are impacted by climate warming (2080–2100 minus 1980–2000): 'Both < 0' means both MEB and OEB decline; 'Both ≥ 0' means both MEB and OEB increase; 'ΔMEB < 0 and ΔOEB ≥ 0' means MEB declines but OEB increases; 'ΔMEB ≥ 0 and ΔOEB < 0' means MEB increases but OEB declines. (c), (d) Corresponding to (a) and (b), respectively, showing the mean air temperature (1980–2000) and interquartile range (IQR) of annual air temperature (1980–2000) at sites under the four scenarios.

number at more sites with warming (Fig. 1, 4). Because of the increase in thermal opportunity (Supporting information), broods of hatchlings will appear earlier and thus contribute more hatchling energy to the OEB with warming. Also, additional broods will appear later in the extended reproductive season. Both empirical and modeling studies have also suggested that squamate species may benefit from climate warming due to increased temperatures allowing for longer activity times (Buckley 2008, Moreno-Rueda et al. 2009, Clarke and Zani 2012, Levy et al. 2016b). However, in regions where species live close to their physiological limits, further warming may reduce the thermal quality of the habitat and induce extirpations (Huey et al. 2009, Sinervo et al. 2010). In addition, our models focus on reproductively matured adults and their offspring, but climate warming may also reduce the age to attain reproductive maturity, which could contribute to population growth (Buckley 2008). However, such prolonged activity may result in a 'live fast and die young' scenario, where early maturation involves a trade-off with future survival (Bestion et al. 2015).

Our modeling predicts a larger increase of OEB for oviparous species, via increased reproductive frequency, than viviparous species at many sites (Fig. 5). However, at many other sites, the OEB of oviparous species is predicted to decline due to reduced developmental success (Fig. 5c). These contradicting results reveal the paradox of opportunity versus risk for oviparous mothers to produce more broods under climate warming. Divergent responses to identical environmental change at different life-history stages highlight the importance of an energetic perspective (Kingsolver et al. 2011). It is noteworthy that, our model predicted zero developmental success in recent climates at some sites because of zero reproductive frequency. Our models generate conservative estimates of reproductive frequency compared with empirical data, which is possibly because we assumed that a postpartum female has to recover to a certain energy balance to start producing a new brood. In addition, not considering local adaptation may also increase the differences between our predictions and empirical data.

We note that our modeling did not consider the death of growing offspring caused by factors other than the depletion of energy reserves (e.g. heat stress and food availability). We made that decision based on the relatively high survival rates in juvenile reptiles (close to those of conspecific adults) (Pike et al. 2008), and also the challenge of quantitatively linking stress to survival rates. Including offspring death in the model may lower (or even cancel out) the magnitude of the predicted increases in OEB under climate warming, and therefore, reduce the advantage for oviparous species at some sites. We included hatchling/neonate energy balance accumulated by offspring from all broods in the calculation of OEB. However, offspring that appear late in the season may not have accumulated enough energy to survive over winter (Civantos et al. 1999, Iraeta et al. 2008). Future modeling could potentially be improved by setting a 'hatchling/neonate energy balance threshold' based on demographic studies (Tinkle and Ballinger 1972), and excluding broods with

hatchling/neonate energy balance less than this threshold in the calculation of OEB (assuming juveniles from these broods would die during hibernation). Excluding late broods from the model may also cancel out the predicted increase in OEB under climate warming, and reduce the potential advantage or disadvantage (depending on sites) for oviparous species over viviparous congeners.

Overall vulnerability under climate warming

Intergenerational trade-offs (Doughty and Shine 1997, Bleu et al. 2013) and variation in the relative importance of maternal and offspring energy reserves based on factors including lifespan and predation (Dean 1981, Candolin 1998, Rivalan et al. 2005) necessitate a synthetic consideration of MEB and OEB to estimate the overall cliamte change vulnerability of sympatric oviparous and viviparous species. One can only conclude with certainty that species will experience a fitness decline or increase under warming when both MEB and OEB decline or increase, respectively.

Our modeling only predicts sites experiencing declines in both MEB and OEB for oviparous species (Fig. 6). These sites are concentrated in the northeastern parts of the sympatric zones, which are warm areas with large temperature variation. This suggests that oviparous species have a higher probability of experiencing fitness declines under climate warming than do viviparous species in sympatric zones. Oviparous species are predicted to have many fewer sites with both increased MEB and OEB than viviparous species (Fig. 6), which suggests a smaller probability of experiencing fitness increases than would be the case for viviparous species in sympatric zones. Interestingly, these sites are concentrated in either cold areas with small temperature variations or warm areas with large temperature variations for oviparous species, but are widespread for viviparous species.

Caveats and future directions

We did not account for potential differences in microhabitat use (e.g. terrestrial and arboreal) between species with the two parity modes due to a lack of appropriate microclimate datasets. However, modifying the voluntary temperature range in our sensitivity analysis indicates that our results are not sensitive to the available thermal opportunity in the habitats (Supporting information). Although *Sceloporus* lizards have short dispersal distances (Massot et al. 2003, Middendorf et al. 2005), they may still shift upslope under climate change (Sinervo et al. 2010), which will somewhat change the sympatric zones. Future studies aiming at making precise distribution predictions for sympatric oviparous and viviparous species may consider applying the model to dynamic sympatric zones and using a dispersal model (Engler et al. 2012) to predict realistic range shifts. Our modeling used one set of biophysical and physiological parameters for both oviparous and viviparous species in order to focus on responses to climate warming directly induced by their divergent reproductive life-histories. In the future, incorporating species-specific

and population-specific traits into the model would allow us to more precisely predict the response of oviparous and viviparous species to climate warming in more specific cases. It is noteworthy that we did not consider potential seasonal variation in food and water availability. For example, the rainy season is bimodal in the western part of the sympatric zones and then becomes summer dominated in the more eastern parts. Reduction of resources may limit maternal energy accumulation and reproduction in both oviparous and viviparous species. It would be interesting to explore whether sympatric oviparous and viviparous species would respond to the variation of food and water availability differently in future research. For example, the egg-laying event of oviparous species may be triggered by both thermal and hydric conditions (Warner and Andrews 2002).

Conclusions

Our synthetic consideration of changes in MEB and OEB highlights the variable climate warming vulnerability of oviparous species in sympatric zones. Oviparous species will increase their reproductive frequency more than viviparous species with warming. However, concurrent decreases in developmental success at many sites, especially in hot areas with high temperature variations, will result in declines in both MEB and OEB.

Preprint

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EDI statement

We declare that the conduct of our study considers equity, diversity and inclusion (EDI).

Author contributions

Liang Ma: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **Ofir Levy**: Methodology (equal); Validation (equal); Writing – review and editing (equal). **Lauren Buckley**: Methodology (equal); Validation (equal); Writing – review and editing (equal). **Chao Hou**: Formal analysis (equal); Methodology (equal). **Wei-Guo Du**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data used in this research are all from the literature and online sources. R codes used in this manuscript are available from the Zenodo Repository: <https://doi.org/10.5281/zenodo.5879411> (Ma et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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