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Breeding phenology drives variation in reproductive output, reproductive costs, and offspring fitness in a viviparous ectotherm

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Abstract

Phenological advances are a widespread response to global warming and can contribute to determine the climate vulnerability of organisms, particularly in ectothermic species, which are highly dependent on ambient temperatures to complete their life cycle. Yet, the relative contribution of breeding dates and temperature conditions during gestation on fitness of females and their offspring is poorly documented in reptiles. Here, we exposed females of the common lizard *Zootoca vivipara* to contrasting thermal scenarios (cold vs. hot treatment) during gestation and quantified effects of parturition dates and thermal treatment on life-history traits of females and their offspring for 1 year. Overall, our results suggest that parturition date has a greater impact than thermal conditions during gestation on life history strategies. In particular, we found positive effects of an earlier parturition date on juvenile survival, growth, and recruitment suggesting that environmental-dependent selection and/or differences in parental quality between early and late breeders underlie seasonal changes in offspring fitness. Yet, an earlier parturition date compromised the energetic condition of gravid females, which suggests the existence of a mother–offspring conflict regarding the optimization of parturition dates. While numerous studies focused on the direct effects of alterations in incubation temperatures on reptile life-history traits, our results highlight the importance of considering the role of breeding phenology in assessing the short- and long-term effects of thermal developmental plasticity.

Keywords: climate change, phenology, parturition date, temperature, reproductive costs, life-history variation, thermal plasticity, parent–offspring conflict

Introduction

For organisms living in seasonal environments, the timing of reproduction during the year is a critical trait strongly associated with fitness (Iler et al., 2021; Visser & Gienapp, 2019). In terrestrial animals, the decision to reproduce early or late during the year can be dictated by numerous environmental and social cues (Watts et al., 2022) and will determine the number of sites available for breeders as well as the number and quality of their mates (e.g., Bensch & Hasselquist, 1992), the timing of the breeding period and thus the length of the juvenile growth season (e.g., Olsson & Shine, 1997), or the availability of resources during the breeding season and early juvenile life (Renner & Zohner, 2018). In fact, much research has focused on the link between breeding phenology and fitness at the individual level since the first comprehensive analysis of this relationship in birds by Perrins (1970). These studies generally show selection for earlier reproduction with regard to the individual reproductive output and the quality of their offspring (de Villemereuil et al., 2020; Radchuk et al., 2019).

At least two non-exclusive mechanisms have been proposed to explain selection for an early laying date in birds and the processes that lead to a seasonal decline in offspring quantity and quality (Verhulst & Nilsson, 2008). First, the seasonal decline in reproductive performance could be explained by the laying date itself, which affects all individuals in the same way ("date hypothesis", Hatchwell, 1991; Moreno, 1998). According to this "date hypothesis", environment-dependent selection occurs through seasonal changes in environmental conditions, such as seasonal shifts in food availability (Verhulst et al., 1995), predation risks (Öberg et al., 2014), or temperatures, which can affect offspring growth and survival during early life (Sauve et al., 2021). Alternatively, the seasonal decline in reproductive performance could also be explained by differences in parental quality between early and late breeders ("quality hypothesis", Brinkhof et al., 1993; Hatchwell, 1991). According to this hypothesis, adults in better condition or with a better-quality territory would reproduce earlier than others and therefore would produce

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better-quality offspring, leading to an apparent causal correlation between the timing of breeding and fitness. Although correlative and experimental studies have challenged these two hypotheses in birds (e.g., Harriman et al., 2017; Pärt et al., 2017; Winkler et al., 2020), the effects of date per se and parental quality on fitness are generally difficult to disentangle and may both contribute to an apparent seasonal decline in reproductive success.

Besides the date and quality hypothesis, the apparent beneficial effects of early breeding dates on fitness-related traits could be the result of environmental conditions experienced by the offspring during their embryonic development, such as variation in microclimatic conditions (e.g., temperature, humidity), parental care (e.g., egg incubation, food provisioning) or predation risks and stress. In ectotherms such as reptiles, reproductive phenology and thermal conditions during incubation are functionally linked, as their essential physiological functions are highly dependent on environmental temperatures (Angilletta et al., 2002). Thus, warmer developmental temperatures caused by warmer climates or an increased thermoregulatory behaviour of pregnant females generally reduce incubation length (in oviparous species) or gestation length (in viviparous species), leading to an earlier hatching date for the offspring (Noble et al., 2018). Beyond this expected temporal impact of the hatching date, developmental thermal conditions during incubation can further directly affect offspring fitness ("thermal hypothesis") by impacting the development of musculoskeletal or brain function (Booth, 2017; While et al., 2009). Generally, warm developmental temperatures and earlier hatching dates have positive effects on offspring viability, growth, survival, and reproduction (Le Henanff et al., 2013; Li et al., 2018; Liu et al., 2022; Olsson & Shine, 1997; Qualls & Andrews, 1999; Uller & Olsson, 2010; Wapstra et al., 2010). Yet, despite the functional link between developmental thermal conditions and hatching dates, few studies have attempted to determine the relative contribution of developmental thermal conditions per se and hatching dates (or parturition date in viviparous species) on fitness in reptiles. In addition, the combined effects of both are rarely considered (Sun et al., 2018), while the effects of developmental temperatures and hatching date could be additive or even interactive if developmental thermal conditions drive the differences in performance between juveniles from early and late breeders.

Although there is evidence for some fitness costs of early breeding in birds (Brown & Bomberger Brown, 2000; Nilsson, 1994), the mechanisms involved in the deleterious effects of an acceleration in reproductive phenology are not yet resolved. Empirical field and experimental studies in the European common lizard (*Zootoca vivipara,* Lichtenstein, 1823) show that warmer populations with an earlier breeding phenology tend to decline over time, despite the advantages for juveniles of being born early and developing in warmer environments (Bestion et al., 2015; Dupoué et al., 2022). In viviparous reptiles, higher temperatures during gestation decrease gestation length and increase basal metabolism in pregnant females due to the increasing oxygen demand of the growing embryos (Foucart et al., 2014). Thus, acceleration of gestation induced by warmer climates or by the selection of higher body temperatures during gestation could increase the energetic costs of pregnancy and negatively affect the body condition of breeding females (Brusch et al., 2023). Hence, acceleration of gestation could induce longer-term costs by affecting mother survival as well as the decision and quality of future reproduction given the known trade-offs between current reproduction, survival, and future reproduction (Stearns, 1992).

In order to improve our understanding of the relative contribution of developmental thermal conditions and parturition date in determining variation in fitness-related traits, we took advantage of the strong thermal plasticity of parturition dates of the European common lizard. By exposing pregnant females to contrasting thermal treatments (cold or hot treatments) during gestation, we advanced or delayed female's parturition date and generated two overlapping gradients of parturition dates between the thermal treatments. We then quantified the effects of thermal treatment and parturition dates both within the breeding season and up to the next breeding season. More specifically, we monitored the body condition, growth, future reproductive traits, and survival of females, as well as offspring morphology at birth, body growth, future survival, and reproduction. To distinguish between the date and thermal hypotheses regarding the impact of phenology on fitness, we then examined the effects of thermal conditions during gestation, the effects of parturition date and the combined effects of both on reproductive performance and life history traits of females and the offspring using model averaging procedures (Figure 1). First, we expect low support for models that do not include developmental conditions and/or parturition date (Figure 1A), as in general, developmental conditions or reproductive phenology are important determinants of female and offspring fitness traits. Second, if the effects of thermal conditions experienced by pregnant females and embryos during gestation are the main determinant of fitness traits ("thermal hypothesis"), we expect higher support for models including only thermal treatment (Figure 1B). Third, if the parturition date ("parturition date hypothesis," which includes date and quality hypothesis) is the main determinant of fitness traits, we expect higher support for models including only the parturition date (Figure 1C). Fourth, if parturition date and thermal treatment equally influence fitness traits, we expect higher support for models including additive effects of thermal conditions during gestation and parturition date ("thermal + parturition date hypothesis"; Figure 1D) or even interactive effects of both ("thermal × parturition date hypothesis"; Figure 1E).

Material and methods

Study species, sampling, and rearing conditions

The European common lizard is a small terrestrial lizard widely distributed in northern Eurasia in highly seasonal, cool, and humid habitats. Natural populations are structured in three main stage classes: juveniles (new-born individuals of the year), yearlings (1- to 2-year-old individuals), and adults (more than 2 years old). The mating period begins shortly after the emergence of sexually mature females from overwintering and occurs later for young than for old females (Bauwens & Verheyen, 1985). At our study site, mated females carry out vitellogenesis (follicular differentiation) during 2 to 3 weeks between mid-April and May, which is followed by ovulation and egg fertilization that mark the onset of gestation. Parturition occurs after an average gestation period of 2 months, that is, between late June and early August, depending on thermal conditions and individual characteristics (Rutschmann et al., 2016). Females lay on average five

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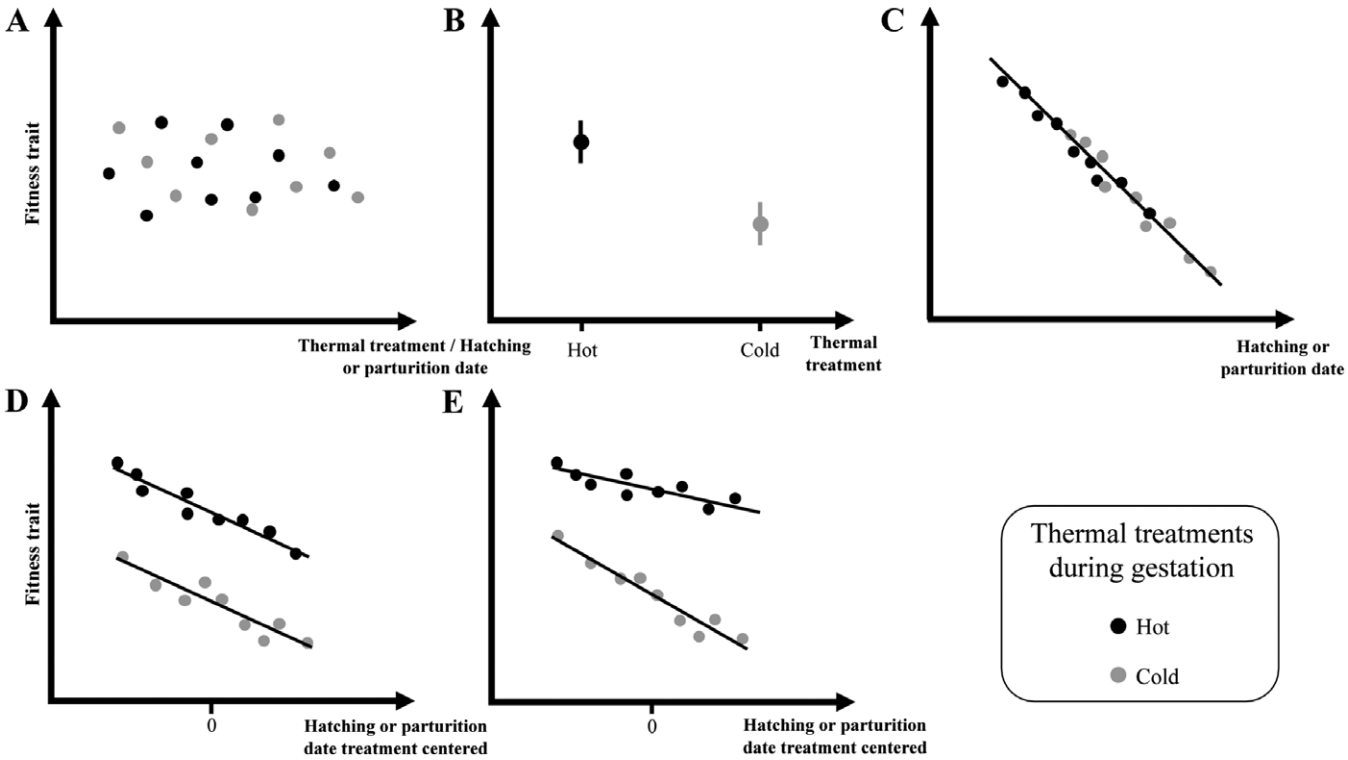

Figure 1. Hypothetical framework of the relationships between thermal treatment, parturition date (or hatching date) and fitness traits of females and the offspring. To test the effects of thermal treatments, parturition date, and combined effects of both on fitness traits, we built and compared the following five types of models: null model without effect of thermal treatment or parturition date ("null hypothesis", scenario A), model including the effect of thermal treatment only ("thermal hypothesis", scenario B), model including the effect of parturition date only ("parturition date hypothesis", scenario C), model including the additive effect of thermal treatment and parturition date ("thermal + parturition date hypothesis", scenario D) and a variation of this model including interactive effects of thermal treatment and parturition date ("thermal × parturition date hypothesis", scenario E). In scenarios D and E, we centred the individual parturition date relative to the parturition dates of females in the same thermal treatment to avoid multicollinearity. The filled black and grey dots represent the fitness traits of individuals exposed to hot and cold conditions respectively.

non-calcified eggs (range 1–12) including both nonviable and live offspring that hatch quickly (a few minutes to a few hours) after parturition.

Lizards were captured inside semi-natural populations maintained in outdoor enclosures at CEREEP-Ecotron IleDeFrance (France, 48°17′11.5″ N, 2°40′45.6″ E). Pregnant adult (n = 84) and subadult females (n = 93) were captured after mating (i.e., between 3rd May and 7th May 2021 for adult females and between 25th May and 11th June 2021 for subadults). We then acclimated females in individual terrariums (adults: 25 × 15 × 15 cm, subadults: 18 × 11 × 12 cm) filled with sterilized peat as substrate, equipped with a shelter, and installed in a temperature-controlled room (23 °C from 9 a.m. to 6 p.m., 16 °C at night). Terrariums were lit automatically between 8:30 a.m. and 5 p.m. by a UVB-enhanced neon tube (30 W) providing white light and by a halogen heating bulb (25 W) placed on one side of the terrarium to generate a thermal gradient. All lizards were acclimatized for a minimum of 2 weeks before the experiments by providing optimal basking conditions (8.5 hr per day), food and water ad libitum, and humid conditions. Reproductive status of females was inferred by the presence of recent male bite marks and ultrasonography (SonoSite M-Turbo, Inc., Bothell, WA, USA). Experiments were performed under the approval of Charles Darwin Animal Experimentation Ethics Committee (APAFIS#2021010121599881) in an animal breeding facility accredited with permit 17/DDPP/SPAE/57.

Experimental design

We exposed females to two contrasted thermal regimes during gestation to change breeding phenology. In the "hot" treatment, females could bask at their preferred temperature for 8.5 hr per day and we imposed a night-time temperature of 18 °C. In the "cold" treatment group, we shortened the daily thermoregulation opportunities of females to 6 hr per day, and imposed night-time temperatures of 14 °C. Basking regime and night-time temperatures were manipulated together to simulate contrasted climate scenarios, induce thermal plasticity in breeding phenology, and create two overlapping parturition date gradients between the thermal treatments. The hot treatment simulates a warming scenario where warmer days are associated with higher night-time temperatures (Zhong et al., 2023), while the cold treatment simulates the current thermal conditions encountered in populations of this species (Dupoué et al., 2022). These two thermal regimes also encompass the variability observed inside natural populations (Dupoué et al., 2022). Experimental manipulations started on 7th June for all adult females after confirmation of their reproductive status. As the ovulation periods of subadults are delayed relative to adults, subadults were distributed into the two experimental groups between 18th June and 5th July after confirmation of their reproductive status. As we were not able to determine the ovulation date of the females, we randomly assigned females to both groups while ensuring a balanced average body mass (which is correlated with the

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progress of gestation), and arranged them randomly in the breeding room. Hot conditions accelerated breeding phenology by 7 days on average in each age group (effect of thermal treatment on parturition date in 2021: $F_{1,147.1} = 47.25$, $p < 0.001$; mean parturition date: 21th July for hot treatment and 28th July for cold treatment), with a broad gradient of parturition dates ranging from 3rd July to 11th August.

Measurements of energetic condition of female

One day before the start of the experiment and one day after parturition, we quantified tail width and limb thickness of females, which are reliable proxies of energetic condition and can therefore be used to assess the energetic costs of reproduction (Bodineau et al., 2024; Brusch et al., 2020). A reduction in tail width and limb thickness indicates muscle catabolism and the mobilization of caudal energy reserves. We took digital pictures of the females ventrally using a flatbed scanner (CanoScan LiDE 700F, Canon) and measured tail width at the 7th sub-caudal scale rows with ImageJ software (Version 1.52v). At the same time, hind limb thickness was measured on both legs using a spessimeter (ID-C1012BS, Mitutoyo, Japan). Following the same method, we measured female limb thickness and tail width before wintering in September 2021, and we also measured limb thickness after wintering in April and May 2022 to estimate long-term effects. We calculated intraindividual changes in limb thickness and tail width by subtracting the final values from the initial values of the trait measured between the beginning and end of gestation and between recapture sessions. For the change in limb thickness, we calculated this change at the right and left hind legs and then averaged them.

Measurements of reproductive effort and offspring quality

After parturition, each female was weighed and the litter was characterized by recording the number of unfertilized eggs, undeveloped embryos, stillborn, and live juveniles. Juveniles were measured for snout to vent length (SVL, with a ruler, to the nearest 0.5 mm), weighted (using a precision scale to the nearest mg), and sexed by counting ventral scales (Lecomte et al., 1992). All live juveniles were marked by toe-clipping. On the day of parturition, we randomly released juveniles from the same litter with their mothers into 1 of 10 outdoor enclosures by standardizing the density and sex ratio of juveniles, subadults, and adults.

Growth, survival, and reproduction up to the following year

We monitored all surviving offspring and females through regular hand capture sessions in outdoor enclosures in September 2021, April 2022, and May 2022. At each capture session, we measured SVL and body mass of all individuals and then released them into their enclosures. We calculated the specific growth rate (specific growth rate (SGR) = [ln (SVL) – ln (initial SVL)]/days) before wintering (between birth and September) and after wintering (between September and May) using established methods (Liu et al., 2022; Sinervo, 1990; Sun et al., 2018). At the end of May 2022, we recaptured all alive individuals to estimate the annual survival. All reproductive females were housed in the laboratory under the same standard rearing conditions (as described in section *Study species, sampling, and rearing conditions*) until parturition. We characterized parturition date, reproductive investment, and litter characteristics (as described in section *Measurements of reproductive effort and offspring quality*).

Statistical analyses

Analyses were performed using R software version 4.2.0 (R Core Team, 2022). In order to test our five hypotheses, we built the following five different types of models (see Figure 1): null model without effect of treatment or parturition date ("null hypothesis", scenario A), model including the effect of thermal treatment only ("thermal hypothesis", scenario B), model including the effect of parturition date ("parturition date hypothesis", scenario C), model including the additive effect of thermal treatment and parturition date ("parturition date + thermal hypothesis", scenario D), and a variation of this model including interactive effects of thermal treatment and parturition date ("parturition date × thermal hypothesis", scenario E). In scenarios D and E, we centred parturition date within thermal treatment as female parturition date minus the average parturition date of females from her thermal treatment to avoid multicollinearity between treatment factor and date. To account for the uncertainty in the model selection of the "nuisance" covariates (i.e., variables that are not of primary interest but should be considered in the analysis), we computed the Akaike weights of models including different nuisance covariates for class of models (see details below) and summed the weights within the different subclasses described. This procedure allowed us to obtain an estimate of a "model-averaged" Akaike weight corresponding to each class of model. We tested these 5 models (scenarios A to E) for each analysis (except for the parturition date analysis in 2021, where we only compared null models [scenario A] and models including the treatment effect [scenario B]), and we added to these five models of interests all covariates as described below. In all cases, we controlled for interindividual and interenclosures variability by including a random effect of individual identity of the mother and/or the enclosure and tested model fitting and model assumptions. All results are reported as means ± *SE* unless otherwise stated and statistical support for each class of model is expressed as a percentage of the cumulative Akaike weights.

Morphological changes of females

We analysed limb thickness changes using linear mixed models (LMMs) with scenarios A to E including the effect of session (i.e., beginning of gestation to parturition, parturition to September, September to April, April to May), age class, and the initial centred value of limb thickness as fixed effects. Tail width changes during gestation were analysed using LMMs including the age class and the initial centred value of tail width as fixed effects.

Immediate and delayed effects on reproductive outputs

Parturition dates in 2021 and 2022 (calculated as day of the year) were analysed using LMMs. We first analysed the effect of thermal treatment on parturition dates in 2021 using models with scenarios A and B including fixed effects of age class and body mass at capture age class-centred. Second, parturition dates of surviving manipulated females in 2022 were analysed with scenarios A to E including mean centred body mass at capture as fixed effect. We added body mass at capture in these models to take account of interindividual differences in the progress of gestation and centred related to age class for the analysis of the 2021 data because the mass of the females is highly dependent on age class.

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We calculated litter size as the total number of reproductive items produced (i.e., fertilized or unfertilized eggs, undeveloped embryos, stillborn, and live offspring), and reproductive success at birth as the number of viable juveniles at birth out of the total number of reproductive items. Litter size was analysed with GLMMs using scenarios A to E with a Poisson distribution, whereas reproductive success at birth was analysed with negative binomial mixed models. We added age class and SVL age class-centred as fixed effects. We further calculated reproductive investment as the difference between the body mass of females before and after the parturition. We then analysed reproductive investment with LMMs using scenarios A to E and including age class and SVL age class-centred as fixed effects. We performed the same analyses of litter size, reproductive success at birth, and reproductive investment in 2022, without testing the effect of age class because all females were adults in 2022.

Effects on offspring morphology at birth, juvenile growth, and reproduction early in life

We fitted LMMs using scenarios A to E to data on offspring SVL and body condition at birth. We added to these models the age class of females and the sex of juveniles as fixed effects. For body condition at birth, we analysed body mass at birth with SVL as a covariate assuming a linear relation between mass and size. In addition, we analysed SGR before and after wintering as well as body size at the end of first year of life (SVL in May 2022) using LMMs with scenarios A to E including fixed effects of juvenile sex and age class of the mother. Finally, since not all juvenile females reproduce at 1 year old, we examined recruitment of juvenile females during the first year of life and their parturition date. We fitted GLMMs with scenarios A to E assuming a binomial distribution to examine recruitment as success/failure events and we used a LMM to study juvenile parturition dates. No variables were added to the base of the models in these two analyses.

Female and juvenile survival

Since all juveniles and females are recaptured in May, lizards not recaptured were considered dead. We analysed survival of juvenile and manipulated females as success/failure events using GLMMs (scenarios A to E) assuming a binomial distribution. We added the age class as a factor in models for manipulated female analyses and we took into account the age class of the mother and the sex of the juvenile as fixed effects for juvenile survival analysis.

Results

Energetic condition changes of female

We found support for an effect of parturition date on female limb thickness and tail width changes ("date hypothesis": 43% and 60%, respectively). Adult and subadult females that gave birth early displayed a stronger reduction of their tail width and limb thickness during gestation than late-breeding females (all $p < 0.05$; Figure 2A and E). This relationship was, however, reversed after breeding and before wintering, a period during which females that gave birth early gained more limb thickness and tail width than late breeding females (all $p < 0.05$; Figure 2B and F). Similarly, after wintering, early breeding females from year 2021 showed a greater increase in limb thickness than late breeding females ($F_{1,67} = 16.3$, $p < 0.001$; Figure 2C). On average, subadult females showed an increase in limb thickness and tail width compared with adult females (limb thickness: 0.03 ± 0.01 and −0.03 ± 0.01 mm respectively; tail width: 0.16 ± 0.02 and −0.02 ± 0.02 mm respectively; all $p < 0.05$).

Reproductive traits of manipulated females

There was strong support for the influence of parturition date on reproductive success at birth (Table 1, "date hypothesis": 55%) but we found a support for null models regarding female's reproductive investment and litter size ("null hypothesis": 44% and 50%, respectively). Reproductive success at birth was greater for females that gave birth early (slope: −0.16 ± 0.08; $\chi^2_1 = 4.26$, $p = 0.03$). Regarding offspring SVL and body condition at birth, we found weak support for models that included parturition date ("date hypothesis": 37%) and treatment ("thermal hypothesis": 32%), respectively. Litters born earlier tended to include larger offspring (slope: −0.17 ± 0.10; $F_{1,96.9} = 3.2$, $p = 0.05$) but the effect of thermal treatment on offspring body condition was not significant ($F_{1,94.1} = 1.7$, $p = 0.20$). Compared with adult females, subadult females show lower reproductive success (4.39 ± 0.38 and 2.77 ± 0.22 viable juveniles at birth respectively; $\chi^2_1 = 5.9$, $p = 0.02$), reproductive investment (2.14 ± 0.09 g and 1.18 ± 0.06 g, respectively; $F_{1,135.6} = 6.2$, $p = 0.01$), and litter size (6.64 ± 0.26 and 3.88 ± 0.15 reproductive items, respectively; $\chi^2_1 = 52.1$, $p < 0.001$).

Body growth, survival, and future reproduction of offspring

We found strong support for models including parturition date regarding annual juvenile survival (Table 1, "date hypothesis": 52%), body size at the end of first year of life (SVL in May, "date hypothesis": 75%), pre-winter and post-winter SGR ("date hypothesis": 67% and 81%, respectively), the recruitment probability of juvenile females ("date hypothesis": 81%) and the breeding dates of juvenile females at the age of 1 year ("date hypothesis": 67%). Annual survival (Figure 3A) and body size at the end of first year of life were greater for early-born juveniles than for late-born juveniles (survival: $\chi^2_1 = 3.8$, $p = 0.05$; body size: slope: −1.28 ± 0.36; $F_{1,46.7} = 12.8$, $p < 0.0001$). In addition, juveniles produced by subadult females have a larger body size at the end of first year of life than those produced by adult females (55.48 ± 0.59 mm and 55.08 ± 0.62 mm, respectively; $F_{1,44.5} = 4.6$, $p = 0.04$). However, the direction of the relationship between SGR and parturition date varied before and after the wintering period (Figure 3B and C). Early-born juveniles had higher pre-winter SGR ($F_{1,58.1} = 14.2$, $p < 0.001$) but lower post-winter SGR than later-born juveniles ($F_{1,40.4} = 40.0$, $p < 0.001$). In addition, we observed a significant decrease in the recruitment probability at 1-year-old for late-born juveniles ($\chi^2_1 = 5.1$, $p = 0.02$) as well as a positive relationship between the breeding date of juveniles and those of their mothers ($F_{1,22.1} = 8.8$, $p < 0.001$; Figure 4).

Survival and future reproduction of manipulated females

There was a strong support for models with long-term effects of thermal treatment on female breeding dates during the next breeding season ("thermal hypothesis": 55%). Females exposed to the cold treatment in 2021 gave birth an average of 5 days earlier the next breeding season in 2022 than females exposed to hot treatment in 2021 ($F_{1,72} = 7.9$,

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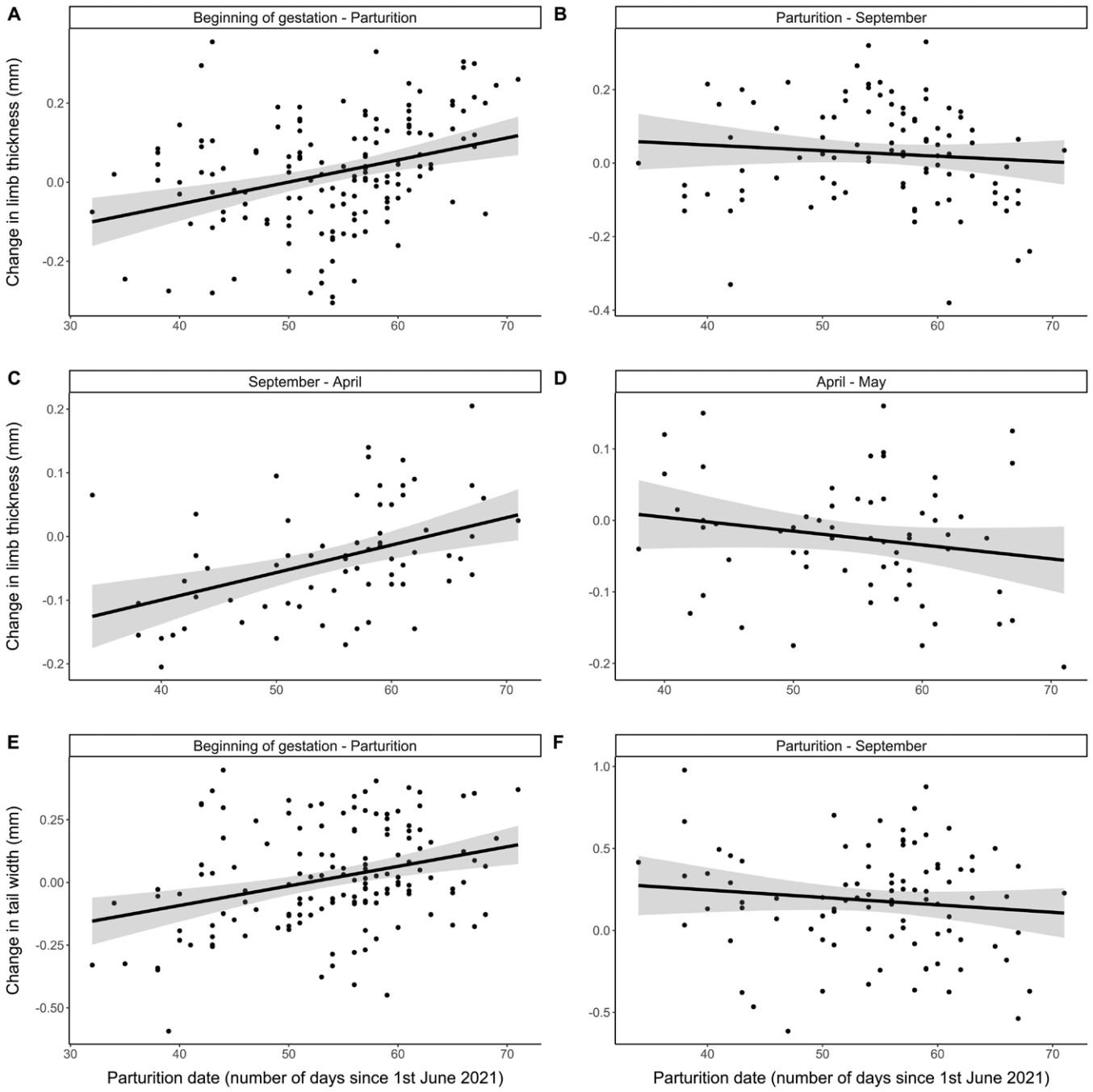

Figure 2. Effects of parturition date on intraindividual changes in limb thickness (A, B, C, D) and tail width (E, F) of breeding females *Zootoca vivipara*. Points represent raw data and a negative change indicates a decrease in the limb thickness or tail width over time. The linear regressions are plotted and shaded areas represent 95% confidence limits.

$p < 0.01$). Apart from this, we found a support for null models regarding female's survival, reproductive investment, litter size, and reproductive success at birth in 2022 ("null hypothesis": 31%, 64%, 50%, and 51%, respectively).

Discussion

In this study, we changed the gestation length of a viviparous lizard by exposing pregnant females to contrasting thermal conditions in order to test the intragenerational and intergenerational effects of thermal conditions and parturition date on life history traits of females and their offspring. In accordance with previous studies in viviparous lizards, colder night-time temperatures and reduced thermoregulation opportunities during the day delayed parturition dates (Brusch et al., 2023; Wapstra et al., 2010). This was observed despite the fact that pregnant females increased their thermoregulation effort in the cold treatment group (see Supplementary Information), probably to counteract the effects of low developmental temperatures on speed of gestation (Atkins et al., 2007; Hare et al., 2008; Qualls & Andrews, 1999). We performed a comparative analysis of five hypotheses (see Figure 1) but statistical support for the "thermal hypothesis", the "parturition date + thermal hypothesis", and the "parturition date

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Table 1. Rounded sums of Akaike weights according to the five hypotheses tested to assess the intragenerational and intergenerational effects of thermal treatment and/or parturition date on fitness traits. The sum of Akaike weights of the model with the highest statistical support for each trait is bolded.

Scenario relating to Figure 1		A	B	C	D	E
Effect category	Trait	Null hypothesis	Thermal hypothesis	Parturition date hypothesis	Thermal + parturition date hypothesis	Thermal × parturition date hypothesis
Intragenerational	Change in tail width	2.03E-06	0.20	**0.60**	0.15	0.05
	Change in limb thickness	5.86E-03	0.33	**0.43**	0.19	0.05
	Parturition date in 2022	0.03	**0.55**	0.01	0.31	0.10
	Reproductive investment in 2021	**0.44**	0.14	0.25	0.09	0.08
	Reproductive investment in 2022	**0.64**	0.19	0.07	0.06	0.03
	Number of viable juveniles at birth in 2021	0.18	0.05	**0.55**	0.21	0.08
	Number of viable juveniles at birth in 2022	**0.51**	0.23	0.17	0.07	0.02
	Litter size in 2021	**0.50**	0.19	0.22	0.07	0.03
	Litter size in 2022	**0.50**	0.23	0.17	0.08	0.03
	Survival	**0.31**	0.14	0.23	0.22	0.09
Intergenerational	Survival	0.16	0.08	**0.52**	0.19	0.05
	Body mass at birth	0.25	**0.32**	0.15	0.21	0.06
	SVL at birth	0.20	0.11	**0.37**	0.23	0.10
	SVL in May	7.76E-03	4.5E-03	**0.75**	0.17	0.07
	Pre-winter specific growth rate	3.11E-03	0.01	**0.67**	0.24	0.08
	Post-winter specific growth rate	7.20E-08	2.25E-07	**0.81**	0.16	0.03
	Recruitment of juvenile females at 1 year old	1.26E-04	1.17E-04	**0.81**	0.11	0.08
	Parturition date at 1 year old	0.04	0.02	**0.67**	0.19	0.08

× thermal hypothesis" was weak, whereas the "parturition date hypothesis" was often strongly supported, especially for most offspring life history traits. Thus, our results suggest that life history strategies were best explained by parturition date rather than by thermal conditions experienced by females during gestation or by additive or interactive effects between thermal conditions and parturition dates. We found strong effects of the parturition date on both female condition traits and reproductive performances, and on juvenile survival, growth, and recruitment. Earlier parturition dates had positive effects on juveniles in accordance with previous studies in reptiles (Le Henanff et al., 2013; Pearson & Warner, 2018; Sinervo & Doughty, 1996; Uller & Olsson, 2010; Wapstra et al., 2010), but had a negative impact on female condition.

Seasonal declines in reproductive investment and litter viability have been observed repeatedly in reptiles, in birds, and in some mammals as well (birds: Dawson, 2008; Verhulst et al., 1995; reptiles: Mitchell et al., 2018; mammals: Green & Rothstein, 1993). In general, the decline in reproductive performances in late-breeding females is explained by a lower quality of these females and/or by less favourable late-season environmental conditions for reproduction (Öberg et al., 2014). In lizards, reproductive investment and litter viability often decrease in females laying eggs later in the season (e.g., Olsson & Shine, 1997) and in females exposed to colder conditions during gestation (e.g., Brusch et al., 2020). In our study, we did not detect an effect of thermal treatment or parturition date on litter size because litter size is determined early in the reproductive cycle before the start of the manipulation (Bauwens & Verheyen, 1985). However, we observed a lower proportion of viable juveniles at birth for late-breeding females. A prolonged incubation or gestation can be harmful to embryos by altering the developmental environment of embryos (Atkins et al., 2007; Hare et al., 2008; Qualls & Andrews, 1999). Finally, lower litter size, reproductive investment, and reproductive success in subadults were probably related to age and reproductive experience.

In addition, while extended literature shows that thermal conditions during embryonic development can significantly influence offspring phenotype (Booth, 2006; Noble et al., 2018; While et al., 2018), our results suggest that juvenile SVL at birth is more influenced by parturition date rather than by developmental thermal conditions per se. Early-born juveniles were slightly larger than late-born juveniles consistent with some previous studies in lizards that found positive effects of earlier hatching date on juvenile body size (Olsson & Shine, 1997; Shine & Olsson, 2003; Sun et al., 2018; Wapstra et al., 2010). However, we didn't find any effect of parturition

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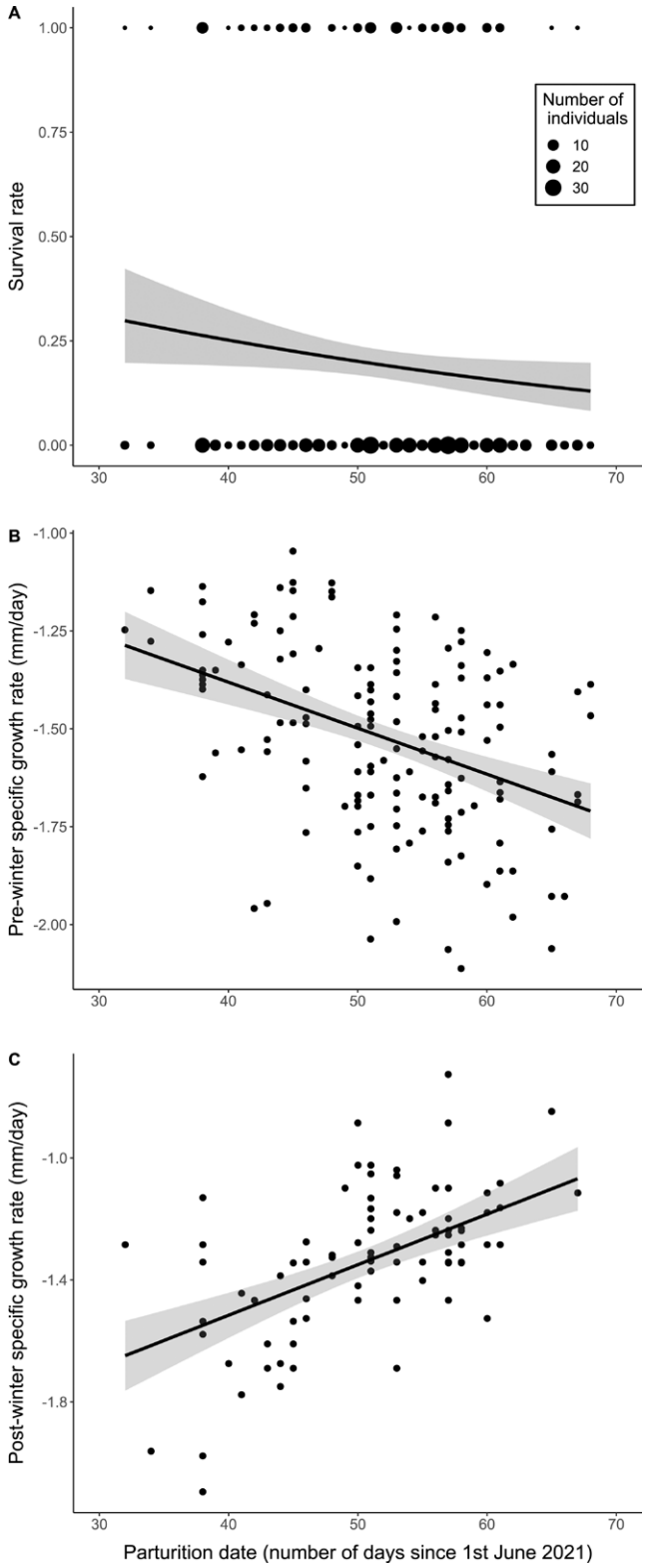

Figure 3. Effects of parturition date on juvenile survival probability (A), pre-winter specific-growth rate (B), and post-winter-specific growth rate (C). In A, solid line represents the average survival probability as a function of parturition date obtained from a logistic regression. The point size corresponds to the number of observations. In B and C, points represent raw data. The linear regression is plotted and shaded areas represent 95% confidence limits.

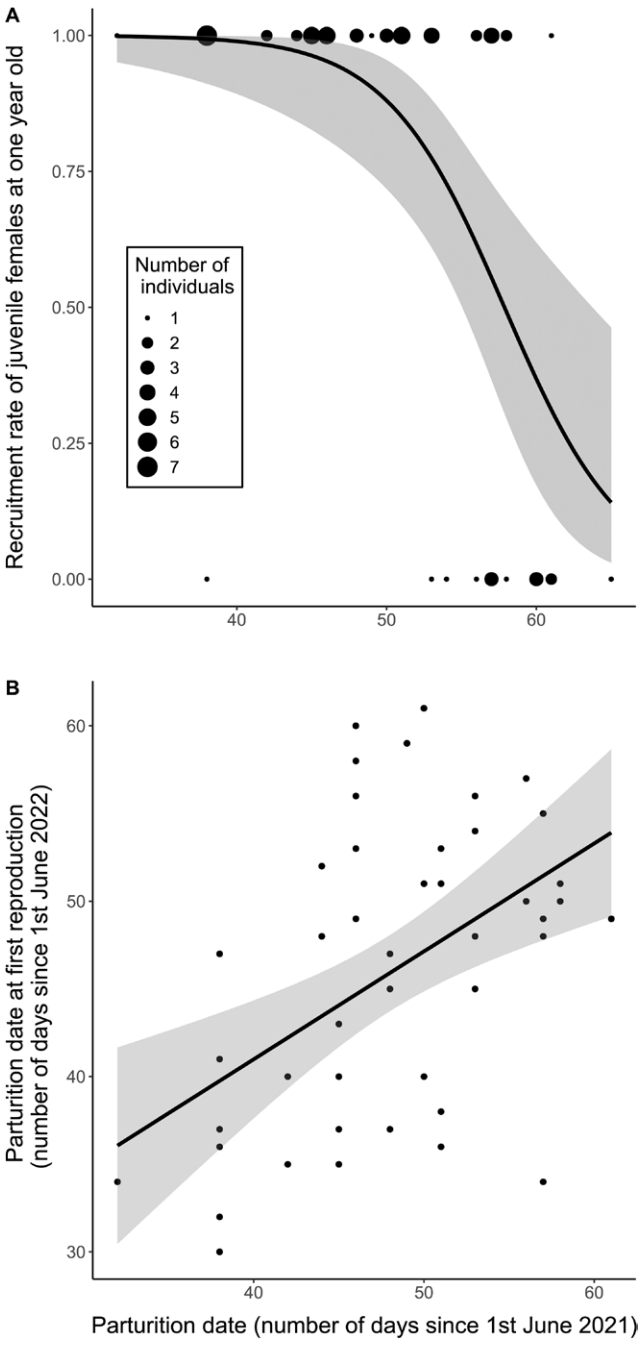

Figure 4. Effects of parturition date on recruitment rate (A) and parturition date (B) of juvenile females at 1 year old. In A, solid line represents the average recruitment of a given parturition date estimated from a logistic regression. The point size corresponds to the number of observations. In B, points represent individual parturition date of juvenile females at 1 year old of a given parturition date. The linear regression is plotted against raw data. Shaded areas represent 95% confidence limits.

date and thermal treatment on juvenile body condition in accordance with a previous study in the European common lizard (Brusch et al., 2020). In general, the extent and direction of the effects of developmental temperatures and hatching dates on juvenile morphology vary between species and the underlying mechanisms of these effects remain poorly understood (reviewed in Booth, 2006; Noble et al., 2018). In some instances, warmer incubation temperatures, longer basking times, and earlier hatching dates increase body mass or size of juveniles at birth (e.g., Doughty & Shine, 1998; Wapstra, 2000; Wapstra et al., 2010). However, in others, eggs laid late in the season and in cold incubation regimes produce larger and/or heavier juveniles (Pearson & Warner,

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2018). Juvenile morphology at birth can be influenced by the amount of yolk provided before ovulation and by temperature-dependent yolk allocation processes towards growth or maintenance (Shine & Harlow, 1993; Wapstra, 2000). Thus, SVL differences at birth between early- and late-born juveniles could result from maternal effects related to the amount of energy allocated in yolk production or to maternal thermoregulation behaviours in line with the quality hypothesis.

Life history traits of juveniles were mainly determined by parturition date and not by thermal treatment alone or in combination with parturition date. As predicted and consistent with previous studies on reptiles, we found positive effects of early parturition date on juvenile survival probability, total growth, summer growth rate, and access to reproduction during the first year of life (Pearson & Warner, 2018; Uller & Olsson, 2010; Wapstra et al., 2010). These advantages of an early birth date on survival and total growth could be linked to prenatal mechanisms linked to female quality ("quality hypothesis") such as the quality of eggs produced or maternal thermoregulation strategies affecting the developmental environment and quality at birth. For example, we found that juveniles born earlier were larger at birth. Benefits of an earlier birth date could be also explained by postnatal mechanisms linked to seasonal changes in climatic conditions, in prey availability and in population density ("date hypothesis"). A longer period of activity before winter combined with more favourable thermal conditions in early summer and less competition among juveniles born early during the season may boost the body growth and energy storage of offspring before wintering and thus positively affect the survival of early-born juveniles (Adolph & Porter, 1993; Pearson & Warner, 2018; Uller & Olsson, 2010; Warner & Shine, 2007). This selective advantage to early individuals may generate strong interindividual differences in fitness unless some compensatory mechanisms exist later in life (Mangel & Munch, 2005; Metcalfe & Monaghan, 2001). As a matter of fact, we found a higher post-winter growth rate in later-born juveniles, which suggests the existence of some compensatory growth strategies developed by late juveniles to offset their disadvantage at birth. Similar compensatory strategies have been demonstrated in several taxa and they generally constitute an adaptive response to a shorter growth period (birds: Hirose et al., 2012; reptiles: Sun et al., 2018; amphibians: Orizaola et al., 2010; fish: Simonin et al., 2016). Despite these compensatory growth responses, early-born lizards maintained a size advantage at 1 year old and we observed a significant decrease in the recruitment probability of late-born juveniles, which shows that birth date is also an important determinant of age at first reproduction. A greater absolute body growth may explain these findings because sexual maturation and breeding dates depend strongly on body size in this species (Heulin, 1985). These results could also be explained by the heritability of parturition dates, as already demonstrated in several bird species (Biquet et al., 2022; Charmantier & Gienapp, 2014), although wild population estimates are scarcer for reptiles.

Despite the beneficial effects of early parturition dates on reproductive quality and juvenile life history traits, we also found negative impacts on females such as greater losses in leg thickness and tail width in females that give birth earlier. In many lizard species, including the European common lizard, the tail is a reserve organ composed mainly of muscle and lipids stored in the form of triglycerides (Price, 2017). Mobilization of caudal lipid reserves and muscle wasting can occur to meet energy and amino acid requirements when dietary intake is insufficient or when energy expenditure is high. In viviparous reptiles, basal metabolism and the resulting energy expenditure increase during gestation due to embryonic development (Foucart et al., 2014). Reptiles can quickly mobilize caudal lipid reserves and/or muscles in response to the acceleration of gestation and the increased demands of embryos (Brusch et al., 2020, 2023; Lourdais et al., 2004). Thus, early breeding is associated with an increase in the immediate energetic costs of reproduction for pregnant females that impact their body condition (this study) but could also change locomotor performances and predation risks (Lourdais et al., 2004). In natural populations, these extra energetic costs could be offset by other advantages of a shorter gestation length in terms of reduced time with a locomotion burden and a high predation risk due to pregnancy, or a longer period before winter to store energy (Shine, 2003). Although we found that early-breeding females restored condition to a greater extent than late-breeding females before winter, the benefits of early parturition to recover energy before winter were not equal to the direct costs imposed by early parturition. Indeed, before and after winter, early breeding females always presented a weaker muscular condition than late females (not shown). In addition, we did not detect any negative effect of early parturition or treatment on future survival and reproduction (but see Bleu et al., 2013) but females exposed to the cold treatment gave birth on average 5 days earlier during the next breeding season than females exposed to the hot treatment. In birds, the condition-dependent individual optimization model of reproductive phenology predicts that females optimize their breeding phenology as a function of arrival condition, arrival date, and the ability to gain in condition on the breeding grounds (Hennin et al., 2016; Rowe et al., 1994). Since female lizards in the cold treatment gave birth later and were on average in better condition when they emerged from winter the following year, this model predicts that they were able to start reproducing earlier as we observed.

Conclusion

Our experimental study examined the effects of breeding phenology and thermal conditions during gestation on life history strategies of mothers and their offspring in a viviparous ectotherm. Our results are consistent with previous studies highlighting directional selection towards early parturition dates, and emphasize that the parturition date, rather than thermal condition during gestation and combined effects of both, is an important determinant of survival, growth, and recruitment of juveniles, which can have a major impact on the population dynamics of viviparous ectotherms. Additionally, our findings suggest the existence of a mother–offspring trade-off concerning the optimization of the parturition dates insofar as reducing the gestation length can entail energy costs for pregnant females. Finally, our findings and field studies highlighting the decline in natural populations of the common lizard with an early phenology call for better consideration of the benefits and costs associated with earlier breeding dates. Future research should quantify the benefits and costs of phenological acceleration in oviparous species, as well as the long-term effects of accelerated life history in order to understand and predict the consequences of phenological changes in response to climate change.

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Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Data are available at Zenodo with doi: https://doi.org/10.5281/zenodo.12673833

Author contributions

Théo Bodineau (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Investigation [equal], Methodology [equal], Validation [equal], Writing—original draft [lead], Writing—review & editing [lead]), Pierre de Villemereuil (Conceptualization [equal], Formal analysis [supporting], Methodology [equal], Validation [equal], Writing—review & editing [equal]), Beatriz Decencière (Investigation [supporting]), Simon Agostini (Investigation [supporting]), Jean-François Le Galliard (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Funding acquisition [equal], Investigation [equal], Methodology [equal], Validation [equal], Writing—review & editing [equal]), and Sandrine Meylan (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Funding acquisition [equal], Investigation [equal], Methodology [equal], Validation [equal], Writing—review & editing [equal])

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Conflict of interest

The authors declare no competing or financial interests.

Ethical statement

Experiments were performed under the approval of Charles Darwin Animal Experimentation Ethics Committee (APAFIS#2021010121599881) in an animal breeding facility accredited with permit 17/DDPP/SPAE/57.

References

Adolph, S., & Porter, W. (1993). Temperature, activity, and lizard life histories. *The American Naturalist*, *142*, 273–295. https://doi.org/10.1086/285538

Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, *27*(4), 249–268. https://doi.org/10.1016/s0306-4565(01)00094-8

Atkins, N., Swain, R., Wapstra, E., & Jones, S. M. (2007). Late stage deferral of parturition in the viviparous lizard *Niveoscincus ocellatus* (Gray 1845): Implications for offspring quality and survival. *Biological Journal of the Linnean Society*, *90*(4), 735–746. https://doi.org/10.1111/j.1095-8312.2007.00770.x

Bauwens, D., & Verheyen, R. F. (1985). The timing of reproduction in the lizard Lacerata vivipara: Differences between individual females. *Journal of Herpetology*, *19*(3), 353–364. https://doi.org/10.2307/1564263

Bensch, S., & Hasselquist, D. (1992). Evidence for active female choice in a polygynous warbler. *Animal Behaviour*, *44*, 301–311. https://doi.org/10.1016/0003-3472(92)90036-9

Bestion, E., Teyssier, A., Richard, M., … Cote, J. (2015). Live fast, die young: Experimental evidence of population extinction risk due to climate change. *PLoS Biology*, *13*(10), e1002281. https://doi.org/10.1371/journal.pbio.1002281

Biquet, J., Bonamour, S., de Villemereuil, P., … Teplitsky, C. (2022). Phenotypic plasticity drives phenological changes in a Mediterranean blue tit population. *Journal of Evolutionary Biology*, *35*(2), 347–359. https://doi.org/10.1111/jeb.13950

Bleu, J., Le Galliard, J. -F., Fitze, P. S., … Massot, M. (2013). Reproductive allocation strategies: A long-term study on proximate factors and temporal adjustments in a viviparous lizard. *Oecologia*, *171*(1), 141–151. https://doi.org/10.1007/s00442-012-2401-1

Bodineau, T., Chabaud, C., Decencière, B., … Le Galliard, J. -F. (2024). Microhabitat humidity rather than food availability drives thermo-hydroregulation responses to drought in a lizard. *Oikos*, *2024*(6), e10535. https://doi.org/10.1111/oik.10535

Booth, D. T. (2006). Influence of incubation temperature on hatchling phenotype in reptiles. *Physiological and Biochemical Zoology*, *79*(2), 274–281. https://doi.org/10.1086/499988

Booth, D. T. (2017). Influence of incubation temperature on sea turtle hatchling quality. *Integrative Zoology*, *12*(5), 352–360. https://doi.org/10.1111/1749-4877.12255

Brinkhof, M. W. G., Cavé, A. J., Hage, F. J., & Verhulst, S. (1993). Timing of reproduction and fledging success in the coot *Fulica atra*: Evidence for a causal relationship. *Journal of Animal Ecology*, *62*(3), 577–587. https://doi.org/10.2307/5206

Brown, C. R., & Bomberger Brown, M. (2000). Weather-mediated natural selection on arrival time in cliff swallows (Petrochelidon pyrrhonota). *Behavioral Ecology and Sociobiology*, *47*(5), 339–345. https://doi.org/10.1007/s002650050674

Brusch, G. A., Gavira, R. S. B., Viton, R., … Lourdais, O. (2020). Additive effects of temperature and water availability on pregnancy in a viviparous lizard. *Journal of Experimental Biology*, *223*(19). https://doi.org/10.1242/jeb.228064

Brusch, G. A. IV, Le Galliard, J. -F., Viton, R., … Lourdais, O. (2023). Reproducing in a changing world: Combined effects of thermal conditions by day and night and of water constraints during pregnancy in a cold-adapted ectotherm. *Oikos*, *2023*(3), e09536. https://doi.org/10.1111/oik.09536

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evolutionary Applications*, *7*(1), 15–28. https://doi.org/10.1111/eva.12126

Dawson, R. D. (2008). Timing of breeding and environmental factors as determinants of reproductive performance of tree swallows. *Canadian Journal of Zoology*, *86*(8), 843–850. https://doi.org/10.1139/z08-065

de Villemereuil, P., Charmantier, A., Arlt, D., … Chevin, L. -M. (2020). Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(50), 31969–31978. https://doi.org/10.1073/pnas.2009003117

Doughty, P., & Shine, R. (1998). Reproductive energy allocation and long-term energy stores in a Viviparous Lizard (*Eulamprus tympanum*). *Ecology*, *79*(3), 1073–1083. https://doi.org/10.2307/176602

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Dupoué, A., Blaimont, P., Angelier, F., … Le Galliard, J. -F. (2022). Lizards from warm and declining populations are born with extremely short telomeres. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(33), e2201371119. https://doi.org/10.1073/pnas.2201371119

Foucart, T., Lourdais, O., DeNardo, D. F., & Heulin, B. (2014). Influence of reproductive mode on metabolic costs of reproduction: Insight from the bimodal lizard *Zootoca vivipara*. *The Journal of Experimental Biology*, *217*(Pt 22), 4049–4056. https://doi.org/10.1242/jeb.104315

Green, W. C. H., & Rothstein, A. (1993). Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology*, *230*(2), 177–186. https://doi.org/10.1111/j.1469-7998.1993.tb02680.x

Hare, K. M., Pledger, S., & Daugherty, C. H. (2008). Low incubation temperatures negatively influence locomotor performance and behavior of the nocturnal lizard *Oligosoma Suteri* (Lacertidae: Scincidae). *Copeia*, *2008*(1), 16–22. https://doi.org/10.1643/cp-06-275

Harriman, V. B., Dawson, R. D., Bortolotti, L. E., & Clark, R. G. (2017). Seasonal patterns in reproductive success of temperate-breeding birds: Experimental tests of the date and quality hypotheses. *Ecology and Evolution*, *7*(7), 2122–2132. https://doi.org/10.1002/ece3.2815

Hatchwell, B. J. (1991). An experimental study of the effects of timing of breeding on the reproductive success of common Guillemots (*Uria aalge*). *Journal of Animal Ecology*, *60*(3), 721–736. https://doi.org/10.2307/5410

Hennin, H. L., Bêty, J., Legagneux, P., … Love, O. P. (2016). Energetic physiology mediates individual optimization of breeding phenology in a migratory arctic seabird. *The American Naturalist*, *188*(4), 434–445. https://doi.org/10.1086/688044

Heulin, B. (1985). Maturité sexuelle et âge à la première reproduction dans une population de plaine de Lacerta vivipara. *Canadian Journal of Zoology*, *63*(8), 1773–1777. https://doi.org/10.1139/z85-266

Hirose, F., Kazama, K., Ito, M., & Watanuki, Y. (2012). Accelerated growth rates in late-hatched Rhinoceros Auklet *Cerorhinca monocerata* chicks depend on food conditions and growth stage: An experimental approach. *Ibis*, *154*(2), 296–306. https://doi.org/10.1111/j.1474-919x.2011.01205.x

Iler, A. M., CaraDonna, P. J., Forrest, J. R. K., & Post, E. (2021). Demographic consequences of phenological shifts in response to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), null. https://doi.org/10.1146/annurev-ecolsys-011921-032939

Le Henanff, M., Meylan, S., & Lourdais, O. (2013). The sooner the better: Reproductive phenology drives ontogenetic trajectories in a temperate squamate (*Podarcis muralis*). *Biological Journal of the Linnean Society*, *108*(2), 384–395. https://doi.org/10.1111/j.1095-8312.2012.02005.x

Lecomte, J., Clobert, J., & Massot, M. (1992). Sex identification in juveniles of *Lacerta vivipara*. *Amphibia-Reptilia*, *13*(1), 21–25. https://doi.org/10.1163/156853892x00193

Li, S. -R., Hao, X., Wang, Y., … Du, W. -G. (2018). Female lizards choose warm, moist nests that improve embryonic survivorship and offspring fitness. *Functional Ecology*, *32*(2), 416–423. https://doi.org/10.1111/1365-2435.12995

Liu, W., Liu, P., Cui, L., … Sun, B. (2022). Moderate climate warming scenarios during embryonic and post-embryonic stages benefit a cold-climate lizard. *Functional Ecology*, *36*(5), 1137–1150. https://doi.org/10.1111/1365-2435.14032

Lourdais, O., Brischoux, F., DeNardo, D., & Shine, R. (2004). Protein catabolism in pregnant snakes (*Epicrates cenchria* maurus Boidae) compromises musculature and performance after reproduction. *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology*, *174*(5), 383–391. https://doi.org/10.1007/s00360-004-0424-6

Mangel, M., & Munch, S. B. (2005). A life-history perspective on short- and long-term consequences of compensatory growth. *The American Naturalist*, *166*(6), E155–E176. https://doi.org/10.1086/444439

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? *Trends in Ecology & Evolution*, *16*(5), 254–260. https://doi.org/10.1016/s0169-5347(01)02124-3

Mitchell, T. S., Hall, J. M., & Warner, D. A. (2018). Female investment in offspring size and number shifts seasonally in a lizard with single-egg clutches. *Evolutionary Ecology*, *32*(2-3), 231–245. https://doi.org/10.1007/s10682-018-9936-5

Moreno, J. (1998). The determination of seasonal declines in breeding success in seabirds. *Etología: Revista de La Sociedad Española de Etología*, *6*, 17–31.

Nilsson, J. -A. (1994). Energetic Bottle-necks during breeding and the reproductive cost of being too early. *Journal of Animal Ecology*, *63*(1), 200–208. https://doi.org/10.2307/5595

Noble, D. W. A., Stenhouse, V., & Schwanz, L. E. (2018). Developmental temperatures and phenotypic plasticity in reptiles: A systematic review and meta-analysis. *Biological Reviews of the Cambridge Philosophical Society*, *93*(1), 72–97. https://doi.org/10.1111/brv.12333

Öberg, M., Pärt, T., Arlt, D., … Low, M. (2014). Decomposing the seasonal fitness decline. *Oecologia*, *174*(1), 139–150. https://doi.org/10.1007/s00442-013-2763-z

Olsson, M., & Shine, R. (1997). The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): Why early clutches are better. *Journal of Evolutionary Biology*, *10*(3), 369–381. https://doi.org/10.1046/j.1420-9101.1997.10030369.x

Orizaola, G., Dahl, E., & Laurila, A. (2010). Compensating for delayed hatching across consecutive life-history stages in an amphibian. *Oikos*, *119*(6), 980–987. https://doi.org/10.1111/j.1600-0706.2009.17956.x

Pärt, T., Knape, J., Low, M., … Arlt, D. (2017). Disentangling the effects of date, individual, and territory quality on the seasonal decline in fitness. *Ecology*, *98*(8), 2102–2110. https://doi.org/10.1002/ecy.1891

Pearson, P. R., & Warner, D. A. (2018). (2018). Early hatching enhances survival despite beneficial phenotypic effects of late-season developmental environments. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1874), 20180256. https://doi.org/10.1098/rspb.2018.0256

Perrins, C. M. (1970). The timing of birds' breeding seasons. *Ibis*, *112*(2), 242–255. https://doi.org/10.1111/j.1474-919x.1970.tb00096.x

Price, E. R. (2017). The physiology of lipid storage and use in reptiles. *Biological Reviews of the Cambridge Philosophical Society*, *92*(3), 1406–1426. https://doi.org/10.1111/brv.12288

Qualls, C. P., & Andrews, R. M. (1999). Cold climates and the evolution of viviparity in reptiles: Cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. *Biological Journal of the Linnean Society*, *67*(3), 353–376. https://doi.org/10.1111/j.1095-8312.1999.tb01939.x

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Radchuk, V., Reed, T., Teplitsky, C., … Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, *10*(1), 3109. https://doi.org/10.1038/s41467-019-10924-4

Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Rowe, L., Ludwig, D., & Schluter, D. (1994). Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist*, *143*(4), 698–722. https://doi.org/10.1086/285627. http://www.jstor.org/stable/2462907

Rutschmann, A., Miles, D. B., Le Galliard, J. -F., … Clobert, J. (2016). Climate and habitat interact to shape the thermal reaction norms

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of breeding phenology across lizard populations. *The Journal of Animal Ecology*, *85*(2), 457–466. https://doi.org/10.1111/1365-2656.12473

Sauve, D., Friesen, V. L., & Charmantier, A. (2021). The effects of weather on avian growth and implications for adaptation to climate change. *Frontiers in Ecology and Evolution*, *9*, 569741. https://www.frontiersin.org/articles/10.3389/fevo.2021.569741

Shine, R. (2003). Locomotor speeds of gravid lizards: Placing 'costs of reproduction' within an ecological context. *Functional Ecology*, *17*(4), 526–533. https://doi.org/10.1046/j.1365-2435.2003.00756.x

Shine, R., & Harlow, P. (1993). Maternal thermoregulation influences offspring viability in a viviparous lizard. *Oecologia*, *96*(1), 122–127. https://doi.org/10.1007/BF00318039

Shine, R., & Olsson, M. (2003). When to be born? Prolonged pregnancy or incubation enhances locomotor performance in neonatal lizards (Scincidae). *Journal of Evolutionary Biology*, *16*(5), 823–832. https://doi.org/10.1046/j.1420-9101.2003.00600.x

Simonin, P. W., Parrish, D. L., Rudstam, L. G., … Sullivan, P. J. (2016). Interactions between hatch dates, growth rates, and mortality of age-0 native rainbow smelt and nonnative alewife in Lake Champlain. *Transactions of the American Fisheries Society*, *145*(3), 649–656. https://doi.org/10.1080/00028487.2016.1143401

Sinervo, B. (1990). Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia*, *83*(2), 228–237. https://doi.org/10.1007/BF00317757

Sinervo, B., & Doughty, P. (1996). Interactive effects of offspring size and timing of reproduction on offspring reproduction: Experimental, maternal, and quantitative genetic aspects. *Evolution*, *50*(3), 1314–1327. https://doi.org/10.1111/j.1558-5646.1996.tb02371.x

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Sun, B. -J., Ma, L., Li, S. -R., … Du, W. -G. (2018). Phenology and the physiological niche are co-adapted in a desert-dwelling lizard. *Functional Ecology*, *32*(11), 2520–2530. https://doi.org/10.1111/1365-2435.13201

Uller, T., & Olsson, M. (2010). Offspring size and timing of hatching determine survival and reproductive output in a lizard. *Oecologia*, *162*(3), 663–671. https://doi.org/10.1007/s00442-009-1503-x

Verhulst, S., & Nilsson, J.-A. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *363*(1490), 399–410. https://doi.org/10.1098/rstb.2007.2146

Verhulst, S., van Balen, J. H., & Tinbergen, J. M. (1995). Seasonal decline in reproductive success of the great tit: Variation in time or quality? *Ecology*, *76*(8), 2392–2403. https://doi.org/10.2307/2265815

Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, *3*(6), 879–885. https://doi.org/10.1038/s41559-019-0880-8

Wapstra, E. (2000). Maternal basking opportunity affects juvenile phenotype in a viviparous lizard. *Functional Ecology*, *14*(3), 345–352. https://doi.org/10.1046/j.1365-2435.2000.00428.x

Wapstra, E., Uller, T., While, G. M., … Shine, R. (2010). Giving offspring a head start in life: Field and experimental evidence for selection on maternal basking behaviour in lizards. *Journal of Evolutionary Biology*, *23*(3), 651–657. https://doi.org/10.1111/j.1420-9101.2009.01924.x

Warner, D. A., & Shine, R. (2007). Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size. *Oecologia*, *154*(1), 65–73. https://doi.org/10.1007/s00442-007-0809-9

Watts, H. E., Robart, A. R., Hahn, T. P., & Gomulkiewicz, R. (2022). Environmental cue integration and phenology in a changing world. *Integrative and Comparative Biology*, *62*(4), 972–979. https://doi.org/10.1093/icb/icac032

While, G. M., Noble, D. W. A., Uller, T., … Schwanz, L. E. (2018). Patterns of developmental plasticity in response to incubation temperature in reptiles. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *329*(4-5), 162–176. https://doi.org/10.1002/jez.2181

While, G. M., Uller, T., & Wapstra, E. (2009). Offspring performance and the adaptive benefits of prolonged pregnancy: Experimental tests in a viviparous lizard. *Functional Ecology*, *23*(4), 818–825. https://doi.org/10.1111/j.1365-2435.2009.01544.x

Winkler, D. W., Hallinger, K. K., Pegan, T. M., … Yoon, H. S. (2020). Full lifetime perspectives on the costs and benefits of lay-date variation in tree swallows. *Ecology*, *101*(9), e03109. https://doi.org/10.1002/ecy.3109

Zhong, Z., He, B., Chen, H. W., … Zhao, X. (2023). Reversed asymmetric warming of sub-diurnal temperature over land during recent decades. *Nature Communications*, *14*(1), Art. 1. https://doi.org/10.1038/s41467-023-43007-6

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