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Théo Bodineau

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*Institut d'Écologie et des Sciences de l'Environnement de Paris - Équipe
Écophysiologie évolutive*

Se reproduire dans des climats changeants : déterminants et conséquences des modifications de la phénologie de la reproduction chez un reptile vivipare

Par **Théo BODINEAU**

Thèse de doctorat en **Sciences agronomiques et écologiques**



Dirigée par **Sandrine MEYLAN** et **Pierre DE VILLEMEREUIL**

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Article 2 - Bodineau, T., Le Galliard, J-F., Rutschmann, A., Richard, M., Massot, M., Clobert, J., Meylan, S. & de Villemereuil, P. High thermal plasticity, low heritability and constant directional selection on breeding phenology in a viviparous ectotherm. **In preparation for *Journal of Animal Ecology*.**

Article 3 - Bodineau, T., de Villemereuil, P., Agostini, S., Decenci re, B., Le Galliard, J.-F. & Meylan, S. (2024). Breeding phenology drives variation in reproductive output, reproductive costs, and offspring fitness in a viviparous ectotherm. ***Journal of Evolutionary Biology***, 37(9),1023-1034. <https://doi.org/10.1093/jeb/voae086>

Article 4 - Bodineau, T., de Villemereuil, P., Lemaire, B., Agostini, S., Decenci re, B., Millet, M., Meylan, S. & Le Galliard, J.-F. A multi-trait evaluation of patterns and fitness consequences of breeding phenology plasticity with nocturnal warming and food restriction in a lizard. **Under review in *Functional ecology*.**

Article 5* (Annexe) - Bodineau, T., Chabaud, C., Decenci re, B., Agostini, S., Lourdais, O., Meylan, S., & 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>

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Communications scientifiques



Influence des ressources nutritives et hydriques sur les comportements de thermo-hydrorégulation d'un ectotherme. Bodineau, T., Chabaud, C., Decencière, B., Agostini, S., Lourdaï, O., Meylan, S. & Le Galliard, J-F. **49^{ème} congrès de la société herpétologique de France – 7 octobre 2022.**

Fitness consequences of breeding phenology plasticity with nocturnal warming and food restriction in a lizard. Bodineau, T., de Villemereuil, P., Lemaire, B., Agostini, S., Decencière, B., Millet, M., Meylan, S. & Le Galliard, J-F. **3rd Joint Congress on Evolutionary Biology – Montréal – 27 juillet 2024.**

Formations

Nom de la formation	Type	Durée
Intégrité scientifique dans les métiers de la recherche	Ethique et intégrité scientifique	15h
Utilisation d'animaux de la faune sauvage non-hébergée à des fins scientifiques	Outils et méthodes pour la thèse	57h
Journées d'intégration et de préparation opérationnelle au projet professionnel	Projet professionnel et valorisation des compétences	24h
Réflexion sur la pédagogie universitaire en biologie	Projet professionnel et valorisation des compétences	2 jours

Enseignements à Sorbonne Université

Unité d'enseignement	Niveau	Type	Heures
Écologie et évolution	Licence 2	TD / TP	106
Interactions durables, écologie et évolution	Licence 3	TD / TP	42
Démarche scientifique et application à l'écologie	Licence 3	TP	26
Écologie marine	Licence 2	TD	18

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Romain SCHILD	Encadrant	L3 - Université de Rouen	Variation de la date de parturition chez le lézard vivipare.
Marie-Ornelia VERGER	Encadrant	L3 - Sorbonne Université	Optimisation des dates de reproduction chez un ectotherme vivipare.
Léon KOENIG	Encadrant	L3 - Université de Strasbourg	Optimisation des dates de reproduction chez un ectotherme vivipare.
Sarah Alves HELENO	Encadrant	L3 - Université de Paris	Optimisation des dates de reproduction chez un ectotherme vivipare.
Sonia ROGER	Encadrant	L3 - Sorbonne Université	Optimisation des dates de reproduction chez un ectotherme vivipare.
Constance BERTRAND	Co-encadrant	M2 -ENSEGID Bordeaux	Approche expérimentale de l'étude de l'optimisation de la date de parturition chez le lézard vivipare.
Leïla BARROUILLET	Encadrant	L2 - Université de Bordeaux	Phénologie de la reproduction et changements climatiques chez le lézard vivipare.
Charline ANDREANI	Encadrant	L3 - Université Paris-Saclay	Effets des températures nocturnes et de la disponibilité alimentaire pendant la gestation sur la fitness des mères et des juvéniles.
Tom COMPAIN	Encadrant	L3 - Université de Poitiers	Effets des températures nocturnes et de la disponibilité alimentaire pendant la gestation sur la fitness des mères et des juvéniles.
Max DELPY	Encadrant	L3 - Université Clermont Auvergne	Étude des effets des températures nocturnes et de la disponibilité alimentaire pendant la gestation sur la fitness des mères et des juvéniles.
Fabien FOURNIER	Encadrant	L2 - Sorbonne Université	Étude du lien causal entre la date de parturition et la fitness des juvéniles et des mères.

Nom prénom	Type d'encadrement	Niveau - Université / école	Sujet
Camille HAMON	Encadrant	L2 - Université Paris-Saclay	Conséquences de la date de parturition sur la survie et la croissance des juvéniles chez le lézard vivipare.
Anaïs MARHUENDA	Encadrant	L2 - Sorbonne Université	Effets des températures nocturnes et de la disponibilité alimentaire pendant la gestation sur la fitness des mères et des juvéniles.
Timothée GAZEAU	Encadrant	M1 - École Pratique des Hautes Études	Étude des déterminants individuels et environnementaux sur la phénologie de la reproduction chez un lézard vivipare.
Matéo MILLET	Encadrant	M1 - Université de Tours	Étude des effets des températures nocturnes et de la disponibilité alimentaire pendant la gestation sur les performances locomotrices des juvéniles.
Marie-Lou CAMPOS	Co-encadrant	M1 - Université Paris-Saclay	Déterminants prénataux et postnataux du mélanisme chez des lézards juvéniles par une approche en jardin commun.
Loïz BOUDARD	Co-encadrant	M1 - Sorbonne Université	Quantification des effets climatiques prénataux et postnataux agissants sur la croissance et la survie chez le lézard vivipare : approche en jardin commun.
Divina BEEJMOHUN	Co-encadrant	M2 - Université Paris-Saclay	Variations géographiques des traits phénotypiques et reproductifs le long d'un gradient environnemental chez le lézard vivipare.

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AVANT-PROPOS

Les changements phénologiques - c'est-à-dire les modifications du timing des activités saisonnières en lien avec le climat - constituent une des manifestations les plus claires des impacts des changements climatiques chez de nombreuses espèces animales et végétales. Chez les ectothermes, c'est-à-dire les animaux ne pouvant pas réguler leur température corporelle via leur métabolisme, les événements phénologiques sont fortement influencés par les conditions thermiques de l'environnement compte tenu de leur thermorégulation comportementale et des effets thermodynamiques sur les processus physiologiques et le cycle de vie de ces organismes. Dans ce contexte, comprendre les effets du réchauffement et de l'avancement des dates de reproduction est essentiel pour quantifier les effets à court et long terme des changements climatiques sur ces organismes. Cette thèse vise à mieux caractériser les effets du climat ainsi que les déterminants et les conséquences de la phénologie de la reproduction chez un ectotherme vivipare. L'introduction de ce mémoire présente brièvement le contexte des changements climatiques présents et futurs, leurs conséquences génériques sur les ectothermes et l'état actuel des connaissances sur les déterminants et les conséquences des dates de reproduction avec un focus sur les reptiles squamates (lézards et serpents). La partie centrale du mémoire présente 4 études rédigées sous la forme d'articles scientifiques qui sont intégrés dans 3 chapitres. Enfin, une discussion générale souligne les apports et les nouvelles questions soulevés par ce travail.

INTRODUCTION GÉNÉRALE



Tourbière des Narcettes – Montselgues. © Théo Bodineau

1. Impact du changement climatique sur les macroclimats

1.1 Modification des macroclimats thermiques et hydriques

Les tendances actuelles du changement climatique sont dominées par l'augmentation des émissions de gaz à effet de serre provenant principalement des activités humaines, telles que la combustion des énergies fossiles, le défrichement et la production alimentaire (Friedlingstein *et al.*, 2019; Hong *et al.*, 2021). Depuis le milieu du 20^e siècle, on assiste à une accélération de l'augmentation de la température moyenne à la surface du globe (Figure 1a), qui pourrait augmenter de 4°C d'ici la fin du 21^e siècle selon l'ampleur des émissions de gaz à effet de serre (Loarie *et al.*, 2009; IPCC, 2023). De plus, le changement climatique entraîne une modification du cycle de l'eau impactant les régimes de précipitations à la surface du globe (Fischer & Knutti, 2016; IPCC, 2023). Les précipitations moyennes dans un monde plus chaud montrent une variation spatiale plus importante : certaines régions connaissent une augmentation (e.g., régions des hautes latitudes) ou au contraire une diminution (e.g., régions subtropicales aride et semi-aride) des précipitations. Au-delà des modifications climatiques moyennes, le changement climatique induit également une augmentation de la fréquence et de l'intensité des événements climatiques extrêmes comme les vagues de chaleur ou de sécheresses (Figure 1b), des inondations et des ouragans (Chen *et al.*, 2018; Stillman, 2019; AghaKouchak *et al.*, 2020).

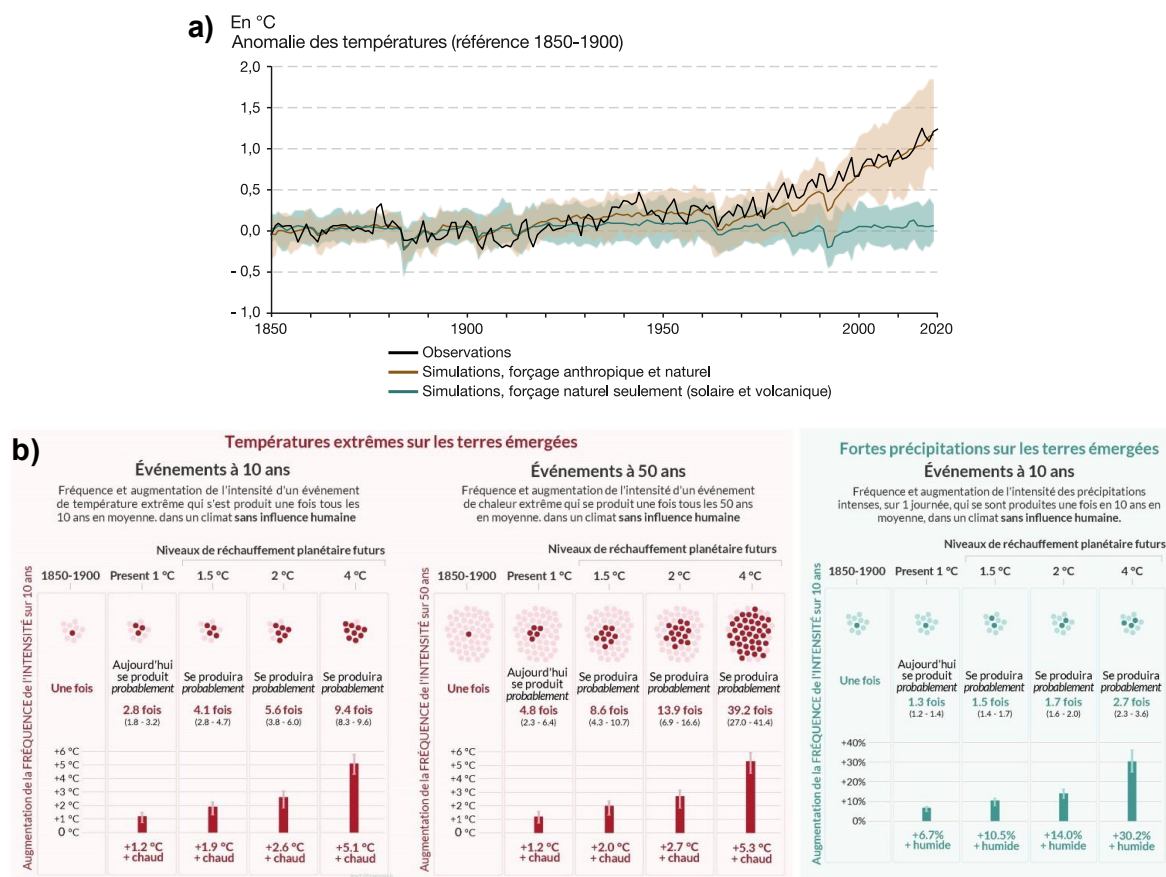


Figure 1 : (a) Changements des températures moyennes annuelles à la surface du globe entre 1850 et 2020 (ligne noire) comparées au modèle de simulation climatique (CMIP6) de la réponse climatique aux facteurs à la fois humains et naturels (marrons), et aux facteurs uniquement naturels (activité solaire et volcanique, verte). (b) Augmentation de la fréquence et de l'intensité des événements extrêmes thermiques en fonction des scénarios de changement climatique. Modifié d'après IPCC, 2021.

1.2 Asymétrie du réchauffement diurne et nocturne

Le changement climatique est également caractérisé par un réchauffement diurne et nocturne asymétrique dans la plupart des régions du globe (Karl *et al.*, 1991; Easterling *et al.*, 1997; Vose *et al.*, 2005; Davy *et al.*, 2017). Cette asymétrie journalière du réchauffement varie spatialement, mais on observe en moyenne une tendance mondiale à une augmentation plus rapide des températures nocturnes que des températures diurnes (Figure 2a; Cox *et al.*, 2020). De plus, les projections climatiques prévoient une augmentation plus intense des températures nocturnes au cours du

siècle et une augmentation du pourcentage de nuits exceptionnellement chaudes enregistrées chaque année de 20 à 40 % d'ici 2100 (Karl *et al.*, 1991; Sillmann *et al.*, 2013). Les raisons sous-jacentes à cette asymétrie restent encore débattues, mais elle pourrait être principalement liée à des changements dans la nébulosité globale, car les nuages ont un impact opposé sur les températures en fonction du moment de la journée (Figure 2b; Easterling *et al.*, 1997; Davy *et al.*, 2017). Durant le jour, l'augmentation de la nébulosité entraîne une diminution des températures diurnes en atténuant le rayonnement solaire au sol alors qu'elle favorise le renvoi du rayonnement infrarouge émis par la Terre vers le sol durant la nuit (Dai *et al.*, 1999; Sun *et al.*, 2000). D'autres facteurs pourraient aussi être impliqués dans le réchauffement asymétrique comme une augmentation des précipitations ou de l'humidité au sol et son effet positif sur l'évapotranspiration diurne (Dai *et al.*, 1999), les variations de circulation atmosphérique et de la couche limite planétaire (Vose *et al.*, 2005; Davy *et al.*, 2017) ou des changements dans l'utilisation des terres (Zhou *et al.*, 2009). Jusqu'à présent, les effets écologiques de cette asymétrie ont été sous-considérés et principalement étudiés chez les plantes et les insectes (Speights *et al.*, 2017; Sadok & Jagadish, 2020; Rutschmann *et al.*, 2024). Puisque le réchauffement diurne et nocturne peuvent affecter différemment les traits développementaux et reproductifs des organismes (e.g., Speights & Barton, 2019; Bruschi *et al.*, 2023) et que le réchauffement nocturne peut accentuer les effets du réchauffement diurne (e.g., Zhao *et al.*, 2014), négliger les effets du réchauffement nocturne pourrait avoir des conséquences importantes sur notre compréhension de la capacité des organismes à faire face aux changements climatiques.

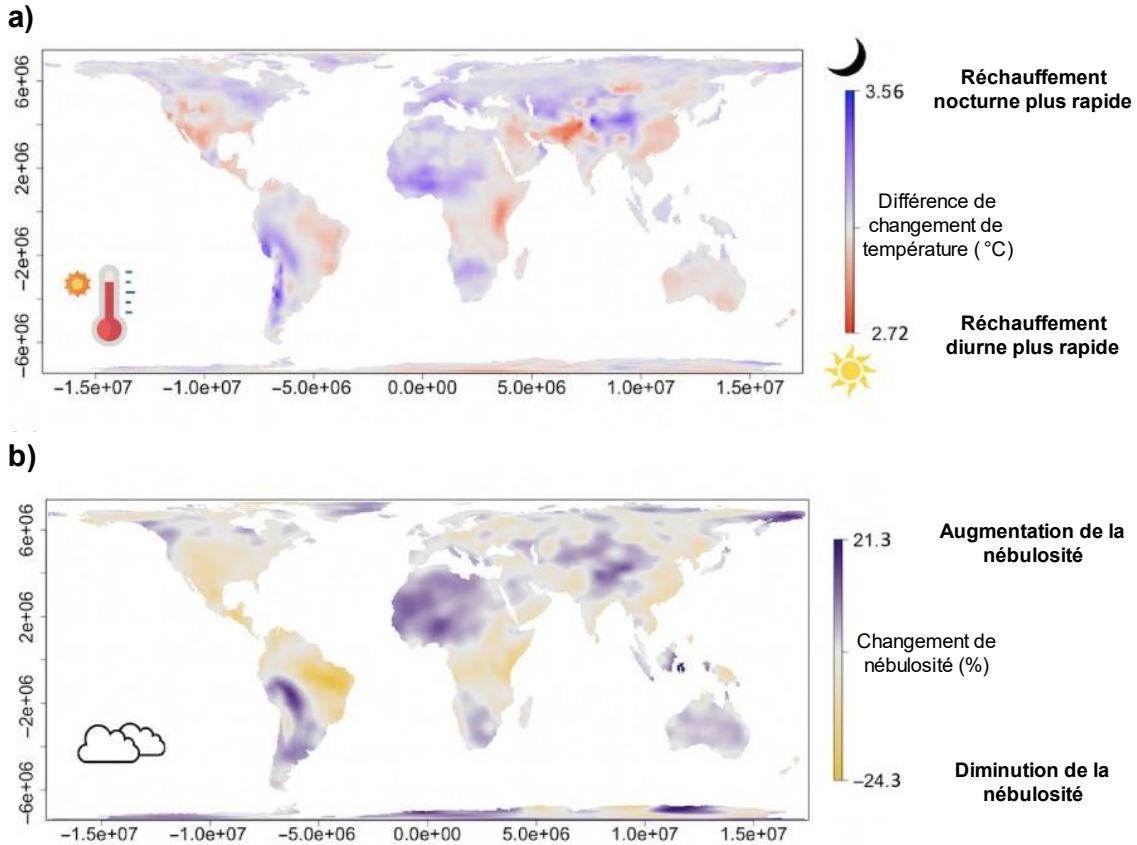


Figure 2 : Variation spatiale de l'asymétrie du réchauffement et de la nébulosité diurne et nocturne entre 1983 et 2017. (a) Variation spatiale de l'asymétrie du réchauffement entre la température maximale diurne et la température minimale nocturne. Le rouge illustre les endroits où le changement diurne a été plus rapide et le bleu les endroits où le changement a été plus rapide pendant la nuit. (b) Variation spatiale du changement de la nébulosité. Le jaune indique les endroits où la nébulosité a diminué et le violet les endroits où la nébulosité a augmenté. Les changements de la température et de la nébulosité ont été calculés en soustrayant le changement de température ou de nébulosité diurne au changement de température ou de nébulosité nocturne. Modifié d'après Cox et al., 2020.

2. Sensibilité des ectothermes au climat

Les ectothermes – c'est-à-dire les organismes ne produisant pas ou peu de chaleur interne via leur métabolisme – constituent la vaste majorité de la biodiversité terrestre (Wilson, 1992). L'ectothermie confère des avantages sur le plan énergétique en limitant les forts coûts de maintenance induits par la production métabolique de

chaleur. Les dépenses énergétiques métaboliques sont ainsi de l'ordre de 12 à 20 fois inférieur chez les ectothermes comparativement aux endothermes de même masse ce qui leur permet d'allouer davantage d'énergie vers la croissance ou la reproduction (Nagy, 2005). En contrepartie, les organismes ectothermes dépendent fortement des sources de chaleur externes pour réguler leur température corporelle, présentent souvent des périodes d'activité plus restreintes au cours de l'année et sont plus sensibles aux fluctuations des conditions thermiques de leur environnement que les endothermes. De ce fait, les ectothermes sont souvent considérés comme des organismes qui seront particulièrement affectés par les modifications climatiques futures (Deutsch *et al.*, 2008; Hayden Bofill & Blom, 2024).

2.1 Sensibilité des performances chez les ectothermes

Toutes les réactions biochimiques au sein d'un organisme sont fortement affectées par la température corporelle (Hochachka & Somero, 2002b). Cette dépendance thermique des réactions métaboliques impacte les performances de l'organisme comme la locomotion (e.g., Lachenicht *et al.*, 2010; Gómez Alés *et al.*, 2018), la capture et l'assimilation des proies (e.g., Van Damme *et al.*, 1991; Avery *et al.*, 1993), la croissance (e.g., Angilletta *et al.*, 2004; Ju *et al.*, 2011) ou la reproduction (Berger *et al.*, 2008; Clarke & Zani, 2012). La sensibilité thermique des performances et plus généralement de la fitness (i.e., valeur sélective) peut être résumée sous la forme d'une courbe de performance thermique décrivant la relation entre les performances d'un organisme (un trait physiologique, comportemental ou lié à la fitness) et sa température corporelle (Figure 3a). Les courbes de performance thermique sont généralement caractérisées par une croissance linéaire à exponentielle des performances avec l'augmentation de la température corporelle jusqu'à ce qu'un maximum soit atteint dans une plage optimale de température. Cet optimum est

ensuite suivi d'une diminution rapide des performances à des températures corporelles supérieures à l'optimum. Les performances sont bornées par des limites thermiques critiques qui correspondent aux seuils thermiques inférieur (CT_{min}) et supérieur (CT_{max}) au-delà desquels les animaux ne peuvent pas survivre sur le long terme.

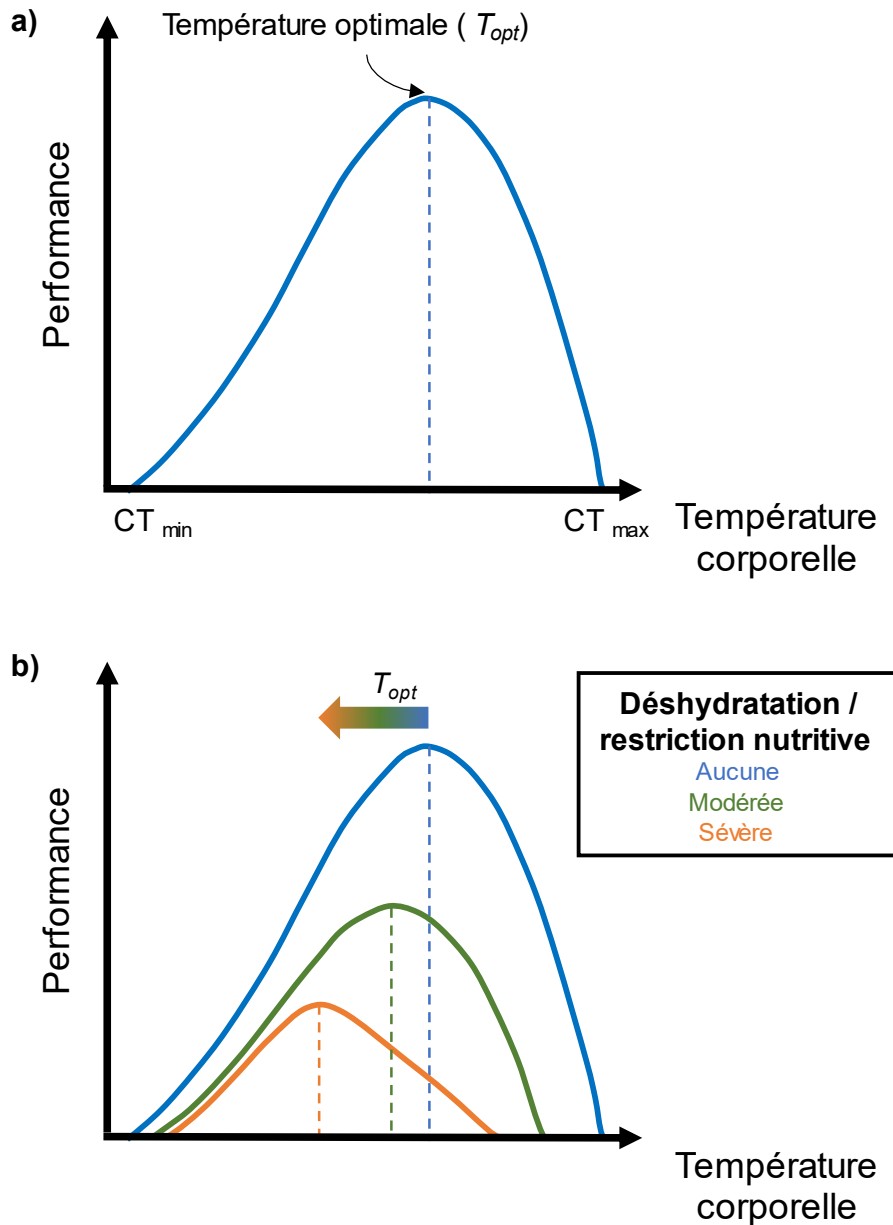


Figure 3 : Courbe de performance thermique hypothétique d'un ectotherme (a) en fonction de son état d'hydratation ou de la disponibilité des ressources nutritives (b). Dans la plage de tolérance de l'animal (i.e., entre les limites thermiques critiques minimales (CT_{min}) et maximales (CT_{max})), les performances augmentent avec la température jusqu'à atteindre une température optimale (T_{opt}) puis diminuent rapidement au-delà de T_{opt} . La déshydratation et la restriction nutritive peuvent à la

fois abaisser les performances d'un organisme à sa température optimale, mais aussi diminuer la température optimale et la plage de tolérance thermique au-delà de laquelle l'animal meurt. Cette figure est inspirée de Rozen-Rechels et al., 2019. Ces courbes de performances thermiques hypothétiques dépendantes de l'état d'hydratation et de la disponibilité des ressources ont été construites à partir d'études sur les capacités locomotrices d'amphibiens déshydratés (e.g., Preest & Pough, 1989; Anderson & Andrade, 2017) et d'études sur les taux de croissance de poissons (e.g., Brett et al., 1969; Elliott, 1982) ou de phytoplanctons (e.g., Thomas et al., 2017).

La sensibilité thermique des performances d'un organisme peut dépendre de facteurs biotiques et abiotiques qui interagissent avec la température pour déterminer les performances (Figure 3b). Premièrement, la disponibilité et les taux d'assimilation des proies peuvent modifier la sensibilité thermique des performances en modifiant la forme de la courbe de performance et la température optimale maximisant les performances. Par exemple, il est bien établi que la température optimale de croissance dépend de la disponibilité et du taux d'ingestion de nourriture (Hardison & Eliason, 2024). En général, des températures élevées maximisent les taux de croissance lorsque l'apport alimentaire est important, mais les taux de croissance diminuent avec l'augmentation de la température lorsque l'apport alimentaire est réduit (e.g., Elliott, 1982; Cui & Wootton, 1988; Letcher & Bengtson, 1993). De plus, la disponibilité de l'eau dans l'environnement peut impacter la sensibilité thermique des performances en influençant l'état d'hydratation de l'organisme. Les effets combinés de la température et de l'état d'hydratation sur les performances ont été principalement étudiés chez les amphibiens (Preest & Pough, 1989; Anderson & Andrade, 2017). Chez ces organismes, une déshydratation modérée ou sévère entraîne généralement une diminution des capacités maximales de performance locomotrice, une diminution de la température corporelle optimale maximisant les performances, ainsi qu'une réduction de l'étendue des performances et de la plage de tolérance thermique. Une explication immédiate des effets interactifs de la température et l'état d'hydratation ou

de la disponibilité de la nourriture est que la déshydratation ou la restriction nutritive modifie la sensibilité et la tolérance thermique du métabolisme (Akerman *et al.*, 2016).

2.2 Le concept de thermo-hydrorégulation

Pour faire face à ces contraintes environnementales, la régulation conjointe de la température corporelle et de l'équilibre hydrique est essentielle pour l'optimisation des performances et la maximisation de la fitness d'un organisme (Figure 4).

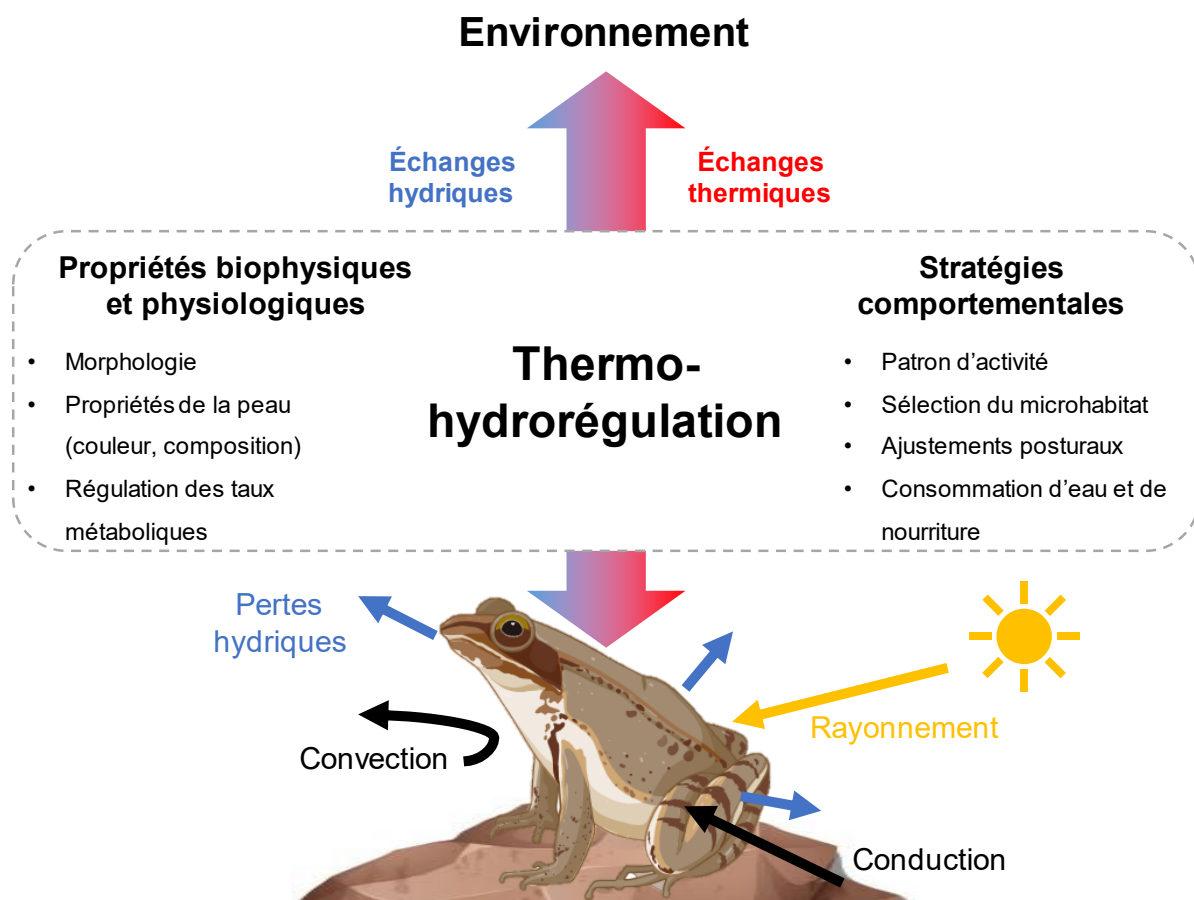


Figure 4 : Principaux échanges thermiques et hydriques entre un ectotherme et l'environnement. Ces échanges sont modulés par les stratégies de thermo-hydrorégulation de l'organisme qui impliquent les propriétés biophysiques et physiologiques de l'organisme ainsi que les stratégies comportementales.

2.2.1 La thermorégulation comportementale

La thermorégulation constitue l'ensemble des processus impliqués dans la régulation de la température corporelle ou du métabolisme énergétique (Angilletta Jr., 2009). La thermorégulation permet de maintenir une température corporelle dans une plage thermique optimale maximisant les processus biologiques essentiels tels que l'activité enzymatique. Chez les organismes ectothermes, la thermorégulation est principalement comportementale et l'animal va réguler sa température corporelle en modulant les échanges de chaleur avec l'environnement par son comportement (Figure 4). Une thermorégulation efficace garantit le maintien d'une température corporelle proche de la température optimale, maximisant les performances de l'organisme et *in fine* sa fitness, même lorsque les températures environnementales sont sous-optimales (Huey, 1982; Kearney *et al.*, 2009; Taylor *et al.*, 2021). Pour atteindre cette température, les animaux ectothermes peuvent tout d'abord s'appuyer sur des changements de patron d'activité journalier (Moore *et al.*, 2018). Par exemple, lorsque les températures environnementales sont trop chaudes, les ectothermes peuvent limiter le risque d'hyperthermie en limitant leur activité aux heures les plus fraîches de la journée (Gunderson & Leal, 2015). Des changements de posture ou d'orientation par rapport à l'irradiance solaire peuvent aussi contribuer à la régulation de la température corporelle en modulant les surfaces d'échanges thermiques entre l'animal et l'environnement (Barton *et al.*, 2014). La coloration et la réflectance de la surface cutanée peuvent également moduler les échanges thermiques (Stuart-Fox *et al.*, 2017). Par exemple, des individus plus mélaniques peuvent se réchauffer plus rapidement et atteindre des températures corporelles plus élevées que les individus plus clairs, ce qui peut conférer des avantages dans des conditions de faible température ambiante (Clusella Trullas *et al.*, 2007; Clusella-Trullas *et al.*, 2009).

Enfin, les ectothermes peuvent aussi réguler leur température corporelle en sélectionnant des microhabitats en fonction de leur température (Sears *et al.*, 2016). La sélection de microhabitats ombragés ou de refuges thermiques peut permettre de réguler sa température corporelle dans des environnements chauds alors que la sélection de microhabitats plus chauds ou ensoleillés peut permettre d'atteindre une température corporelle optimale dans des environnements froids (Sunday *et al.*, 2014).

2.2.2 L'hydrorégulation

L'hydrorégulation englobe l'intégralité des processus liés à la régulation de l'équilibre hydrique de l'organisme afin de maintenir un état d'hydratation optimal. Chez les ectothermes, les pertes hydriques respiratoires sont fortement corrélées aux taux métaboliques et les pertes hydriques cutanées dépendent du gradient de pression de vapeur d'eau entre l'environnement et l'organisme ainsi que de la perméabilité de la barrière cutanée (Lillywhite, 2006; Chown *et al.*, 2011). Ainsi, des environnements secs ou une température corporelle élevée peuvent augmenter les pertes hydriques totales et perturber l'équilibre hydrique de l'organisme (Seebacher & Alford, 2002; Bodineau *et al.*, 2024). Le maintien d'un état d'hydratation optimal implique la régulation des pertes et des apports hydriques via des ajustements comportementaux (Figure 4). Par exemple, des modifications des comportements de thermorégulation, des patrons d'activité ou de la posture peuvent limiter les pertes hydriques (Pough *et al.*, 1983; Rozen-Rechels *et al.*, 2020; Le Galliard *et al.*, 2021) et la sélection de microhabitats humides (Pintor *et al.*, 2016; Dezetter *et al.*, 2023) ou avec de l'eau de boisson disponible peut favoriser le maintien d'un bon état d'hydratation. Des mécanismes physiologiques favorisant la conservation d'eau sont aussi impliqués dans la régulation de l'équilibre hydrique comme la réduction des pertes hydriques cutanées via des modifications de la composition et de la structure de la peau

(Lillywhite, 2006; Wegener *et al.*, 2014) ou la réduction des taux métaboliques (Chown, 2002). Enfin, certaines espèces peuvent stocker de l'eau ou utiliser l'eau issue des réactions cataboliques pour maintenir leur équilibre hydrique (Chown, 2002; Davis & DeNardo, 2007).

2.2.3 Liens fonctionnels entre la thermorégulation et l'hydrorégulation

Longtemps étudiées séparément, la thermorégulation et l'hydrorégulation sont des processus fonctionnellement liés, car les conditions thermiques et hydriques (e.g., humidité, disponibilité de l'eau) varient souvent conjointement dans l'environnement et, car de nombreux processus physiologiques et comportements sont conjointement impliqués dans la régulation de la balance thermique et hydrique (Rozen-Rechels *et al.*, 2019). Par exemple, au niveau physiologique, les pertes hydriques cutanées augmentent avec la température corporelle tandis que la perte d'eau respiratoire s'accroît avec l'augmentation du métabolisme et de la fréquence respiratoire due à la chaleur. Au niveau comportemental, bien que certains comportements peuvent à la fois optimiser la thermorégulation et l'hydrorégulation (e.g., sélection d'un microhabitat chaud et humide, restriction de l'activité comportementale lors des phénomènes de vagues de chaleur ou de sécheresse), l'interdépendance de la température corporelle et des pertes hydriques peut conduire à un compromis comportemental où une stratégie thermorégulatrice optimise les performances au détriment de l'équilibre hydrique. L'existence de réponses comportementales et physiologiques partagées entre l'hydrorégulation et la thermorégulation ainsi que l'existence de compromis entre ces deux processus a abouti à la proposition du concept de « thermo-hydrorégulation » (Rozen-Rechels *et al.*, 2019). La thermo-hydrorégulation peut être définie comme un ensemble interactif de processus physiologiques et comportementaux permettant le

maintien conjoint d'un équilibre hydrique et thermique qui optimise les performances, la reproduction et la survie d'un organisme (Rozen-Rechels *et al.*, 2019).

2.3 Impacts des changements climatiques

L'augmentation des températures moyennes, de la fréquence des vagues de chaleur ou de sécheresse prévue dans les prochaines décennies (IPCC, 2023) pourraient atteindre les limites thermiques et hydriques supérieures de nombreux ectothermes et avoir des conséquences létales sur ces organismes (Gunderson & Stillman, 2015). Ces risques peuvent être tamponnés par des ajustements plastiques ou adaptatifs de la physiologie et des comportements (Huey *et al.*, 2012; Seebacher *et al.*, 2015; Logan & Cox, 2020; Enriquez-Urzelai & Gvoždík, 2024). Toutefois, si la plasticité ou si les changements adaptatifs sont insuffisants ou trop lents, les modifications climatiques vont compromettre le maintien de l'homéostasie (i.e., l'ensemble des paramètres physiologiques essentiels à la vie) ce qui peut affecter négativement les performances, la survie et la reproduction des individus (Figure 5) et entraîner un risque accru d'extinction des populations (Huey *et al.*, 2010; Sinervo *et al.*, 2010; Kingsolver *et al.*, 2013; Zhang *et al.*, 2022).

Effets potentiels des changements climatiques sur les ectothermes

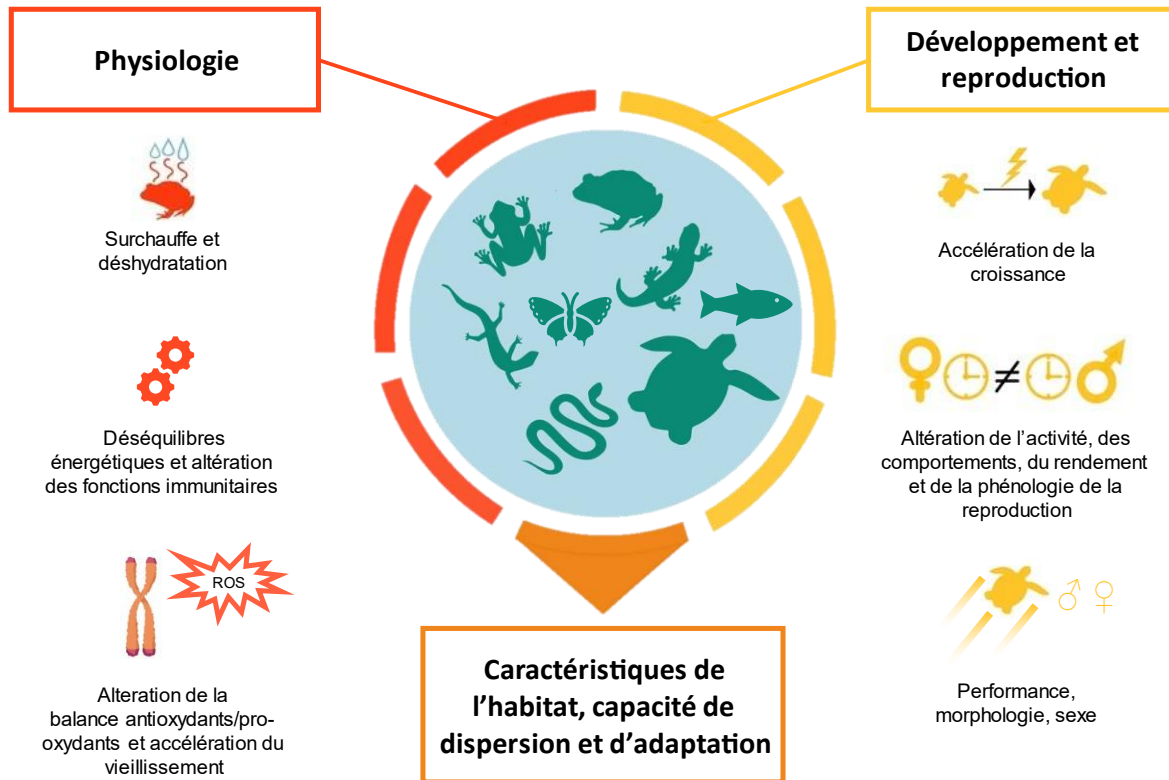


Figure 5 : Conséquences potentielles des changements climatiques sur les ectothermes. Cette figure illustre les effets potentiels de la modification des régimes thermiques (e.g., augmentation moyenne des températures, vagues de chaleur) et hydriques (e.g., diminution de la disponibilité de l'eau, sécheresse) sur les processus physiologiques, développementaux et reproductifs des ectothermes. Les effets des changements climatiques dépendent des caractéristiques de l'habitat, de la capacité de dispersion et de la capacité des organismes à s'adapter aux contraintes de l'environnement. ROS : Espèces réactives de l'oxygène. Modifié d'après Hayden Bofill & Blom, 2024.

2.3.1 Altérations physiologiques

Les changements climatiques peuvent affecter les patrons de croissance et le bilan énergétique des ectothermes (Figure 5). Compte tenu de la dépendance thermique de leur métabolisme qui augmente généralement de manière exponentielle avec la température (Arrhenius, 1889; Gillooly *et al.*, 2001), les environnements plus chauds entraînent une augmentation des taux de croissance et des dépenses énergétiques

(Dillon *et al.*, 2010; Burraco *et al.*, 2020) qui doivent être compensées par une augmentation des apports énergétiques. Ces effets peuvent être modifiés par des épisodes de sécheresse ou de vagues de chaleur. En effet, une faible disponibilité de l'eau dans l'environnement et des températures environnementales supérieures aux seuils thermiques critiques peuvent réduire les fenêtres d'activité journalière des ectothermes et diminuer les apports alimentaires (Kearney, 2013; Kearney *et al.*, 2018; Doucette *et al.*, 2023). La diminution de l'apport énergétique due aux restrictions d'activité associée à l'accélération des coûts métaboliques à des températures élevées pourrait ainsi entraîner un « effondrement métabolique » impactant les performances individuelles et la viabilité des populations (Huey & Kingsolver, 2019). D'ailleurs, ces phénomènes de restriction d'activité en réponse à la restriction hydrique et au stress thermique ont été proposés comme des mécanismes explicatifs des extinctions de populations observées chez des lézards mexicains du genre *Sceloporus* (Sinervo *et al.*, 2010).

Les stress thermique et hydrique peuvent également affecter les processus de vieillissement des ectothermes (Burraco *et al.*, 2020) en causant des déséquilibres entre la production de substances pro-oxydantes et la capacité antioxydante des cellules entraînant ainsi un stress oxydatif sur le long terme (Yang *et al.*, 2010; Madeira *et al.*, 2013; Dupoué *et al.*, 2020a; Zhang *et al.*, 2023b). Le stress oxydatif peut causer des dommages à des biomolécules essentielles telles que les lipides membranaires, les protéines et l'ADN (Halliwell, 2007). Par exemple, le stress oxydatif est généralement considéré comme un mécanisme majeur de l'attrition des télomères qui sont des structures nucléoprotéiques répétées coiffant l'extrémité des chromosomes et permettant le maintien de la stabilité du génome (Shay & Wright, 2019). Ces dommages entraînent un vieillissement accéléré des cellules et de l'organisme entier

avec l'apparition de pathologies au cours du vieillissement (Halliwell & Gutteridge, 2015; Burraco *et al.*, 2020).

Enfin, les stress thermique et hydrique peuvent affecter l'immunocompétence - la capacité d'un individu à résister aux agents pathogènes et aux parasites grâce à la réponse de son système immunitaire - qui est une composante essentielle à la survie de l'individu en conditions naturelles (Lafferty, 2009; Graham *et al.*, 2011). D'une part, les températures environnementales et la déshydratation peuvent impacter l'immunocompétence via des effets directs des températures environnementales ou de l'état d'hydratation sur l'activité des cellules phagocytaires et cytotoxiques de l'immunité innée et adaptative (Rios & Zimmerman, 2015). D'autre part, les températures élevées ou la déshydratation peuvent avoir des effets indirects sur l'immunocompétence en affectant les dépenses métaboliques et la quantité d'énergie pouvant être allouée au système immunitaire (Segerstrom, 2007) ou en affectant le statut oxydatif, car certaines réponses immunitaires reposent sur la production de substances pro-oxydantes (e.g., rôle antimicrobien des espèces réactives de l'oxygène lors de la réponse inflammatoire (Sorci & Faivre, 2008)). Par exemple, des études mettent en évidence une diminution de l'immunocompétence lors d'une exposition aiguë ou chronique à des températures élevées chez des espèces de poissons (Vinagre *et al.*, 2012; Dittmar *et al.*, 2014), de gastéropodes (Seppälä & Jokela, 2010) et de lézards (Han *et al.*, 2020a). Néanmoins, l'effet des conditions thermiques sur l'immunocompétence des ectothermes semble variable en fonction des espèces considérées. Dans certains cas, l'exposition à des températures plus chaudes n'a pas d'effet (Stahlschmidt *et al.*, 2017a) ou augmente l'immunocompétence (Martins *et al.*, 2011; Zimmerman *et al.*, 2017). Enfin, plusieurs études chez des espèces distinctes de squamates (reptiles non aviens comprenant les espèces de lézards et de

serpents) suggèrent que le manque d'eau et la déshydratation augmentent l'immunocompétence (Moeller *et al.*, 2013; Brusch & DeNardo, 2017; Brusch IV *et al.*, 2019; Sandfoss *et al.*, 2022).

2.3.2 Effets sur la reproduction et la progéniture

Les changements des régimes thermiques et hydriques affectent les activités reproductrices des ectothermes (Figure 5). L'exposition à de fortes chaleurs peut perturber les comportements de parade nuptiale, la communication et les comportements de reproduction (Boullis *et al.*, 2016; Sales *et al.*, 2018). Par exemple, des études chez les abeilles solitaires et domestiques montrent que des températures élevées perturbent les vibrations des ailes lors des parades nuptiales, les profils olfactifs impliqués dans la reconnaissance pré-accouplement et le succès reproducteur des mâles (Stürup *et al.*, 2013; Conrad *et al.*, 2017). Les activités reproductrices dépendent également fortement des épisodes pluvieux en particulier pour les espèces ayant des stades de vie aquatiques et qui dépendent de retenues d'eau éphémères pour pondre, comme les amphibiens (Jensen *et al.*, 2003; Blaustein *et al.*, 2010; Dalpasso *et al.*, 2023).

Les conditions climatiques peuvent également impacter de manière importante les traits reproductifs comme l'investissement reproducteur total, la fécondité et le succès reproducteur (Grazer & Martin, 2012; Bhagarathi *et al.*, 2024). Les effets de la température sur les traits reproductifs sont variables et dépendent en grande partie de l'adéquation entre la biologie thermique et les températures environnementales. De nombreuses études en milieu contrôlé chez les ectothermes suggèrent l'existence d'une plage thermique étroite autour d'une température optimale, où des changements de seulement +2° ou -2 °C entraînent une détérioration de l'investissement reproductif,

de la fécondité et du succès reproducteur (Grazer & Martin, 2012). Les conditions thermiques peuvent également affecter les compromis entre les traits reproductifs comme la taille et le nombre d'œufs par exemple (e.g., reptiles : Starostová *et al.*, 2012; Rutschmann *et al.*, 2016a; arthropode: Marty *et al.*, 2022).

Les températures durant le développement embryonnaire ou larvaire ont aussi des effets sur le phénotype et les performances futurs de la progéniture (Booth, 2006; Angilletta Jr., 2009; Noble *et al.*, 2018). En effet, les températures d'incubation peuvent affecter de nombreux processus ontogéniques comme la vitesse du développement embryonnaire (While *et al.*, 2018), les dépenses énergétiques embryonnaires (Pettersen *et al.*, 2024), le degré de conversion du vitellus en tissu (Storm & Angilletta, 2007) ou la détermination du sexe chez certaines espèces de reptiles (Warner, 2011). Les températures développementales peuvent également influencer le développement des fonctions musculo-squelettiques ou cérébrales (While *et al.*, 2009; Booth, 2017). Ainsi, plusieurs études mettent en évidence des effets persistant des températures développementales au cours de la vie sur la morphologie, les taux de croissance, les comportements, les performances locomotrices et la survie (Booth, 2006; Angilletta Jr., 2009; Noble *et al.*, 2018; Singh *et al.*, 2020). Une méta-analyse récente chez les reptiles suggère que les effets des températures développementales sur la survie (succès d'éclosion, survie post-éclosion), les performances (e.g., endurance, vitesse de course ou de nage) et la morphologie (e.g., taille, corpulence) suivent généralement une courbe concave avec des valeurs phénotypiques plus faibles aux températures les plus froides et les plus chaudes (Noble *et al.*, 2018). Les conditions d'humidité dans l'environnement d'incubation (chez des insectes, certains amphibiens et les reptiles ovipares) ainsi que l'état d'hydratation de la mère (chez les organismes vivipares) peuvent aussi influencer le succès d'éclosion, la morphologie et

les performances des larves (e.g., insectes: Al-Saffar *et al.*, 1996; Norhisham *et al.*, 2013; Johnsen *et al.*, 2021; Frooninckx *et al.*, 2024) ou des juvéniles (amphibien: Salica *et al.*, 2017; reptiles: Marco *et al.*, 2004; Dezetter *et al.*, 2021). La disponibilité en eau est en effet essentielle au bon déroulement du développement embryonnaire et à la croissance somatique des tissus.

2.4 Rôle de l'habitat dans l'atténuation des effets des changements climatiques

Les caractéristiques et la complexité de l'habitat influencent fortement la vulnérabilité des organismes ectothermes aux changements climatiques en particulier chez les espèces présentant des capacités de dispersion limitées comme certains amphibiens et reptiles (Neel *et al.*, 2021; Stark *et al.*, 2023). En effet, la structure de l'habitat peut générer des écarts importants entre les conditions macroclimatiques et les conditions microclimatiques auxquels sont réellement exposés les organismes (Helmuth *et al.*, 2005; Suggitt *et al.*, 2011; Figure 6). Les conditions microclimatiques sont en grande partie déterminées par l'exposition du substrat au rayonnement solaire, par la composition du substrat, par la couverture végétale ainsi que par la disponibilité de l'eau dans l'environnement (Sears *et al.*, 2011; Suggitt *et al.*, 2011). La végétation et la présence d'eau dans l'habitat peuvent par exemple générer de forts gradients d'ombrage, de température et d'humidité générant des microhabitats favorables tamponnant les effets des conditions macroclimatiques plus chaudes (Scheffers *et al.*, 2014; Woods *et al.*, 2015; Pincebourde *et al.*, 2016; Stark *et al.*, 2023). La présence d'abris (e.g., zone ombragée, abri souterrain) peut également fournir des zones de retraits pour éviter la surchauffe ou la déshydratation lors de vagues de chaleur ou de sécheresse (Beck & Jennings, 2003; Moore *et al.*, 2018; Rozen-Rechels *et al.*, 2019; Dezetter *et al.*, 2023). Par exemple, nous avons mis en évidence chez le lézard vivipare que la présence d'un abri humide dans un environnement desséchant et

dépourvu d'eau tamponne fortement les altérations physiologiques et comportementales induites par la restriction hydrique (Bodineau *et al.*, 2024; **Article 5 en Annexe**). Dans l'ensemble, la complexité et l'hétérogénéité de l'habitat peuvent tamponner les effets de conditions environnementales plus chaudes et du manque d'eau (Kearney *et al.*, 2009; Sears *et al.*, 2016).

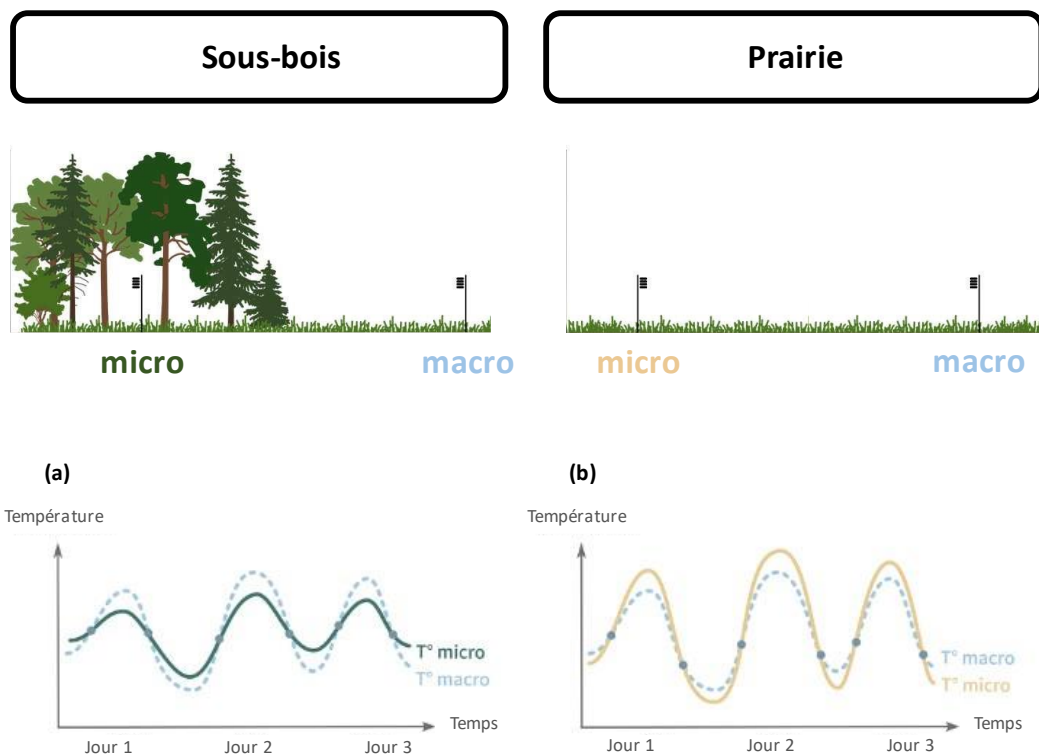


Figure 6 : Variation des conditions thermiques à l'échelle micro- et macroclimatique entre deux types d'habitats. (a) Sous-bois où la variabilité de la température du microclimat est atténuée par rapport à la température du macroclimat. (b) Prairie ouverte où la variabilité de la température est amplifiée. Modifié d'après De Frenne et al., 2021 et Gril et al., 2023.

3. Phénologie de la reproduction dans des climats changeants

Pour de nombreuses espèces, les événements du cycle vital se produisent à des moments spécifiques de l'année ou dans des conditions environnementales spécifiques avec une périodicité des événements critiques du cycle vital (comme la

reproduction, la migration ou la floraison). Les changements dans la phénologie - c'est-à-dire dans le timing des activités saisonnières des espèces - est l'une des réponses écologiques les plus répandues aux effets des changements climatiques (Parmesan, 2006; Thackeray *et al.*, 2016; Chmura *et al.*, 2019). Par exemple, de nombreuses espèces vivant dans des environnements saisonniers présentent une tendance globale à des activités printanières et des dates de reproduction plus précoces. Néanmoins, il existe des variations considérables dans la direction et l'ampleur de ces changements phénologiques au sein des groupes taxonomiques et entre eux (Parmesan, 2007; Ge *et al.*, 2015; Thackeray *et al.*, 2016). Les modifications phénologiques sont ainsi plus marquées chez les consommateurs primaires et les ectothermes terrestres (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Vitasse *et al.*, 2021). Bien que les changements temporels des événements phénologiques soient bien documentés, de nombreuses incertitudes persistent quant aux indices environnementaux et aux mécanismes sous-tendant les réponses phénologiques des ectothermes aux changements climatiques (Forrest & Miller-Rushing, 2010; Chmura *et al.*, 2019) ainsi qu'à leurs conséquences au niveau individuel et populationnel (Chuine, 2010; Iler *et al.*, 2021).

3.1 Principaux facteurs environnementaux affectant la phénologie de la reproduction des squamates

3.1.1 Effets de la température et des ressources sur l'initiation de la reproduction

Alors que la photopériode – c'est-à-dire la durée du jour – est probablement le prédicteur environnemental le plus précis du temps annuel et un signal prédominant pour les activités de reproduction chez la plupart des animaux (Gorman *et al.*, 2001; Gwinner, 2003), l'implication de ce signal dans l'initiation de l'activité reproductrice des squamates est plus variable (Van Dyke, 2014). Chez les squamates vivant dans des

régions tempérées, les changements saisonniers des conditions thermiques constituent le principal indice de déclenchement de la reproduction par rapport aux changements saisonniers de la photopériode (Van Dyke, 2014). En général, l'activation des comportements reproducteurs et la recrudescence gonadique nécessitent une exposition à des températures froides durant l'hiver puis à des conditions plus chaudes au printemps (Marion, 1970, 1982; Lutterschmidt, 2012). Par exemple, l'induction de la vitellogenèse printanière chez le lézard vivipare dépend d'une exposition obligatoire à des températures inférieures à 8-10°C pendant l'hiver (Gavaud, 1986) et un réchauffement printanier tardif retarde l'initiation de la reproduction chez *Acanthodactylus erythrurus* (Castilla *et al.*, 1992). Néanmoins, certaines espèces n'ont pas besoin d'exposition à des périodes froides, mais la reproduction est suivie d'une période réfractaire après laquelle seule une hausse des températures stimule la recrudescence gonadique (e.g., Cuellar & Cuellar, 1977).

De plus, la reproduction nécessite un investissement particulièrement important de la part des femelles. La production des œufs est coûteuse en énergie et la gestation entraîne une augmentation des taux métaboliques et des dépenses énergétiques maternelles en particulier chez les espèces vivipares où l'intégralité du développement embryonnaire a lieu au sein de la femelle (Van Dyke & Beaupre, 2011; Foucart *et al.*, 2014). Par conséquent, la quantité d'énergie précédemment stockée et la quantité de nourriture disponible sont des déterminants importants des décisions de reproduction chez les squamates. La fréquence des événements reproductifs est variable chez les squamates avec des espèces se reproduisant une fois ou plusieurs fois par an (e.g., le lézard des murailles (*Podarcis muralis*)), et des espèces avec des écarts de plusieurs années entre les événements de reproduction (e.g., la vipère aspic (*Vipera aspis*)). Les squamates se répartissent le long d'un continuum « *income* » - « *capital* »

(Bonnet *et al.*, 1998), où les « *income breeders* » sont des espèces qui dépendent des ressources collectées pendant la période de reproduction pour soutenir l'investissement reproductif, tandis que les « *capital breeders* » dépendent de l'énergie collectée et stockée avant la reproduction en vue d'une utilisation ultérieure. Les mécanismes sous-tendant la décision d'initiation de la reproduction en fonction de la quantité d'énergie stockée ou récemment acquise ne sont pas totalement connus chez les squamates. Néanmoins, il existe probablement un seuil de condition corporelle au-dessus duquel la reproduction débute et une faible quantité de proies disponibles au début du cycle reproductif peut retarder l'initiation de la reproduction (Vitt *et al.*, 1978; Bonnet *et al.*, 1998).

3.1.2 *Plasticité thermique du cycle reproductif*

On observe chez les squamates une forte variation interannuelle de la phénologie de la reproduction (Ljungström *et al.*, 2015; Cunningham *et al.*, 2020). Cette plasticité des dates de reproduction est principalement expliquée par les effets de la température sur les processus biochimiques essentiels (e.g., réaction cinétique, régulation hormonale (Hochachka & Somero, 2002a)) et les comportements (e.g., période d'activité (Adolph & Porter, 1993)) qui régissent les étapes clés du cycle reproductif comme l'émergence post-hivernale, la vitellogenèse (i.e., phase d'accumulation du vitellus dans les ovocytes), ou le développement des embryons. D'une part, des températures plus élevées durant la vitellogenèse accélèrent de façon directe le développement folliculaire et la formation des œufs (Duvall, 1982), mais peuvent aussi accroître les périodes d'activité, la capture et l'assimilation des proies ce qui peut accélérer la formation des œufs (Price, 2017). D'autre part, des températures élevées durant la gestation (chez les espèces vivipares) ou l'incubation (chez les espèces ovipares) vont accélérer le développement embryonnaire, réduire la durée de la

gestation ou d'incubation et provoquer des dates de parturition ou d'éclosion plus précoces (Noble *et al.*, 2018).

3.2 Déterminants individuels des dates de reproduction chez les squamates

Plusieurs études chez des lézards font aussi état de variations interindividuelles importantes dans les dates de reproduction (Olsson & Shine, 1997; Wapstra *et al.*, 2010; Ljungström *et al.*, 2015; Cunningham *et al.*, 2020). Premièrement, la taille corporelle est un déterminant important des dates de parturition chez certains lézards. En général, les femelles de grande taille pondent ou mettent bas plus tôt (Bauwens & Verheyen, 1985; Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016a; Hall & Warner, 2017). Les mécanismes sous-jacents ne sont pas bien connus, mais pourraient inclure l'expérience de reproduction (car la taille est corrélée à l'âge chez les espèces à croissance continue) ou la compétitivité des femelles plus grandes et plus âgées pour l'accès aux ressources (e.g., proies, sites de thermorégulation, sites de ponte). Deuxièmement, la condition corporelle des femelles reproductrices semble également être un déterminant important de la date de ponte. Par exemple, les femelles avec une plus forte condition corporelle pondent plus tôt chez le lézard des souches (*Lacerta agilis*; Olsson & Shine, 1997) et l'anolis brun (*Anolis sagrei*; Hall *et al.*, 2018). Enfin, des déterminants génétiques pourraient aussi expliquer les différences interindividuelles des dates de reproduction. Bien que des études chez un scinque vivipare (*Niveoscincus ocellatus*) suggèrent que les femelles présentent des dates de parturition répétables d'une année sur l'autre (Wapstra *et al.*, 2010; Cunningham *et al.*, 2020), aucune étude n'a estimé l'héritabilité des dates de ponte ou de parturition dans une population naturelle de squamates.

3.3 Conséquences de la phénologie sur le succès reproducteur et la progéniture

La phénologie de la reproduction contribue de manière importante à la fitness individuelle car elle détermine la capacité d'un organisme à exploiter les ressources qui varient dans le temps au cours de la saison. Chez les reptiles squamates, les conséquences de la phénologie de la reproduction sur la fitness des individus reproducteurs et de leur progéniture ont principalement été étudiées chez les lézards. Ces études mettent en évidence l'existence d'une sélection directionnelle favorisant des dates de ponte ou de parturition plus précoces (Olsson & Shine, 1997; Wapstra *et al.*, 2010). On observe ainsi une diminution saisonnière de l'investissement reproductif et du nombre de juvéniles viables produit par les femelles (Olsson & Shine, 1997; Mitchell *et al.*, 2018) ainsi qu'un effet positif d'une date d'éclosion précoce sur la survie, la croissance et la reproduction des juvéniles (Olsson & Shine, 1997; Qualls & Andrews, 1999; Uller & Olsson, 2010; Wapstra *et al.*, 2010; Le Henanff *et al.*, 2013; Li *et al.*, 2018; Sun *et al.*, 2018; Liu *et al.*, 2022).

Deux hypothèses principales et non exclusives, initialement développées chez les oiseaux, peuvent expliquer la sélection directionnelle vers des dates de ponte plus précoces (Figure 7). « L'hypothèse de la date » ("Date hypothesis", Hatchwell, 1991; Moreno, 1998) suggère que la diminution saisonnière du succès reproductif est une conséquence du temps en soi qui affecte de manière similaire tous les individus. Selon cette hypothèse, la sélection s'opère via une dégradation des conditions environnementales au cours de la saison. Par exemple, les reproducteurs précoces peuvent accéder à une plus grande quantité de nourriture (e.g., Perrins, 1965), à un nombre de partenaires sexuels plus important (e.g., Veiga & Salvador, 2001), être exposés à des températures plus clémentes ou à des taux de prédation plus faibles (e.g., Götmark, 2002) ou disposer d'une fenêtre temporelle plus importante pour les

activités post-reproduction comme le stockage d'énergie avant l'hiver (Bleu *et al.*, 2012). De même, une période d'activité plus longue avant l'hiver combinée à des conditions thermiques plus favorables au début de l'été et une compétition plus faible entre les juvéniles peut favoriser la croissance corporelle, le stockage d'énergie et la survie des juvéniles nés tôt dans la saison (Adolph & Porter, 1993; Warner & Shine, 2007; Uller & Olsson, 2010; Pearson & Warner, 2018). La sélection directionnelle peut aussi résulter d'une variation saisonnière de la qualité des reproducteurs ("Quality hypothesis", Hatchwell, 1991; Brinkhof *et al.*, 1993). Selon cette hypothèse, les reproducteurs présentant une condition corporelle plus élevée (Descamps *et al.*, 2011), plus âgés, expérimentés, ou compétitifs pour utiliser les ressources de l'environnement ou disposant d'un meilleur territoire (Shutt *et al.*, 2022) seraient capables de se reproduire plus tôt entraînant une covariation apparente entre le moment de la reproduction et la fitness indépendamment des effets du temps en soi. La contribution de ces deux hypothèses au déclin saisonnier de la fitness a été principalement étudiée chez les oiseaux (Verhulst & Nilsson, 2008), et nous avons peu de connaissances sur la contribution de ces mécanismes chez les squamates (Sun *et al.*, 2018).

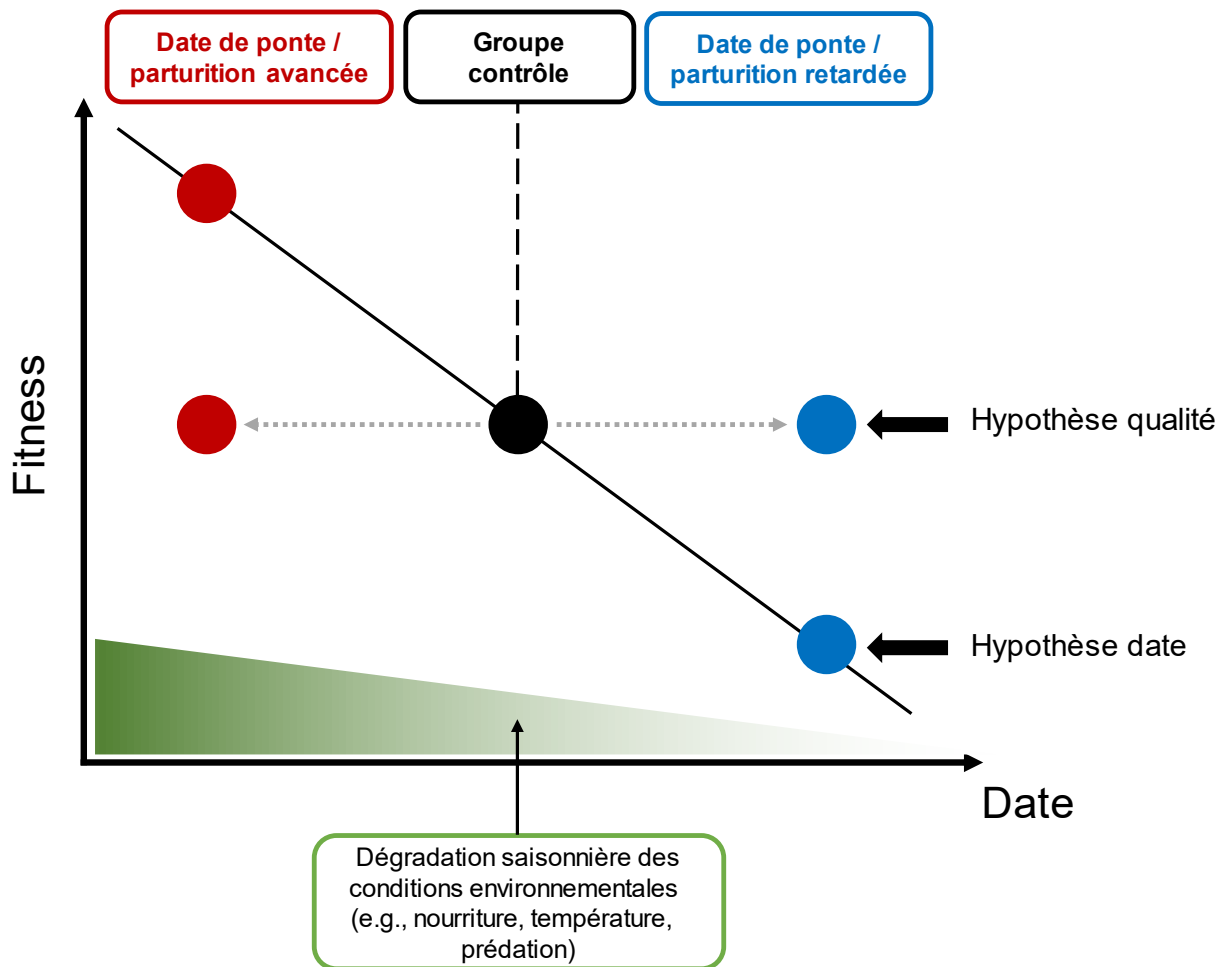


Figure 7 : Variation hypothétique de la fitness en fonction de l'hypothèse de la date et de l'hypothèse de la qualité suite à une manipulation expérimentale des dates de ponte ou de parturition. L'hypothèse de la date prédit un déclin saisonnier de la fitness causé par la détérioration des conditions environnementales. L'hypothèse de la qualité prédit que le déclin saisonnier de la fitness est causé par des différences de qualité entre les individus reproducteurs précoces et tardifs. Il est à noter que la fitness des groupes retardé et avancé peut être intermédiaire entre les deux résultats présentés, ce qui suggérerait que l'hypothèse de la date et de la qualité sous-tendent le déclin saisonnier de la fitness. Modifié d'après Verhulst & Nilsson, 2008.

4. Objectifs et hypothèses de la thèse

4.1 Problématiques et objectifs généraux

Les impacts écologiques des changements climatiques chez les ectothermes peuvent se manifester à différentes échelles biologiques par une perturbation des processus physiologiques, des traits fonctionnels (i.e., traits morphologiques, physiologiques,

comportementaux et phénologiques qui influencent indirectement la fitness (Violle *et al.*, 2007)) et des stratégies de reproduction et d'histoire de vie. Face aux changements climatiques, les ectothermes terrestres présentent des changements phénologiques marqués avec des dates de reproduction avancées de plusieurs jours à plusieurs semaines par décennie en raison de la plasticité thermique du cycle reproductif (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Vitasse *et al.*, 2021). Comprendre les conséquences de l'accélération de la phénologie de la reproduction est donc essentiel pour anticiper les changements démographiques et la vulnérabilité des populations d'ectothermes exposées au réchauffement climatique. **Cette thèse vise à identifier et comprendre les effets du climat et de la phénologie de la reproduction sur les traits physiologiques, comportementaux, reproductifs et les traits d'histoire de vie d'un ectotherme terrestre dans différents contextes populationnels.**

Plus précisément, les objectifs de cette thèse sont de :

- (i) Déterminer comment les conditions environnementales locales entraînent des variations intraspécifiques dans les phénotypes et les traits reproductifs des femelles reproductrices.
- (ii) Comprendre les déterminants environnementaux et individuels de la phénologie de la reproduction.
- (iii) Comprendre les conséquences de la phénologie de la reproduction et du climat sur les traits d'histoire de vie des femelles reproductrices et de leur progéniture.

Afin de répondre à ces objectifs, nous avons utilisé une approche intégrative combinant des études corrélatives et expérimentales en s'intéressant à des processus

cellulaires, physiologiques, comportementaux et reproductifs dans différents contextes populationnels.

4.2 Espèce modèle: le lézard vivipare

4.2.1 Modèle d'étude

Dans le cadre de cette thèse, nous avons utilisé le lézard vivipare (*Zootoca vivipara*, Lichenstein 1823) comme modèle d'étude. Le lézard vivipare est un petit lézard diurne et terrestre de la famille des lacertidae présentant une large répartition en Eurasie allant du Nord de l'Espagne au cercle polaire arctique, et des côtes atlantiques de l'Europe Occidentale aux côtes Pacifiques de la Sibérie (Surget-Groba *et al.*, 2006). Sur le territoire métropolitain français, cette espèce est majoritairement vivipare, mais la forme ovipare de cette espèce (non étudiée dans cette thèse) est présente dans la zone pyrénéenne en marge sud de la distribution de l'espèce. Cette espèce est inféodée aux milieux frais et humides comme les tourbières, les zones marécageuses ou les prairies humides (e.g., Lorenzon *et al.*, 2001; Rozen-Rechels *et al.*, 2020). Les populations naturelles sont structurées en trois grandes classes d'âge : les juvéniles (nouveau-nés de l'année), les subadultes (individus âgés d'un à deux ans) et les adultes (âgés de plus de deux ans).

4.2.2 Populations étudiées

Au cours de ce projet de thèse, nous avons réalisé plusieurs études sur des populations semi-naturelles et naturelles de lézard vivipare. L'ensemble des études expérimentales présentées dans ce manuscrit (**Articles 3 et 4**) ont été réalisées sur des individus maintenus toute l'année en conditions semi-naturelles dans des macrocosmes terrestres au Centre de Recherche en Écologie Expérimentale et Prédictive (CEREEP-Ecotron, Saint-Pierre-lès-Nemours, 77140, France (48° 17' N, 2°

41' E)). Les enclos sont constitués d'une végétation permanente (principalement de l'herbe), d'un accès permanent à de l'eau libre, de refuges et de sites de thermorégulation (Figure 8). Les principales sources de mortalité dans les enclos sont les interactions sociales, l'épuisement énergétique et le parasitisme, car la prédation terrestre et aviaire est évitée grâce à des parois en chlorure de polyvinyle (PVC) et à des filets. L'intégralité des individus sont codés, ce qui permet d'effectuer des suivis longitudinaux des individus tout au long de leur vie grâce à des sessions de recaptures régulières.

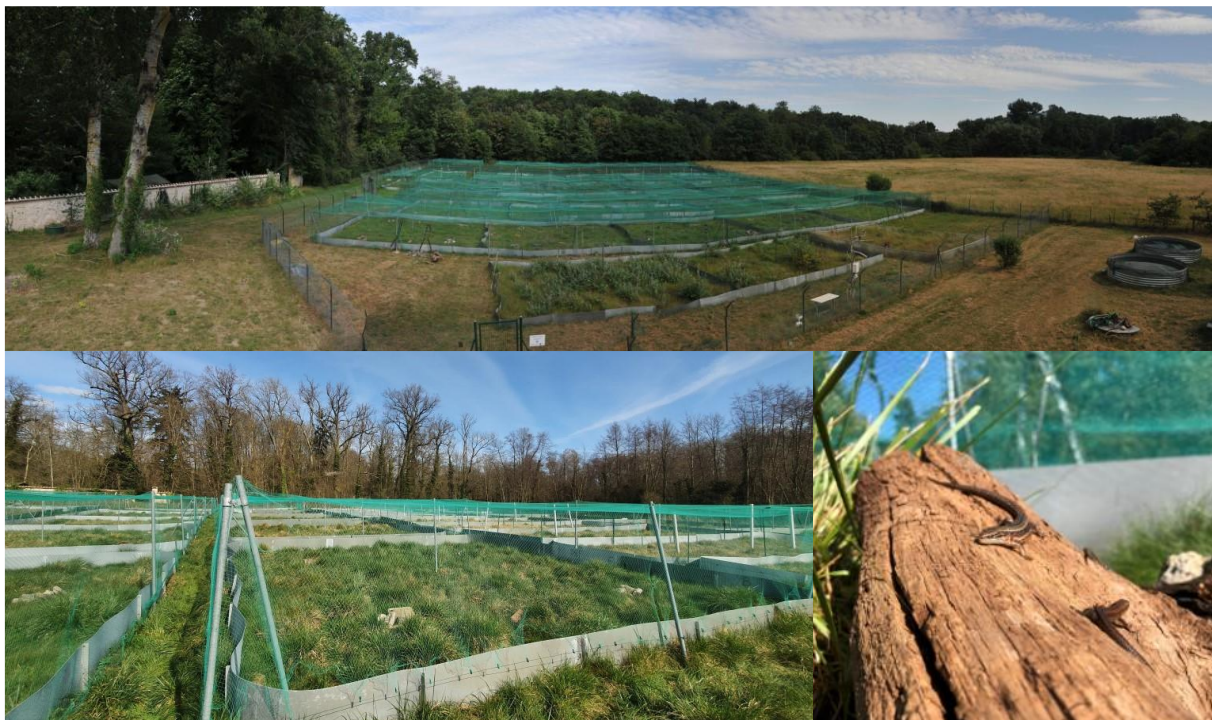


Figure 8 : Photographies des macrocosmes terrestres dans lesquels sont maintenues les populations de lézard vivipare. Les macrocosmes sont implantés sur une prairie humide et disposent d'une végétation et de sites de thermorégulation (pierriers, branches) favorables à l'espèce. Chaque enclos de 100 m² est séparé par des plaques en plastique enfouies profondément dans le sol afin d'éviter les mouvements des lézards vers l'extérieur et la prédation terrestre. Des filets sont utilisés pour éviter la prédation aviaire.

Les études corrélatives (**Articles 1 et 2**) ont quant à elles été réalisées sur des populations naturelles de lézard vivipare en marge sud de la distribution de l'espèce dans le Massif central (Figure 9). Ces populations ont déjà fait l'objet d'études par le passé (e.g., Lorenzon *et al.*, 1999; Massot *et al.*, 2017; Rozen-Rechels *et al.*, 2020; Dupoué *et al.*, 2022) et présentent des conditions thermiques, une couverture forestière et une disponibilité de l'eau contrastées. Parmi ces populations, une population (ROB) localisée sur le Mont-Lozère fait l'objet d'un suivi à long terme par marquage-recapture depuis 1986. Chaque année les individus sont capturés et un suivi des événements de reproduction est réalisé sur les femelles reproductrices. On possède pour cette population un pedigree génétique depuis les années 2000.

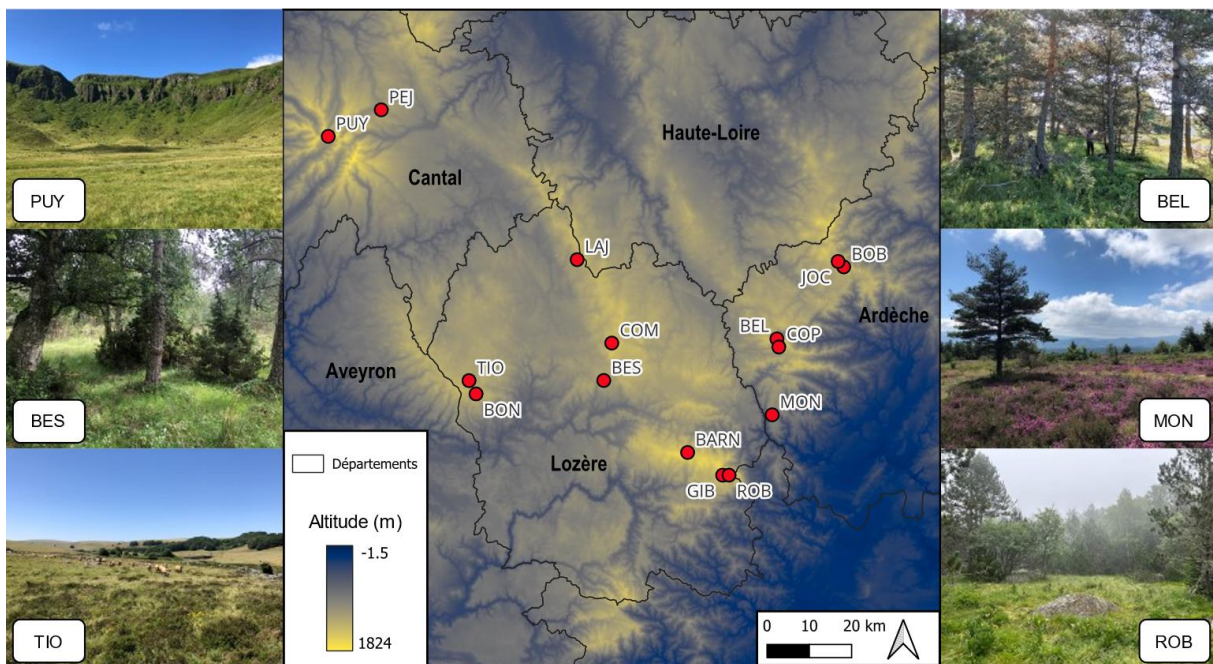


Figure 9 : Localisation et diversité des populations naturelles de lézard vivipare (*Zootoca vivipara*) échantillonnées dans le Massif central.

4.2.3 Reproduction

Dans les populations naturelles que nous avons étudiées dans le Massif central, les lézards hibernent environ 7 mois entre la fin du mois de septembre et le milieu du mois

d'avril (Figure 10). Les mâles sont les premiers à émerger après l'hibernation au milieu du mois d'avril, suivis par les femelles adultes et subadultes à la fin avril - début mai suivant les conditions météorologiques. La période d'accouplement commence au mois de mai quelques jours après l'émergence post-hivernale des femelles sexuellement matures. La vitellogenèse (différenciation des follicules et stockage du vitellus dans les ovocytes) se produit en moyenne au cours des 3 premières semaines après l'émergence post-hivernale (3 premières semaines de mai). La vitellogenèse est suivie de l'ovulation et de la fécondation des œufs ce qui marque le début de la gestation (en moyenne à la fin mai). L'essentiel du développement embryonnaire (organogenèse) a lieu au cours du premier tiers de la gestation (Hubert, 1962). Au cours du second tiers de la gestation a lieu la phase fœtale avec l'essentiel de la croissance embryonnaire qui marque une forte croissance des besoins hydriques et respiratoires des embryons (Foucart *et al.*, 2014). Après une période de gestation d'environ 2 mois en fonction des conditions thermiques locales et des caractéristiques individuelles (Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016b), la parturition a lieu entre la mi-juillet et le début du mois d'août. Dans nos populations expérimentales maintenues au CEREEP-Ecotron à basse altitude, la phénologie de la reproduction est plus précoce compte tenu des conditions plus chaudes sur site. Dans ces populations, la vitellogenèse débute généralement à la mi-avril, l'ovulation au début/milieu du mois de mai et la parturition a lieu entre la mi-juin et la fin juillet en moyenne. Ces populations semi-captives sont également caractérisées par le fait que certaines femelles subadultes se reproduisent à l'âge d'un an, ce qui est rare en population naturelle. Les femelles pondent 1 à 12 œufs (en moyenne 5) non calcifiés comprenant à la fois des juvéniles non viables et des juvéniles vivants complètement

formés. Quelques minutes ou quelques heures après la parturition, les juvéniles percent la fine enveloppe coquillière de l'œuf et sont autonomes.

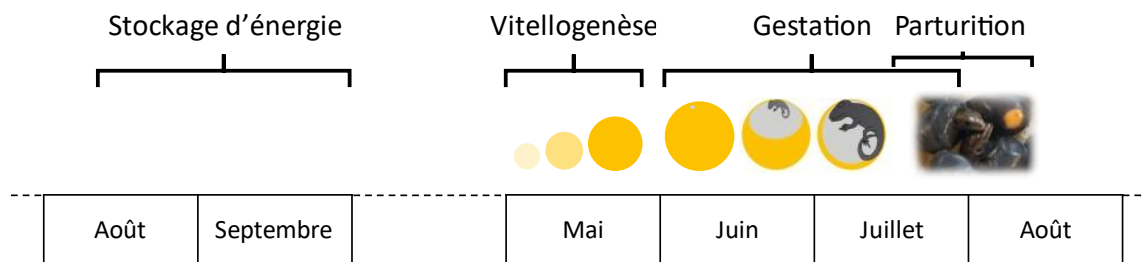


Figure 10 : Cycle reproducteur du lézard vivipare (*Zootoca vivipara*, (Jacquin 1787)) dans les populations naturelles du Massif central, France. La phénologie de la reproduction peut varier en fonction des conditions climatiques locales. Modifié d'après Bleu et al., 2013.

4.3 Études réalisées et hypothèses

4.3.1 Approches corrélatives

Tout d'abord, nous avons utilisé une approche corrélative afin d'examiner les variations géographiques de traits cellulaires (longueur relative des télomères), morphologiques (taille, condition), physiologiques (taux métaboliques, pertes hydriques évaporatives, mélanisme dorsal), comportementaux (température préférée, heure d'émergence) et reproductifs (date de parturition, investissement reproductif total, taille et viabilité de la portée) de femelles reproductrices le long d'un gradient environnemental (**Article 1** ; voir Figure 13 et Table 1 ci-après). Nous avons échantillonné 14 populations présentant des conditions climatiques (températures diurnes et nocturnes), une couverture forestière et un accès à l'eau libre (accès permanent ou temporaire) contrastés et quantifié l'effet de ces paramètres environnementaux sur l'ensemble des traits mesurés. Les objectifs de ce projet étaient de comprendre les mécanismes physiologiques et comportementaux par lesquels les femelles reproductrices répondent aux conditions environnementales locales et

comprendre comment ces facteurs influencent les traits reproductifs. Nous avons fait l'hypothèse que les traits phénotypiques et reproductifs (1) varient entre les populations, (2) sont corrélés aux conditions climatiques locales et (3) sont influencés par la structure de l'habitat (couverture forestière et accès à l'eau libre).

Dans une seconde étude, nous avons examiné les tendances phénologiques, les variations interindividuelles des dates de reproduction ainsi que la sélection agissant sur les dates de parturition. Pour ce faire, nous avons utilisé une base de données de marquage-recapture d'un suivi longitudinal de plus de 30 ans d'une population naturelle (ROB, mentionnée ci-dessus) de lézard vivipare dans le Massif central (**Article 2** ; voir Figure 13 et Table 1 ci-après). Plus précisément, nous avons examiné comment les conditions thermiques diurnes et nocturnes ainsi que les traits individuels façonnent les dates de parturition, quantifié l'héritabilité des dates de parturition ainsi que la forme, l'intensité et la variation temporelle de la sélection sur les dates de parturition. Nous avons fait l'hypothèse que les températures maximales journalières durant la période d'activité post-hivernale ainsi que la taille corporelle sont les principaux déterminants des dates de parturition. Nous prédisons que les dates de parturition sont hérissables et nous nous attendons à une sélection directionnelle vers les dates de parturition précoces qui peut fluctuer annuellement en fonction des conditions thermiques.

4.3.2 Approches expérimentales

Des études expérimentales au CEREAP-Ecotron IleDeFrance nous ont permis de quantifier les conséquences des conditions thermiques et des dates de parturition sur les traits morphologiques, physiologiques et comportementaux des femelles reproductrices ainsi que sur les traits d'histoire de vie de leur progéniture. En effet,

grâce aux structures expérimentales du CEREEP Ecotron, nous avons pu modifier les conditions thermiques au cours de la gestation et examiner les effets des traitements expérimentaux pendant un an en suivant les individus dans des macrocosmes terrestres (voir Figure 13 et Table 1 ci-après). Ces études ont pour but de progresser dans notre compréhension des bénéfices et des coûts associés à l'accélération thermique de la gestation. Nous avons émis l'hypothèse générale que (1) les conditions thermiques et la date de parturition sont des déterminants importants des traits reproductifs des femelles et des traits d'histoire de vie de la progéniture et (2) que l'accélération thermique de la gestation peut avoir des effets négatifs sur l'homéostasie des femelles, mais positifs sur les juvéniles en favorisant la croissance, la survie et l'accès à la reproduction.

Dans l'**Article 3**, nous avons utilisé une technique d'ingénierie phénotypique afin de modifier expérimentalement les dates de parturition et d'étudier les effets des conditions thermiques et de la date de parturition en soi sur les traits d'histoire de vie des femelles et de leur progéniture (voir Figure 13 ci-après). Nous avons accéléré ou retardé les dates de parturition en exposant les femelles à deux régimes thermiques contrastés (froid ou chaud) pendant la gestation. Les femelles exposées à des conditions chaudes disposaient d'une période de thermorégulation optimale de 8.5h par jour et d'une température nocturne de 18°C. Les femelles exposées à des conditions froides disposaient d'une période de thermorégulation restreinte de 5h par jour et étaient exposées à des températures nocturnes de 14°C. Nous avons suivi l'état corporel, les traits reproductifs immédiats et futurs, la survie des femelles, ainsi que la morphologie à la naissance, la survie, la croissance et la reproduction des juvéniles. Puisque les conditions thermiques de développement et les dates de parturition sont fonctionnellement liées et qu'ils peuvent tous deux influencer les traits de fitness, nous

avons comparé la contribution relative des conditions thermiques et de la date de parturition en soi sur ces traits.

Alors que les changements climatiques sont caractérisés par une tendance plus forte au réchauffement nocturne et qu'ils peuvent entraîner des altérations concomitantes de la disponibilité alimentaire, nous présentons dans l'**Article 4** une étude visant à déterminer les effets de l'augmentation des températures nocturnes et de la diminution de l'apport énergétique durant la gestation (voir Figure 13 ci-après). Nous avons exposé des femelles gestantes à des températures nocturnes (21°C, 16°C, 13°C) et une disponibilité de la nourriture (*ad libitum* ou restriction nutritive modérée) contrastées durant la gestation. Nous avons quantifié les impacts du réchauffement nocturne et de la disponibilité alimentaire sur la condition, la physiologie et les comportements maternels ainsi que sur la phénologie, l'investissement reproductif et les traits d'histoire de vie de la progéniture. Nous avons émis l'hypothèse que le réchauffement nocturne et la restriction nutritive impacte négativement l'homéostasie maternelle en altérant la condition énergétique, les processus physiologiques et les paramètres de reproduction. Nous nous attendons à un impact négatif de la restriction alimentaire sur la progéniture à la naissance, tandis que le réchauffement nocturne pourrait augmenter les performances, la croissance et la survie de la progéniture en générant des dates de naissance plus précoces. Enfin, la restriction alimentaire pourrait accentuer les effets du réchauffement nocturne sur les caractéristiques maternelles et le rendement reproductif en raison de l'optimum thermique inférieur des performances en cas d'apport alimentaire restreint.

4.3.3 *Expériences non valorisées*

Deux autres études expérimentales ont également été réalisées dans le cadre de ce projet doctoral, mais n'ont pas encore été valorisées et ne seront pas présentées dans ce manuscrit. Une étude complémentaire au chapitre 3 (**Expérience 5**) visait à mettre en évidence expérimentalement les impacts physiologiques de l'accélération de la gestation sur les femelles reproductrices, sur le développement et la physiologie embryonnaire ainsi que sur les traits d'histoire de vie et la dynamique des télomères des juvéniles. Pour ce faire, nous avons exposé les femelles à trois régimes thermiques simulant des opportunités de thermorégulation restreintes, similaires aux conditions extérieures ou augmentées (durée d'allumage des lampes chauffantes de 5h, 8h et 11h respectivement) durant la gestation (Figure 11). Des suivis physiologiques (condition, immunocompétence, stress oxydatif) et comportementaux (activité et température corporelle) ont été réalisés pour suivre l'état physiologique des femelles et caractériser les stratégies de thermorégulation durant la gestation. Un suivi échographique a été réalisé durant toute la durée de la gestation pour suivre le développement et la physiologie embryonnaire (taille des œufs, stade de développement, rythme cardiaque des embryons). Après la parturition des femelles, nous avons caractérisé les traits de reproduction (investissement reproducteur, viabilité de la portée), les traits morphologiques des juvéniles (taille, masse) et prélever des échantillons de tissus caudaux pour des mesures ultérieures de la longueur relative des télomères. Les juvéniles et les femelles ont été relâchés en jardin commun dans les macrocosmes terrestres puis recapturés à l'âge d'un an afin d'estimer les effets différés des traitements et de la date de parturition sur la survie, le phénotype (taille, condition) et la longueur des télomères des juvéniles.

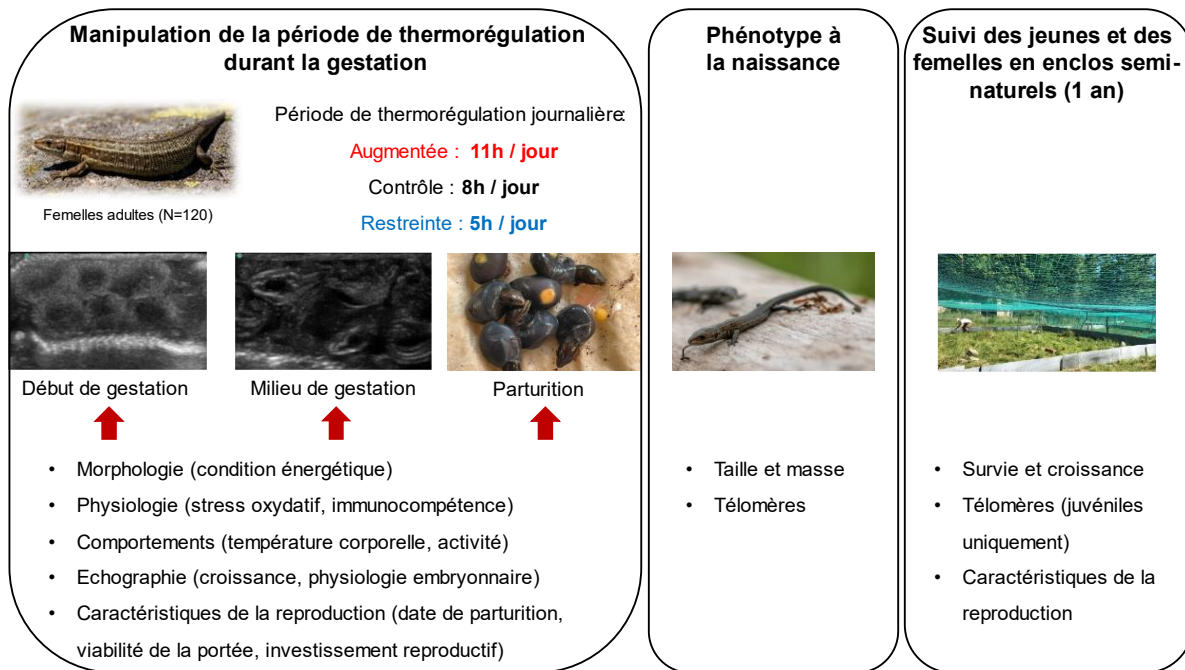


Figure 11 : Résumé graphique de l'expérience 5. Nous avons exposé 120 femelles à trois régimes thermiques contrastés simulant des opportunités de thermorégulation restreintes, similaires aux conditions extérieures ou augmentées pendant la gestation. Un suivi morphologique, physiologique, comportemental et échographique a été effectué sur les femelles durant la gestation. Après la parturition, nous avons caractérisé les traits reproductifs des femelles et les caractéristiques des juvéniles à la naissance avant de les relâcher en jardin commun dans des enclos semi-naturels. Un suivi de la survie, des traits phénotypiques et de la reproduction a été réalisé l'année suivante sur les juvéniles et les femelles.

Enfin, une expérience de jardin commun (**Expérience 6**) a été réalisée en collaboration avec Julien Côte et Luis San-Jose à la Station d'Écologie Théorique et Expérimentale de Moulis (Figure 12). Cette expérience a été réalisée sur les juvéniles (N=1067) produits par femelles gestantes capturés lors de l'étude de la variation géographique des traits fonctionnels et reproductifs le long d'un gradient environnemental (**Article 1**). Tout d'abord, des traits cellulaires (longueur relative des télomères), morphologiques (taille, condition), comportementaux (heure d'émergence, préférence thermique) et physiologiques (pertes hydriques, métabolisme, mélanisme dorsal) similaires à ceux mesurés sur les femelles ont été mesurés sur les juvéniles à

leur naissance. Les juvéniles ont ensuite été relâchés en jardin commun au sein de grands enclos semi-naturels où les conditions thermiques ont été manipulées par un système de volets générant de l'ombre au-dessus des enclos (dispositif expérimental appelé « Métatron terrestre », voir Bestion *et al.*, (2015)). Trois traitements climatiques estivaux ont été appliqués aux enclos : un traitement climatique « actuel » simulant des températures moyennes équivalentes aux températures actuelles extérieures (fermeture des volets à partir de 28°C), un traitement climatique « intermédiaire » (fermeture des volets à partir de 33°C) et un traitement climatique « chaud » simulant une augmentation de +2°C par rapport au climat actuel (fermeture des volets à partir de 38°C). La cohorte de juvéniles a été suivie pendant 2 ans jusqu'à leur première reproduction avec deux sessions de recapture par an (septembre et mai) où l'intégralité des traits mesurés à la naissance ont été remesurés. Les objectifs généraux de ce projet sont de mesurer les changements phénotypiques et la fitness des individus dans les différents traitements climatiques pour déterminer si (1) les syndromes d'extinction accumulés dans les populations chaudes de cette espèce sont réversibles (voir Dupoué *et al.*, 2022) et (2) si les populations les plus froides sont les plus sensibles à l'augmentation des températures. Au cours de cette expérience, j'ai coordonné les captures des femelles gestantes en milieu naturel et participé aux mesures réalisées sur les juvéniles à la naissance.

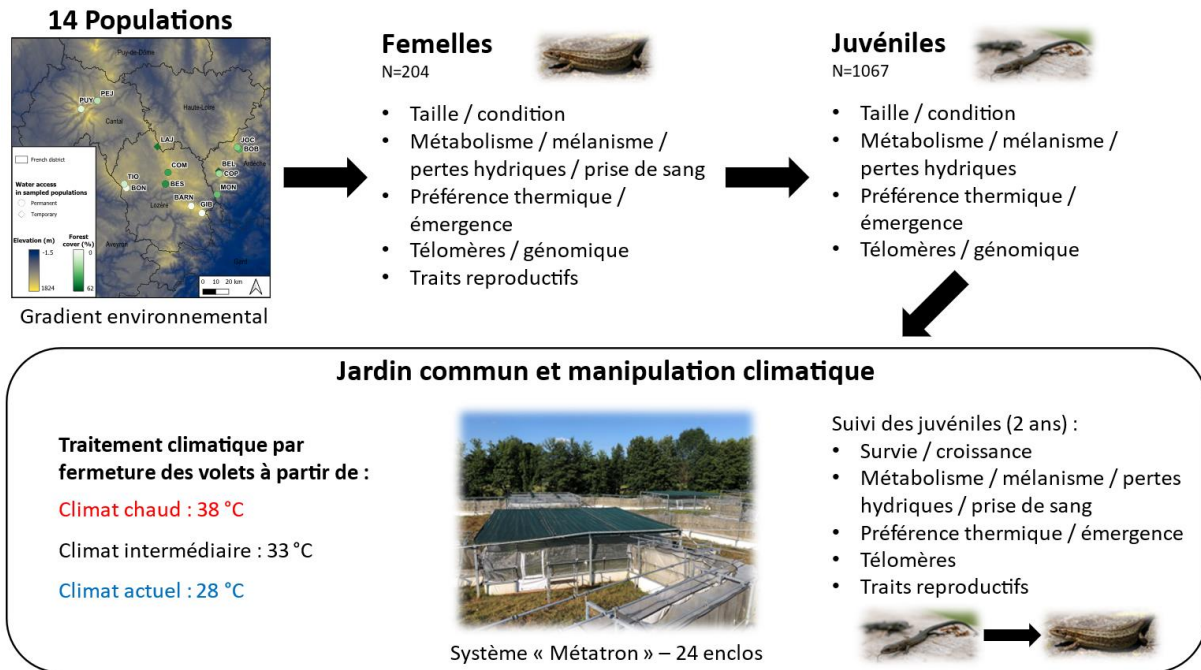


Figure 12 : Résumé graphique de l'expérience 6. Une expérience de jardin commun a été réalisée sur 1067 juvéniles produits par des femelles capturées dans 14 populations présentant des conditions climatiques, une couverture forestière et un accès à l'eau libre contrastés. Des traits cellulaires, morphologiques, physiologiques et comportementaux ont été mesurés sur les femelles et leurs juvéniles à la naissance. Les juvéniles ont été relâchés en jardin commun dans des enclos semi-naturels où les conditions climatiques ont été manipulées afin de simuler un climat actuel, intermédiaire ou chaud. La survie et les traits phénotypiques des juvéniles ont été suivi pendant 2 ans jusqu'à leur première reproduction avec deux sessions de recapture par an (septembre et mai) où les traits phénotypiques mesurés à la naissance ont été remesurés.

4.3.4 Synthèse des études réalisées durant la thèse

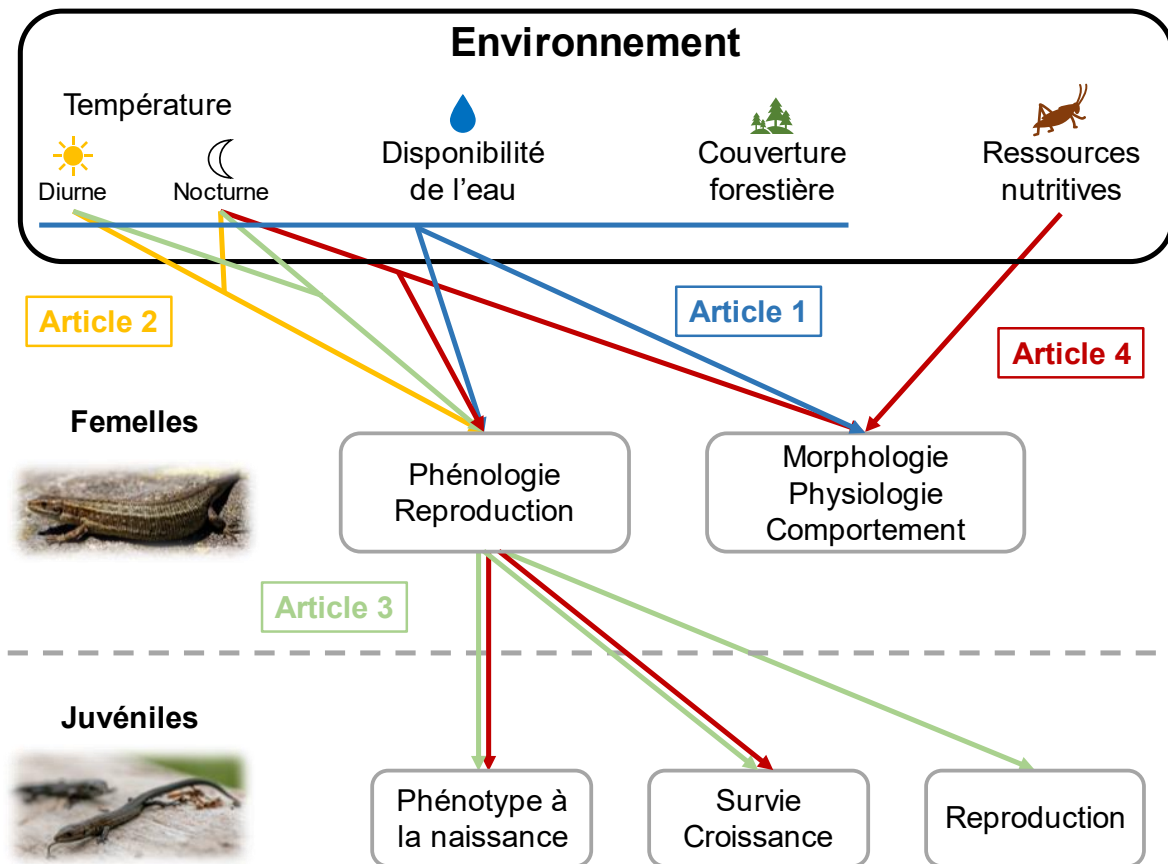




Figure 13 : Représentation schématique des relations testées et des articles de la thèse. L'article 1 examine les effets des conditions thermiques (diurne et nocturne), de la couverture forestière et de la disponibilité de l'eau sur les variations géographiques des traits cellulaires, morphologiques, physiologiques, comportementaux et reproductifs des femelles en milieu naturel. Dans l'article 2, nous avons étudié les déterminants environnementaux et individuels de la phénologie de la reproduction, quantifié l'héritabilité des dates de parturition ainsi que la forme, l'intensité et la variation temporelle de la sélection sur les dates de parturition en milieu naturel. L'article 3 quantifie expérimentalement les effets des conditions thermiques durant la gestation et de la date de parturition sur les traits morphologiques et reproductifs des femelles ainsi que sur les traits d'histoire de vie de leur progéniture. L'article 4 examine expérimentalement les effets de l'augmentation des températures nocturnes et de la diminution de l'apport énergétique durant la gestation sur les traits morphologiques, physiologiques, comportementaux et reproductifs des femelles ainsi que sur le phénotype à la naissance, la survie et la croissance des juvéniles.

Table 1 : Tableau récapitulatif des études réalisées et des données collectées.

	Article 1	Article 2	Article 3	Article 4	Expérience 5*	Expérience 6*
Données collectées	Juin - août 2022	1989 - 2019	Mai 2021 - août 2022	Mai - septembre 2023	Mai 2022 - août 2023	Juin 2022 - août 2024
Contribution	Complète - collecte des données et analyse	Complète - analyse des données	Complète - collecte des données et analyse	Complète - collecte des données et analyse	Complète - collecte des données	Collaboration - Collecte partielle des données
Design	Variations géographiques des traits (14 populations - gradient environnemental)	Suivi longitudinal par marquage - recapture + pedigree	Traitements thermiques durant la gestation puis jardin commun en enclos semi-naturels	Traitements thermiques et nutritifs durant la gestation puis jardin commun en enclos semi-naturels	Traitements thermiques durant la gestation puis jardin commun en enclos semi-naturels	Jardin commun + traitements thermiques en enclos semi-naturels (Métatron)
Effectif	204 femelles adultes	2119 évènements de reproduction	84 femelles adultes et 93 subadultes	138 femelles adultes	120 femelles adultes	1067 juvéniles
Traitements expérimentaux			<div style="border: 1px solid blue; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Période de thermorégulation restreinte 5h30 / jour T° nuit : 14 °C</div> <div style="border: 1px solid red; border-radius: 10px; padding: 5px; display: inline-block; margin-top: 5px;">Période de thermorégulation standard 8h30 / jour T° nuit : 18 °C</div>	<div style="border: 1px solid blue; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Nuit froide 11°C</div> <div style="border: 1px solid black; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Nuit intermédiaire 16°C</div> <div style="border: 1px solid red; border-radius: 10px; padding: 5px; display: inline-block; margin-top: 5px;">Nuit chaude 21°C</div> <div style="text-align: center; margin-top: 10px;">  <i>Ad-libitum</i>  <i>Restriction</i> </div>	<div style="border: 1px solid blue; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Période de thermorégulation restreinte 5h / jour</div> <div style="border: 1px solid black; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Période de thermorégulation standard 8h / jour</div> <div style="border: 1px solid red; border-radius: 10px; padding: 5px; display: inline-block; margin-top: 5px;">Période de thermorégulation standard 11h / jour</div>	<div style="border: 1px solid blue; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Climat actuel Fermeture volets à 28°C</div> <div style="border: 1px solid black; border-radius: 10px; padding: 5px; display: inline-block; margin-bottom: 5px;">Climat intermédiaire Fermeture volets à 33°C</div> <div style="border: 1px solid red; border-radius: 10px; padding: 5px; display: inline-block; margin-top: 5px;">Climat chaud Fermeture volets à 38°C</div>
Trait cellulaire maternel						
Télomère						
Traits physiologiques maternels						
Taux métabolique						
Pertes hydriques						
Mélanisme dorsal						
Stress oxydatif						
Corticostérone						
Immunocompétence						
Traits comportementaux maternels						
Thermorégulation						
Heure d'émergence						

	Article 1	Article 2	Article 3	Article 4	Expérience 5*	Expérience 6*
Traits morphologiques maternels						
Taille/masse						
Épaisseur muscle/queue						
Traits reproductifs maternels						
Phénologie, investissement reproducteur total, taille et viabilité de la portée						
Développement embryonnaire						
Traits des juvéniles						
Taille/masse						
Télomères						
Taux métabolique						
Pertes hydriques						
Mélanisme dorsal						
Thermorégulation						
Endurance						
Survie, croissance						
Reproduction						
Données climatiques						
Collecte						
Mise en forme						

* : Expérience non valorisée dans ce manuscrit

RÉSULTATS



Femelle gestante en position de thermorégulation. © Arnaud Badiane

Chapitre 1 - Variations géographiques des traits phénotypiques et reproductifs



Femelle post-parturiente relâchée dans sa population d'origine (Puy Mary – Cantal)
après les épisodes de sécheresse de l'été 2022. © Théo Bodineau

Article 1

Local climate conditions and forest cover drive geographic variation of functional and reproductive traits in a viviparous ectotherm

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Abstract

1. Ecological impacts of climate warming in ectotherms can manifest across various biological levels with heat stress disrupting cellular processes, functional traits and life-history strategies. Using space-for-time substitutions where one examines geographic variation in population phenotypes allows to make predictions for biotic responses to climate warming over time. Yet, this approach must rely on a multivariate description of the local environment to infer a causal relationship between climate conditions and phenotypes.

2. Here, we examined the geographical variation in cellular, morphological, physiological, behavioural and reproductive traits of adult female common lizards (*Zootoca vivipara*) across 14 natural populations along an environmental gradient with contrasting daytime and nighttime temperatures, forest cover and free-standing water access.

3. We found significant geographical variations in all traits of females, with the exception of resting metabolic rates. Geographic trait variation was mainly correlated with local thermal conditions and forest cover, but not with access to free-standing water.

4. Females from populations with warm nighttime temperatures had lower total evaporative water losses and tended to have a lower dorsal darkness, while females from populations exposed to higher daytime temperatures had lower preferred body temperatures. Females from populations with higher forest cover had a higher body condition at capture and an earlier emergence time. In addition, female telomere length (a biological marker of ageing) was higher in populations with lower temperatures and a high forest cover.

5. Reproductive traits were mainly determined by the forest cover and to a lesser extent by nighttime local temperature. Females from populations with high forest cover had delayed parturition dates, higher reproductive investment and a higher post-partum condition. However, the number of viable juveniles at birth was negatively correlated with high local nighttime temperatures.

6. Our integrative study suggests that local diurnal and nocturnal thermal conditions as well as forest cover can lead to changes in cellular, physiological, behavioural and reproductive traits. While thermal stress and habitat alteration are growing threats to terrestrial ectotherms, taking into account intraspecific variations in functional and reproductive traits together with changes in diurnal, nocturnal temperatures and vegetation will be essential for predicting ectotherms responses to current and future climates.

Keywords: ectotherm, forest cover, geographic variation, life-history traits, reproduction, temperature, thermal biology, water balance.

1. Introduction

Metabolic theory predicts that global warming should lead to an acceleration of ectotherms pace of life, causing accelerated growth and reproduction, as the regulation of their body temperature and metabolic rate depends on external thermal conditions (Brown et al., 2004; Burraco et al., 2020). As global warming is expected to increase and heatwaves and droughts become more frequent (IPCC, 2023), the thermal acceleration of pace of life combined with water restriction may lead to physiological alterations at different scales in terrestrial ectotherms (Hayden Bofill & Blom, 2024; Zhang et al., 2022). Increases in body temperature are associated with higher energy expenditure and water loss (Rozen-Rechels et al., 2019; Schulte et al., 2011), which

can disrupt the energy and water balance of ectotherms during both active and resting phases. Heatwaves and droughts may also restrict ectotherms' activity periods to the cooler hours of the day, thereby reducing food intake (Kearney, 2013; Kearney et al., 2018). In consequence, cumulatively, heatwaves and drought could lead to a "metabolic meltdown" (Dillon et al., 2010; Huey & Kingsolver, 2019). These environmental stressors can also disrupt organismal homeostasis and subsequently affect longevity (reviewed in Burraco et al. 2020). For example, water deprivation and the thermal acceleration of metabolism can cause oxidative damage to essential biomolecules such as membrane lipids, proteins, or telomeres, thereby accelerating ageing (Costantini, 2014; Dupoué et al., 2020).

Adaptive behavioural and physiological plasticity may allow ectotherms to mitigate these negative effects of climatic stressors (Huey et al., 2012). The most well-documented plastic responses of ectothermic squamates to thermal and hydric stress are energy and water conservation mechanisms including thermal depression (i.e., a downregulation of thermoregulatory behaviours; (e.g., Ladyman et Bradshaw 2003)), metabolic depression (i.e., a downregulation of metabolic rates; (e.g., Christian, Bedford, et Schultz 1999; Muir, Costanzo, et Lee 2007)), and the reduction of transcutaneous water losses (reviewed in Lillywhite 2006). Acclimation responses for these traits have largely been observed under controlled conditions, leaving gaps in our understanding of how natural populations acclimate to local thermal environments. So far, field studies on the geographical variations of physiological and behavioural traits in relation to climate have focused on thermal physiology (e.g., thermal preferences, field body temperatures) or evaporative water losses in reptiles (Chabaud et al. 2022; Dupoué et al. 2017; Gilbert et Miles 2019; Gvoždík 2002; Rozen-Rechels et al. 2020; Trochet et al. 2018). However, the impacts of local thermal conditions on

other climate-relevant traits such as metabolic rates (e.g., Chabaud et al. 2022; Muñoz et al. 2022), activity patterns, or dorsal melanisation (e.g., Alho et al. 2010; Martínez-Freiría et al. 2020), which influence thermoregulation and energy balance, have received far less attention. Therefore, examining intraspecific variation in a broader spectrum of physiological and behavioural traits that may influence squamates' performance in future climates is crucial for understanding how they will adapt to shifting environmental conditions (Wong & Carmona, 2021).

Additionally, changes in thermal regimes can impact the reproductive traits of squamates and consequently affect population dynamics (Bestion, Teyssier, et al., 2015). Phenological changes are probably one of the most well-documented consequences of changing thermal conditions on reproductive traits in reptiles. Warmer thermal conditions generally advance post-hibernation emergence (Moss & MacLeod, 2022) and reduce incubation or gestation length (Booth, 2006; Noble et al., 2018), leading to earlier laying, parturition and hatching dates during the breeding season (J. F. Le Galliard et al., 2010; Ljungström et al., 2015; Pearson & Warner, 2018). In addition, thermal conditions can affect reproductive quality and investment, as developmental temperatures may influence energy allocation to eggs or embryos and the quality of embryonic development (Meiri et al., 2012; Noble et al., 2018; Starostová et al., 2012). Reduced water availability during gestation can also increase embryonic mortality and reproductive failure (Dezetter et al., 2021; Zani & Stein, 2018). While several studies have reported extended geographical variations in reproductive traits in reptiles (Díaz et al., 2012; DU et al., 2005; Gregory & Larsen, 1993), fewer have quantified the climatic determinants behind inter-population variations in reproductive traits (Ramírez-Bautista et al., 2021; Rutschmann, Miles, Le Galliard, et al., 2016).

The climate sensitivity of ectotherm populations could depend on the structure and quality of their habitat (Marshall et al., 2015; Stark et al., 2023). The heterogeneity of the thermal and hydric environment is largely determined by differences in substrate exposure, vegetation cover, composition of the underlying substrate, and water availability in the environment (Sears et al., 2011; Suggitt et al., 2011). Vegetation can create sharp gradients of shade, temperature, and humidity, generating favourable microclimates that may buffer the effects of heatwaves or droughts (Pincebourde et al., 2016; Scheffers et al., 2014; Stark et al., 2023; Woods et al., 2015). Additionally, the presence of free-standing water can create cooler, more humid microhabitats and mitigate the effects of drought by providing drinking water (Rozen-Rechels, Badiane, et al., 2020). For instance, previous studies in lizards have highlighted covariations between forest cover or water availability and functional traits related to homeostasis (Chabaud et al. 2022; Dupoué et al. 2017) or reproductive traits (Rutschmann et al. 2016). To estimate the role of habitat structure in the response of ectotherm populations to climate change, it is necessary to conduct comparative analyses of climate-relevant and reproductive traits along environmental gradients in sites with contrasting habitat characteristics.

In this study, we conducted an integrative analysis of geographical variation in multiple climate relevant traits of female common lizards (*Zootoca vivipara*) across 14 natural populations in the Massif Central Mountain range (France). We sampled reproductive females from populations with different habitat features (e.g., forest cover and free-standing water access) along an environmental gradient. In this area, local warming induces changes in life-history with populations at the warm margins characterized by a faster pace of life, accelerated ageing and higher extinction risk (Chamaillé-Jammes et al., 2006; Dupoué et al., 2022; Dupoué, Rutschmann, Le

Galliard, Clobert, et al., 2017). In addition, previous studies have highlighted geographical variations in growth rates (Lorenzon et al., 1999), evaporative water loss rates (Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017), thermoregulatory behaviour (Rozen-Rechels, Rutschmann, et al., 2020) and parturition dates (Massot et al., 2017; Rutschmann, Miles, Le Galliard, et al., 2016), caused by local climatic conditions, access to free-standing water and forest cover. Here, we used an integrative analysis to study the influence of environmental temperatures, forest cover and free-standing water access on broader spectrum of cellular (telomere length), morphological (SVL, body and muscle condition), behavioural (preferred body temperature and emergence time), physiological (metabolism, dorsal darkness, total evaporative water losses), and reproductive traits (parturition date, reproductive investment, litter size and litter viability) of female common lizard. We tested whether these traits: (1) varied among populations, (2) were correlated with local climatic conditions, and (3) were influenced by habitat structure (forest cover and free-standing water access).

2. Material and methods

2.1. Studied species, populations and rearing conditions

The European common lizard (*Zootoca vivipara*, *Lichtenstein, 1823*), is a small terrestrial lizard widely distributed in northern Eurasia in highly seasonal, cool and humid habitats. In our study area of the Massif Central Mountains in south-central France, reproduction is viviparous and annual (Horreo et al., 2021). The mating period begins shortly after the emergence of sexually mature females from overwintering (i.e., in May). Parturition occurs after an average gestation period of ca. 7-8 weeks (i.e., between July and early August) depending on thermal conditions and individual

characteristics (Bauwens & Verheyen, 1985). Females lay on average five non-calcified eggs (range 1-12) including both nonviable offspring (fertilised or unfertilised eggs, undeveloped embryos and stillborn) and live offspring which hatch quickly after parturition.

Between the 15th June to the 30th June 2022, we captured 204 reproductive females in 14 natural populations ($N = 10 - 15$ lizards per population; see Figure 1). Sampled populations were distributed along an environmental gradient with heterogeneous forest cover, access to free-standing water and local climatic conditions (see Supplementary Table S1). We used aerial high-resolution photographs (Rozen-Rechels, Rutschmann, et al., 2020) to calculate the proportion of trees in each population (forest cover). This index ranged from 0 % (open grasslands, mainly grass) to 62 % (sites in forested environments). It indicates the degree of shading in the habitat that influences importantly the opportunity for thermoregulation behaviour of lizards (Sears et al., 2016). We further distinguished the populations with permanent access to free-standing water in peat bogs or humid meadow habitats from those with periodic access in meadows with no water during summer except from intermittent precipitations and morning dew. Previous studies have shown that intermittent water access constrains thermo-hydroregulation strategies, growth and reproduction in this species (Chabaud et al., 2022; Lorenzon et al., 1999). In addition, we used two temperature data loggers (iButtons, Maxim Integrated Products, Sunnyvale, CA, USA, $\pm 0.06^{\circ}\text{C}$) per population, placed at 1m20 above ground level and in the shade, to measure air temperature every hour during a standardised sampling period from 1st May to 15th June 2022. We extracted the mean daily minimum, mean and maximum temperatures (T_{\min} , T_{mean} and T_{\max} , respectively) to assess thermal conditions during the active spring season before we captured lizards. Weather conditions in 2022 were

characterized by a persistent lack of rainfall during late winter and spring, exceptional temperature anomalies of +3-4°C above seasonal averages during spring and persistent excess insolation (unpublished data, Météo France).

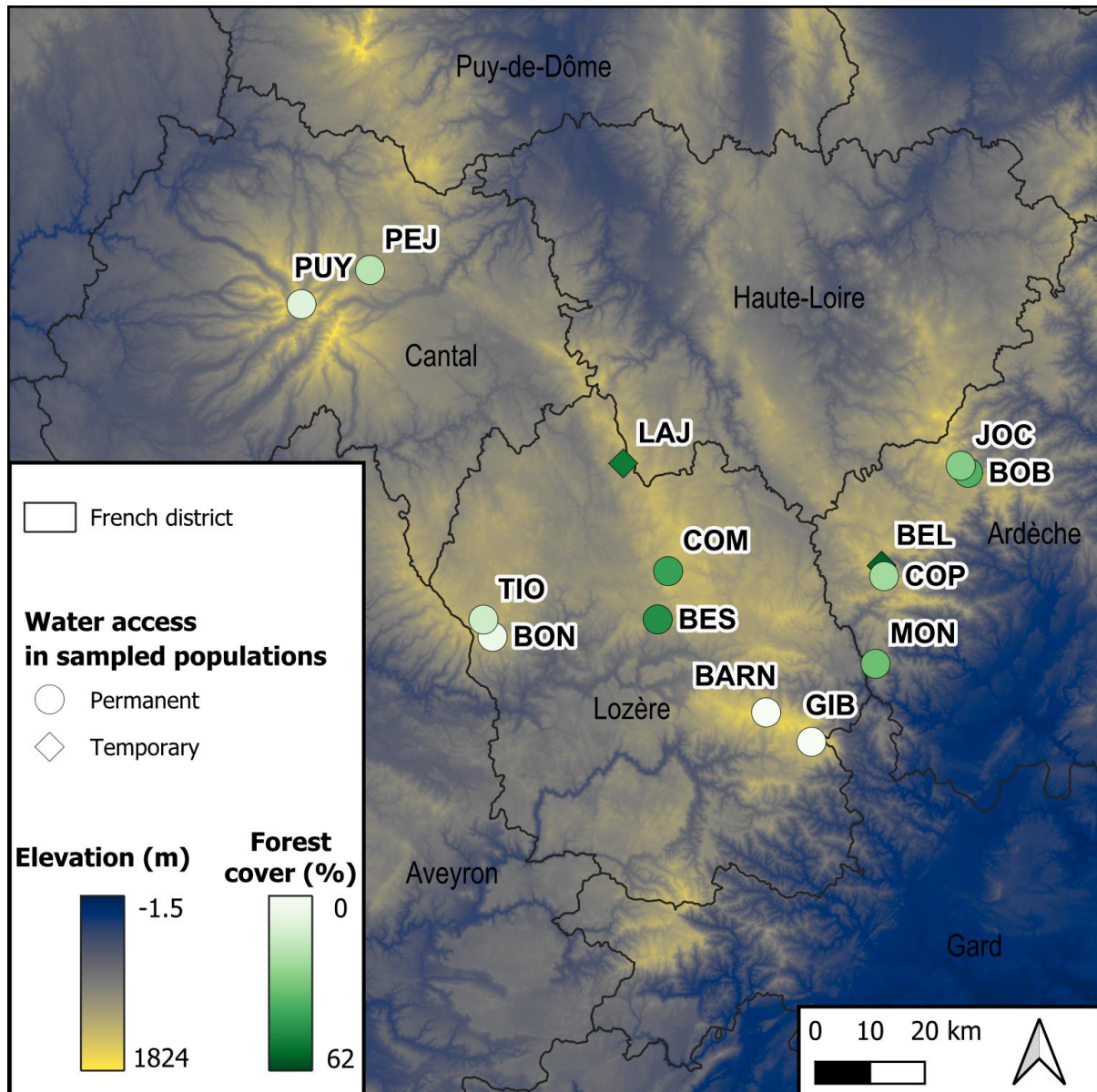


Figure 1: Geographic location of 14 sampled populations in the Massif Central mountain range from France along an environmental gradient with contrasting forest cover and access to free-standing water.

All adult pregnant females were measured at capture for snout-vent length (SVL) and body mass, then housed in a field laboratory in standard rearing conditions

(Rutschmann, Miles, Clobert, et al., 2016) and transported to the final laboratory (CNRS, Moulis, Ariège) within a week after capture. Females were scanned dorsally using a flatbed scanner (Canon Canoscan Lide 110, resolution 400 dpi) for subsequent measurement of dorsal melanisation (see below) and we collected tail tip tissues (< 3-4 mm) using sterilised scissors for telomere assays (see below). All females tail tip tissues were put into liquid nitrogen and subsequently stored at -80°C until molecular assays. Note that the tail regrows rapidly after autotomy. Then, females were housed until parturition in individual terrariums (35 x 18 x 23 cm) filled with sterilised peat as substrate, equipped with a shelter, and installed in a temperature-controlled room. Terrariums were lit and heated automatically from 9:00 a.m. to 12:00 a.m. and from 2:00 p.m. to 5:00 p.m. by a UVB-enhanced neon tube (30 W) and a halogen heating bulb (25W) placed on one side of the terrarium to generate a thermal gradient relevant to this species (20-35°C). We provided *ad libitum* food (2 crickets (*Acheta domesticus*) every two days), *ad libitum* water and a humid environment (three water sprays per day).

2.2 Measurements of reproductive output and postpartum condition of female

Right after parturition (“day 0”), each female was weighed and the litter was characterised by recording the number of unfertilised eggs, undeveloped embryos, stillborn and live juveniles. We further calculated litter size as the total number of unfertilised eggs, undeveloped embryos, stillborn and live juveniles. We calculated reproductive investment as the difference between the body mass of females before and after parturition, and litter viability as the proportion of live juveniles at birth. On average one day after parturition (“day + 1”), we measured left and right hind limb thickness of females using a spessimeter (ID-C1012BS, Mitutoyo, Japan). Limb thickness provides a reliable proxy of muscular condition and responds to changes in

food intake, water supply and reproductive effort (Bodineau, Chabaud, et al., 2024; Bruschi, Gavira, Viton, Dupoué, Leroux-Coyau, Meylan, Le Galliard, et al., 2020).

2.3. Behavioural measurements

Five days after parturition (“day +5”), we measured the females' emergence time with an instantaneous sampling every 15 minutes from 8:15 a.m. to 10:45 p.m. where we noted if the female was active (visible in the terrarium) or not. Emergence time was calculated as the first time when the female was seen active and is importantly related to the thermoregulation behaviour and daily activity pattern (Rozen-Rechels, Badiane, et al., 2020). The next morning (“day +6”), we measured the preferred body temperature of fasting females with a standard protocol (Bestion, Clobert, et al., 2015). Briefly, we used 80 x 20 x 40 cm terraria divided in eight 10 cm zones by black marks on the floor and heated by a halogen heating bulb (60W) placed on one side of the terrarium to generate a thermal gradient (20 °C to 45 °C). The temperature of each zone was continuously quantified thanks to thermometers in a terrarium without lizards. Before measurements, all females were placed in the cold zone of the terrarium for acclimation for 30 minutes and then, video cameras above terraria recorded females' position for 30 minutes. Video data was analysed using the Observer software (Noldus, 1991). Preferred temperature was calculated as the mean compartment's temperatures weighted by the time spent by the lizard in each compartment.

2.4. Physiological measurements

2.4.1. Resting metabolic rate

In the evening of “day +6” and “day +11”, we measured resting metabolic rate as overnight oxygen consumption using closed-system respirometry methods in fasting animals as in an earlier study (Foucart et al., 2014). We measured the resting

metabolic rate of each female at 22°C (resting body temperature) and 32°C (activity body temperature), randomising the order of trials and allowing for 5 days between each trial. Females were weighed and then placed individually in test containers (1000 ml) in a climatic chamber at the desired temperature. All individuals were allowed a 2 hours acclimation period in late afternoon before starting each trial. After collecting a baseline outside air sample with 140 mL syringes at the onset of trial (Medtronic Monoject Luer Lock), we closed test containers, flushed air inside containers with outside air using an air pump and maintained lizards overnight at testing temperatures (12:00 p.m. to 10:30 a.m. at 22°C and 12:00 p.m. to 7:30 a.m. at 32°C). At the end of each trial, we collected a final air sample from each container. Oxygen proportion in air samples was determined using an O₂ analyser (FOXBOX, Sable Systems, Las Vegas, NV, USA). Using an infusion pump (KDS 200, KD Scientific Inc., Holliston, MA, USA), air dried in a column of Drierite was sent at a constant flow (60 mL.min⁻¹) to the O₂ analyser, which was calibrated before each trial using outdoor air. We calculated oxygen consumption (mL.h⁻¹) as the difference between final O₂ and baseline O₂ multiplied by the chamber volume divided by trial duration.

2.4.2. Total evaporative water losses

We quantified total evaporative water losses using gravimetric method on fasted animals without any access to water because variation in body mass at rest is strongly correlated with water losses in squamate reptiles (DeNardo, 2004; Dupoué et al., 2015). In the evening of “day + 7”, we weighed females at 8:00 p.m. (± 1 mg) and maintained them overnight at 22°C climate chamber with controlled humidity (65.5 ± 3.1 %). After 12 hours, all individuals were weighed again and we calculated the water loss rate (in mg.h⁻¹) as mass loss overnight at rest per hour.

2.4.3. Dorsal darkness

Dorsal darkness was quantified using dorsal scans taken after capture using the ImageJ software (Schneider et al., 2012) and following the protocol of Bestion et al. (2023). Briefly, we defined three standardised sections on the median part of the back and flanks between the legs. Sections were then converted to 32-bit black and white and we quantified the dorsal darkness as the proportion of black pixels in the delimited parts using the greyscale threshold option (threshold set at 45). We calculated mean dorsal darkness by averaging the dorsal darkness of the medial and lateral parts.

2.4.4. Telomere estimation

DNA was extracted and purified using DNAAdvance kit (Beckman Coulter) following manufacturer protocol for animal tissues. We assessed the concentration of DNA extracted from all samples with Qubit fluorometer and evaluated DNA quality and integrity by optical density spectrophotometry (NanoDrop) on a subset of samples (N=24, absorbance ratio A260/280 = 1.85 ± 0.04 , ratio NanoDrop/Qubit = 1.60 ± 0.27). For all samples, we quantified telomere length from 10 ng DNA using a real-time qPCR method (Cawthon, 2002) with PCR conditions and primers designed and tested in earlier studies (Dupoué et al., 2020, 2022; McLennan et al., 2019). We amplified telomeric DNA repeat sequences (T) with universal Tel1b and Tel2b primers, and DNA sequences of the single copy gene (S) recombination activating gene 1 (RAG-1) with primers designed for *Zootoca vivipara* (GenBank accession number: KY762205.1). All samples were randomly distributed on eight plates and telomere and single-copy gene assays were performed on separate plates in duplicate with a qPCR thermocycler (Bio-Rad CFX96). The analysis was repeated in case of strong variation between the two replicates (Δ cycle threshold $\geq |0.3|$) or atypical amplification profile. We calculated relative telomere length following Pfaffl (2001) using qBase software (Hellemans et al.,

2007) and *qpcR* R package (Spiess, 2018). Telomere assays were highly repeatable (intra-assay repeatability: $r = 0.94$ [CI: 0.895 - 0.937], inter-assay repeatability: $r = 0.848$ [CI: 0.411 - 0.937]). RAG-1 and Tel PCR efficiencies ranged from 95% to 104% and 102.9% to 114.7% respectively, within the acceptable range (85% - 115%).

2.5. Statistical analysis

Analyses were performed using R software version 4.2.0 (R Core Team, 2022) using an identical model selection approach for all traits. Firstly, we determined if morphological (SVL, body condition at capture and limb thickness), physiological (resting metabolic rate, total evaporative water losses, dorsal darkness, relative telomere length), behavioural (preferred body temperature, emergence time) and reproductive traits (parturition date, reproductive investment, litter size, litter viability) varied among populations. To do so, we compared generalised linear mixed models fitted with population as random effect with a null model using likelihood ratio tests (LRT). Resting metabolic rate, total evaporative water losses, dorsal darkness and relative telomere length were log-transformed as their distribution was not Gaussian. Specifically, for resting metabolic rate analysis which was measured repeatedly at two temperatures, we fitted a model with body mass and temperature as fixed effects as well as a nested random effect of individual identity and population. We then compared these models to a simplified model with same fixed effects but with only individual identity as random effect. We then calculated the proportion of variance explained by the population effect as the ratio between the variance explained by the random effect of population and total variance (including residual and random effects variance).

If the random population effect was retained in the model, we next investigated the environmental factors underlying geographic variation in morphological, behavioural, physiological and reproductive traits. We focused on the effects of climatic

conditions, forest cover and free-standing water access rather than on elevation. Since T_{mean} was correlated with T_{max} we chose to study the effects of T_{min} as a climatic proxy related to nighttime temperatures and T_{max} as the climatic proxy related to daytime temperatures (see Supplementary Figure S1). We build a first full (generalised) linear mixed model including fixed additive effects of climate (T_{min} and T_{max}), forest cover and female SVL, as well as the population effect in the random part of the model. Only two populations had temporary access to water and this was correlated with high forest cover (see Supplementary Figure S2). We thus built a second full model including same covariates but by replacing the forest cover effect by the free-standing water access effect. Female body size was included in all models, as body size of lizards is often correlated with their physiological and reproductive traits (e.g., water loss: (J.-F. Le Galliard et al., 2021); dorsal darkness: (Clusella Trullas et al., 2007), reproductive traits: (Bodineau, Chabaud, et al., 2024; J. F. Le Galliard et al., 2010)). All continuous covariates were mean centred. We then built all possible models from full models (see Table S2 of Supplementary information) and compared the relative importance (sum of Akaike weights over all models in which the variable appears ($\sum w_i$)) of climate variables (T_{min} and T_{max}), forest cover and access to free-standing water using the Akaike information criterion corrected for small sample size (AICc). We tested model fitting and model assumptions (e.g., normality, when relevant, and homogeneity of variance of the residuals) with the full model. A Gaussian distribution was assumed for all traits, except for litter size, which assumed a Poisson distribution with a log link, and viability which assumed a binomial distribution with a logit link. Full model fits were satisfactory. We estimated model parameters using a model averaging procedure with the “natural average” method (Burnham & Anderson, 2004) implemented in *Mumin*

package (Bartoń, 2024). All results are reported as means \pm SE unless otherwise stated.

3. Results

3.1. Morphology at capture

Female SVL varied significantly among populations (proportional variance explained = 20%; LRT= 21.83, $p < 0.0001$), but none of our environmental covariates explained this variation (Table 1). We also identified differences in female body condition among populations (proportional variance explained = 8%; LRT = 5.14, $p = 0.02$) and the forest cover was the most supported environmental variable to explain this variation ($\Sigma w_i = 0.67$; Table 1). Females from populations with a higher forest cover had a higher body condition at capture (slope= 0.75 ± 0.24 g; $z = 2.8$, $p = 0.005$; Figure 2a).

3.2. Behaviour

Female preferred body temperature varied weakly among populations (proportional variance explained = 7%; LRT = 4.48, $df = 1$, $p = 0.03$). T_{max} was the most supported variable to explain geographic variation of preferred body temperature ($\Sigma w_i = 0.85$; Table 1) and preferred body temperature decreased with T_{max} (slope= -0.65 ± 0.24 °C; $z = 2.4$, $p = 0.02$; Figure 2b). In addition, we found significant geographic differences in emergence time between populations (i.e., activity start time; proportional variance explained = 7%; LRT = 4.95, $df = 1$, $p = 0.03$). The forest cover was the most supported as explanatory variables of this variation ($\Sigma w_i = 0.63$; Table 1). Females from populations with a higher forest cover had an earlier emergence time (slope= -51.3 ± 16.8 minutes; $z = 2.7$, $p = 0.006$).

3.3. Cellular and physiological traits

Resting metabolic rate at 22°C and 32°C did not vary significantly among populations (proportional variance explained = < 0.1%; LRT = 1.27E-07, df = 1, p = 0.99). In addition, we found marginal differences in total evaporative water losses among populations (proportional variance explained = 6%; LRT= 3.01, df = 1, p = 0.08). Total evaporative water losses were weakly correlated with T_{\min} ($\Sigma w_i = 0.80$; slope= $-0.05 \pm 0.02 \mu\text{g}\cdot\text{h}^{-1}$; $z = 2.07$, $p = 0.04$) with slightly lower total evaporative water losses in populations with a higher T_{\min} . We also found variation in dorsal darkness among populations (proportional variance explained = 29%; LRT = 40.39, df = 1, $p < 0.0001$). T_{\min} was the most supported variable to explain this variation ($\Sigma w_i = 0.69$; Table 1) with a marginally significant decrease in dorsal darkness in populations with higher T_{\min} (slope= $-0.13 \pm 0.06 \%$; $z = 1.8$, $p = 0.06$; Figure 2c). Finally, females' relative telomere length differed substantially among populations (proportional variance explained = 64%; LRT = 118.28, $p < 0.0001$). The most supported variables explaining variation in relative telomere length across populations included the forest cover index ($\Sigma w_i = 0.96$), T_{\min} ($\Sigma w_i = 1.0$) and T_{\max} ($\Sigma w_i = 0.98$; Table 1). In specific, female relative telomere length increased with the forest cover (slope= 0.75 ± 0.19 ; $z = 3.0$, $p < 0.001$; Figure 2d) but decreased with T_{\max} (slope= -0.08 ± 0.02 ; $z = 3.1$, $p = 0.002$; Figure 2e) and T_{\min} (slope= -0.26 ± 0.04 ; $z = 4.8$, $p < 0.0001$; Figure 2f).

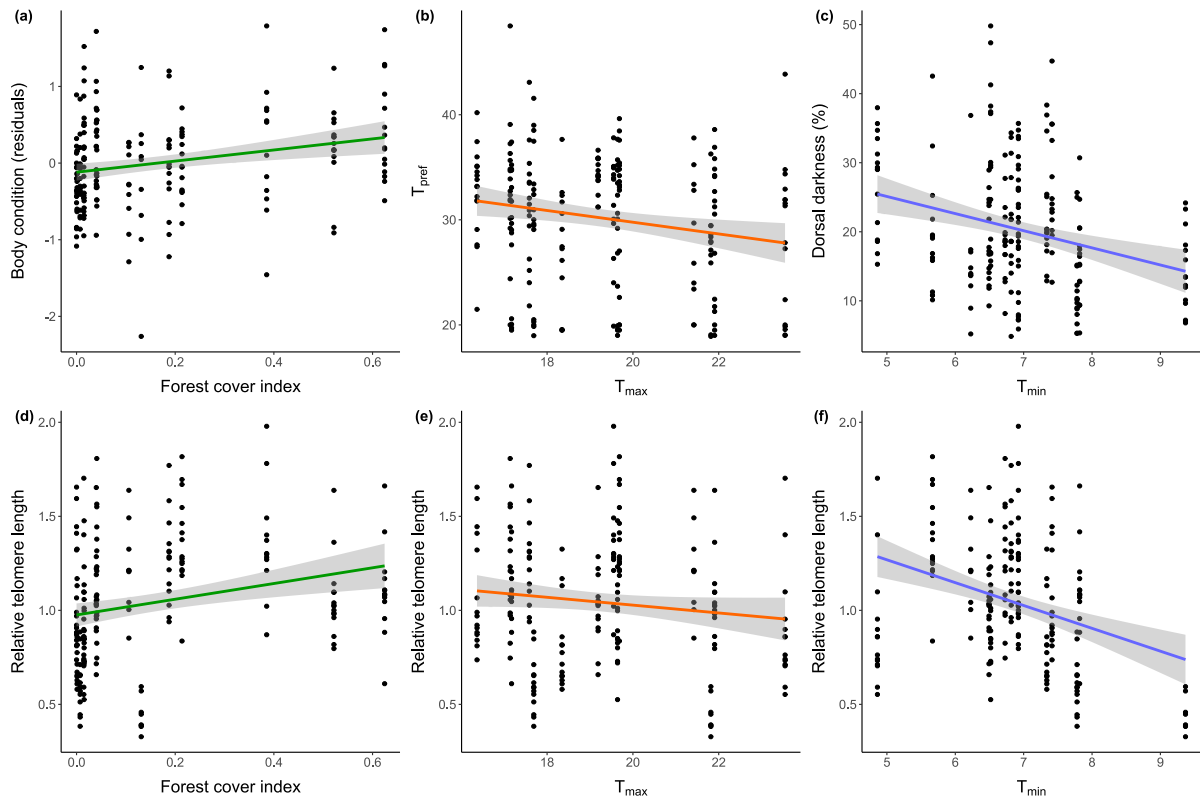


Figure 2: Variation in morphological and physiological traits of breeding females in natural populations of *Zootoca vivipara* along an environmental gradient. Variation of body condition at capture (residuals of a linear regression between female body mass and SVL) as a function of forest cover index (a). Variation of dorsal darkness as a function of mean daily minimum temperature (T_{\min}) during activity period (b). Variation of preferred body temperature (T_{pref}) as a function of mean daily maximum temperature (T_{max}) during activity period (c). Variation of relative telomere length as a function of forest cover index (d), T_{\min} (e) and T_{max} (f) during activity period. Points represent individual data and regression lines are displayed with their 95% confidence bands and coloured green when traits are correlated with forest cover index, blue if correlated with T_{\min} and orange if correlated with T_{max} .

3.4. Reproductive traits

Litter size varied weakly among sampled populations (proportional variance explained = 7%; $\chi^2_1 = 5.16$, $p = 0.02$). Although forest cover was the strongest explanatory variable for these variations ($\Sigma w_i = 0.40$; Table 1), its slope was not significant ($z = 1.4$, $p = 0.15$). In addition, we found variation across populations in parturition date (proportional variance explained = 39%; LRT = 64.24, $p < 0.0001$), reproductive

investment (proportional variance explained = 14%; LRT = 11.63, df = 1, $p < 0.001$), postpartum body condition (proportional variance explained = 15%; LRT = 12.22, df = 1, $p < 0.001$) and postpartum limb thickness (proportional variance explained = 15%; LRT = 13.36, df = 1, $p < 0.001$). The forest cover was the most supported explanatory variable to explain geographic variations in parturition dates, reproductive investment, postpartum limb thickness and postpartum body condition ($\Sigma w_i = 0.68$; $\Sigma w_i = 0.89$; $\Sigma w_i = 0.80$ and $\Sigma w_i = 0.87$ respectively; Table 1). Females from populations with a higher forest cover gave birth later (slope= 10.5 ± 4.32 days; $z = 2.2$, $p = 0.03$; Figure 3a), had a higher reproductive investment (slope= 0.66 ± 0.18 g; $z = 3.3$, $p = 0.001$; Figure 3b), a higher postpartum limb thickness (slope= 0.10 ± 0.04 mm; $z = 2.58$, $p = 0.01$) as well as post-partum body condition (slope= 0.62 ± 0.18 g; $z = 3.16$, $p = 0.002$; Figure 3c). Furthermore, litter viability differed among populations (proportional variance explained on the latent scale = 22%; $\chi^2_1 = 22.81$, $p < 0.0001$) and T_{\min} was the most supported explanatory variable to explain this variation ($\Sigma w_i = 0.77$). Litter viability was lower in populations with higher T_{\min} (slope= -0.57 ± 0.22 ; $z = 2.6$, $p = 0.009$; Figure 3d).

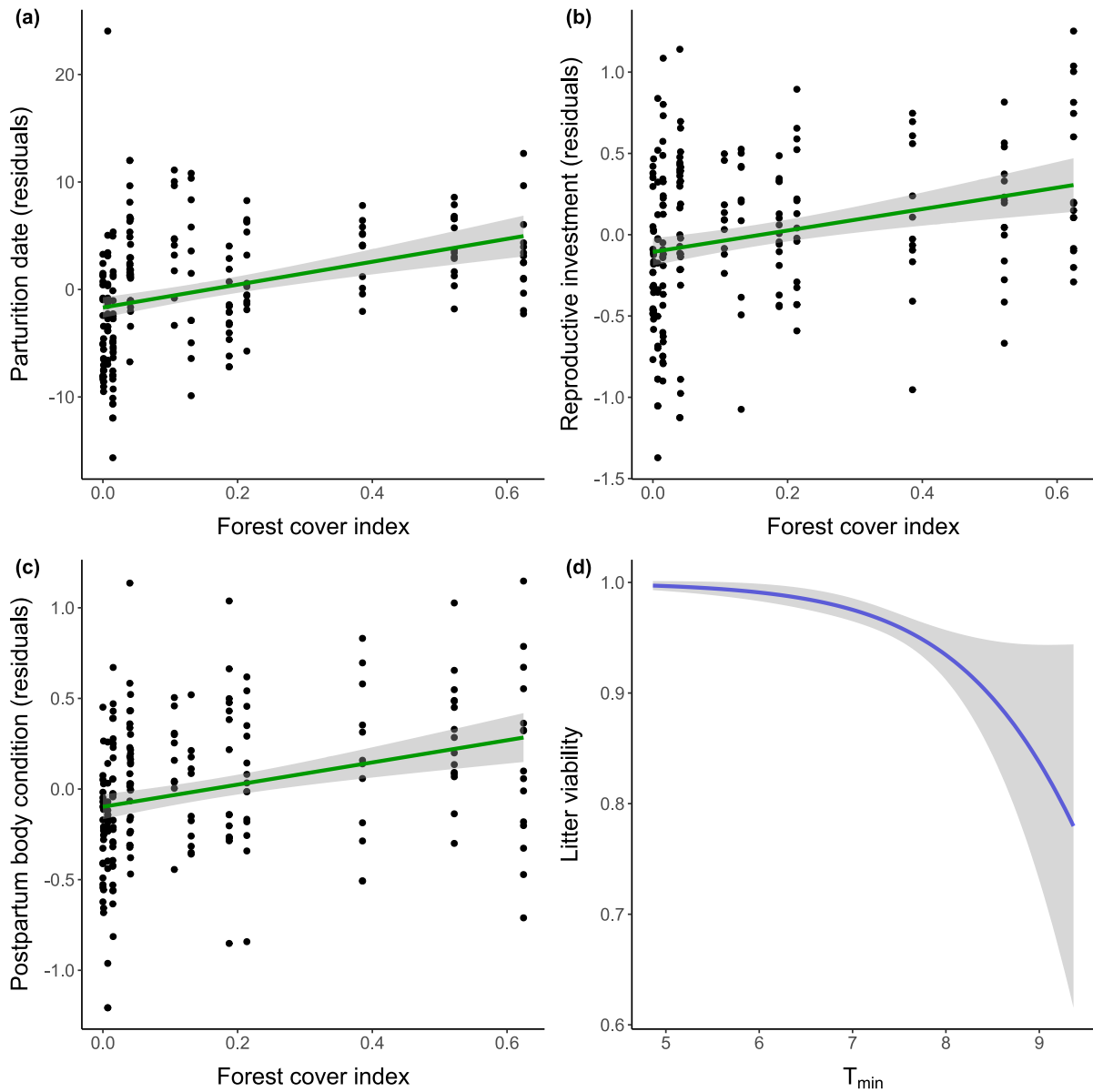


Figure 3: Variation in female reproductive traits in natural populations of *Zootoca vivipara* along an environmental gradient. Variation of parturition date (a), reproductive investment (b) and post-partum body condition (c) corrected by SVL (residuals) as a function of the forest cover index. Variation of litter viability (i.e., proportion of viable juveniles in the litter) as a function of mean daily minimum temperature (T_{min}) during activity period (d). In (a, b, c), points represent individual data and regression lines are displayed with their 95% confidence bands. In (d), predictions of the final model were fitted on the data together with the 95% confidence interval. Regression lines are coloured green when traits are correlated with forest cover index and blue if correlated with T_{min} .

Table 1: Rounded sum of Akaike weights (Σw_i) for each environmental explanatory variable of morphological, behavioural, physiological and reproductive traits. Σw_i was calculated by summing the weights of models where the variable appears. Σw_i are bold where covariates have a significant effect on traits.

		Forest cover	Water presence	T_{min}	T_{max}
Morphological, behavioural and physiological traits	SVL	0.20	0.22	0.30	0.26
	Body condition at capture	0.67	0.28	0.37	0.31
	Emergence time	0.63	0.32	0.28	0.46
	Preferred body temperature	0.20	0.25	0.56	0.85
	Total evaporative water losses	0.29	0.39	0.80	0.34
	Dorsal darkness	0.21	0.23	0.69	0.27
	Relative telomere length	0.96	0.02	1.0	0.98
Reproductive traits	Parturition date	0.68	0.16	0.29	0.26
	Reproductive investment	0.89	0.09	0.27	0.26
	Litter size	0.40	0.19	0.27	0.27
	Litter viability	0.47	0.39	0.77	0.46
	Post-partum body condition	0.87	0.10	0.37	0.28
	Post-partum limb thickness	0.80	0.12	0.38	0.57

4. Discussion

In this study, we investigated the geographical variation in cellular, morphological, behavioural, physiological and reproductive traits across wild populations of the common lizard (*Zootoca vivipara*), which differed in their local climatic conditions, forest cover, and access to free-standing water. We identified inter-population differences in all measured traits, except for resting metabolic rates. Overall, relative telomere length varied strongly across populations, while morphological and reproductive traits were moderately variable, and behavioural and physiological traits were surprisingly weakly variable. Diurnal and/or nocturnal thermal conditions covaried with a range of functional traits (preferred body temperature, dorsal darkness, total evaporative water losses), with relative telomere length and with litter viability. Females from populations exposed to warmer nocturnal temperatures had reduced total evaporative water losses and dorsal darkness, as well as lower relative telomere length and litter viability. Moreover, females exposed to warmer daytime temperatures showed reduced preferred body temperature and had shorter relative telomere length. Furthermore, forest cover covaried with female emergence behaviour, relative telomere length, body condition and was the main driver of geographic variation in reproductive traits whereas access to open water did not covary with studied traits. Females from populations with greater forest cover showed better body condition at capture, earlier emergence time, delayed parturition dates, increased reproductive investment and better post-partum condition. These results can be understood if lizards from habitats with a high forest cover were buffered against some negative effects of the exceptional 2022 spring and early summer heat wave on energy balance and reproductive effort.

Females from populations exposed to higher minimum daily temperatures (i.e., higher nocturnal temperatures) had shorter relative telomere length and lower total water losses. During the night, diurnal ectotherms are exposed to surrounding environmental conditions for a long period and have limited behavioural capacities because they rest in the soil or vegetation (e.g., nocturnal microhabitat selection (Davis & DeNardo, 2007; Dezetter et al., 2023)). Thus, nocturnal temperatures have more direct effects on body temperatures and energy balance in this species than diurnal conditions. Reduced relative telomere length in populations exposed to warm nights is in line with two recent studies on common lizards (Dupoué et al., 2022; Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017) and the general hypothesis that relative telomere length may shorten faster with age under warmer climates in ectotherms (reviewed in Burraco et al. 2020). For example, increased metabolic activity due to warmer nights could lead to increased oxidative stress and telomere shortening due to sustained mitochondrial activity and impaired antioxidant defences (Burraco et al., 2020). Furthermore, since respiratory and cutaneous water losses are functionally linked to body temperature in squamates (see Rozen-Rechels et al. 2019), increasing nighttime temperatures can significantly increase total evaporative water losses and affect water balance. Reduced total evaporative water losses in populations exposed to warmer minimum temperatures could reflect physiological acclimatisation and/or genetic adaptations of skin barrier permeability via changes in its thickness (e.g., lipid content) or composition (e.g., type, proportion and geometry of lipids (Lillywhite, 2006)). While previous studies have shown that ectothermic species can adjust their water loss in response to daytime temperatures (e.g., Dezetter et al., 2022; Riddell et al., 2019), modifications in water loss due to nocturnal thermal conditions have, to our knowledge, not been documented.

Moreover, nighttime temperatures were the main driver of geographical variations in dorsal darkness and females exposed to warm nighttime local temperatures tended to have a lower dorsal darkness. The intensity of integument darkness may influence heating rates in lizards and confer an advantage in cold environments by allowing darker individuals to maintain larger activity windows favouring foraging, or embryo development during gestation for example (thermal melanism hypothesis: reviewed in Clusella Trullas, van Wyk, et Spotila 2007). On the contrary, the increased heating rate induced by darker skin can be disadvantageous in warm environments where the overheating risk is greater, which should favour lighter colour forms (Clusella-Trullas & Nielsen, 2020). Although the thermal advantage of darker integument is limited during the night, warmer nocturnal temperatures can increase sensitivity to diurnal heat stress (Speights et al., 2017) and a recent experiment showed that exposure to nocturnal warming leads to plastic downward changes of skin darkness in the common lizard (Rutschmann et al., 2021). An alternative hypothesis is that nocturnal temperatures affect physiological processes closely linked to integument melanisation, such as the immune system (Sacchi et al., 2017; Stahlschmidt et al., 2017). Overall, our results underline the importance of considering nocturnal warming in the responses of ectotherms to climate change (reviewed in Rutschmann et al. 2024)

Relative telomere length also covaried with local daytime maximum temperatures. Thus, both daytime and nighttime warming may contribute to telomere shortening in the common lizard (Burraco et al., 2020). The effects of local thermal conditions on females relative telomere length may reflect intragenerational effects of annual thermal conditions (Axelsson et al., 2020) and/or intergenerational accumulated effects of past thermal conditions experienced by previous generations in the

population ("aging loop hypothesis"; Dupoué et al., 2022). In addition, according to the thermal adaptation hypothesis, we expected that thermal preferences should covary with environmental temperatures (Angilletta et al., 2002). Yet, we found no evidence of higher preferred body temperatures in warmer populations. On the contrary, females from populations exposed to warmer daytime maximum temperatures had lower preferred body temperature, a counter-intuitive gradient reported in some other studies of ectotherms (e.g., Fangué et al., 2009; Hodgson & Schwanz, 2019; Trochet et al., 2018). One potential explanation is that reduced preferred body temperatures could be an effective response to avoid overheating risk and physiological imbalances (e.g., increased energy expenditure and oxidative stress) in warmer climates. Such differences in preferred body temperature between populations are probably linked to plastic adjustments in thermoregulatory behaviour rather than permanent differences between populations and could be context-dependent (Clusella-Trullas & Chown, 2014). Indeed, other studies on the common lizard have failed to report significant geographical variation in preferred body temperature (Chabaud et al., 2022; Gvoždík & Castilla, 2001; Rozen-Rechels et al., 2021) and thermoregulation-related traits are generally weakly heritable in reptiles (Logan et al., 2018; Paranjpe et al., 2013).

Finally, litter viability covaried with local nighttime temperatures and females exposed to warmer nighttime temperatures produced fewer viable juveniles at birth. In general, the effects of developmental temperatures on juvenile viability follow a concave shape (Noble et al., 2018), where too cold or too hot temperatures increase embryonic mortality and developmental abnormalities (Cui et al., 2022; Ji et al., 2002; Qualls, 1999). Effects of developmental conditions on offspring quality have often been studied by manipulating diurnal thermal regimes, and we do not know to what extent nocturnal acceleration of embryonic development at suboptimal temperatures can

impact offspring quality (Rutschmann et al., 2024). For example, increased physiological activity at suboptimal temperatures may increase oxidative stress (Ritchie & Friesen, 2022), which could impact embryo viability (Dennerly, 2007). The relationship between nighttime temperatures and litter viability could also be linked to some effects of nighttime temperatures on the intrinsic quality of breeding females and consequently on the quality of juveniles produced, given the link between telomere length, individual quality and reproductive success (Angelier et al., 2019; Cheron et al., 2021; Dupoué et al., 2022).

Surprisingly, local thermal conditions were not the main driver of geographical variations in parturition dates, reproductive investment and post-partum body condition of females. In viviparous reptiles, breeding phenology is generally strongly influenced by thermal conditions as developmental temperatures affect the speed of embryonic development and gestation length (Ljungström et al., 2015). In addition, reproduction is a critical period during which female common lizards use their stored and recently acquired resources (capital and income mixed strategy) to fuel egg formation and energy expenditure related to embryonic development (Bleu et al., 2013; Foucart et al., 2014; Van Dyke & Beaupre, 2011). Given the thermal dependence of metabolism (i.e., energy expenditure), prey capture and assimilation rates (Van Damme et al., 1991), thermal conditions during vitellogenesis or gestation should influence reproductive allocation strategies and postpartum body condition in females (Brusch, Gavira, Viton, Dupoué, Leroux-Coyau, Meylan, Galliard, et al., 2020; Brusch IV et al., 2023; Rutschmann, Miles, Clobert, et al., 2016). The limited impact of thermal conditions on the geographical variation in reproductive traits reported here may be attributed to behavioural thermoregulation or sufficiently abundant prey availability, which could mitigate temperature effects on reproduction (Beltrán et al., 2021;

Bodineau, de Villemereuil, et al., 2024). In addition, the exceptional heat wave during our sampling year potentially increased thermoregulatory opportunities even in the usually colder populations, allowing females to more easily reach an optimal temperature for embryonic development and reproductive investment (Rutschmann, Miles, Clobert, et al., 2016). Finally, reproductive traits are influenced by both diurnal and nocturnal temperatures (Brusch IV et al., 2023), and we found that some populations had opposite diurnal and nocturnal thermal profiles, maybe due to differences in nighttime cooling and cloud regimes (hot daytime temperature but cold nighttime temperature, or vice versa; see Table S1). Thus, this may have reduced the effect of diurnal and nocturnal temperatures on these traits.

Nevertheless, forest cover contributed significantly to the geographic variation in cellular, morphological, behavioural, physiological and reproductive traits. We found that females from populations with high forest cover had higher relative telomere length, earlier emergence time, delayed parturition date, higher reproductive investment and were in better condition at capture or after parturition. The forest cover can influence local microclimatic conditions (Sears et al., 2011; Suggitt et al., 2011) through the attenuation of solar radiation and evapotranspiration, generally buffering thermal and hydric stress at ground level (De Frenne et al., 2021). In heliothermic ground-dwelling species that actively thermoregulate such as the common lizard (Gvoždík, 2002), microclimate quality and heterogeneity are essential for optimal thermoregulation (Sears et al., 2016). A higher forest cover may constrain behavioural thermoregulation by increasing shaded areas, which could explain the permanent behavioural adjustments in activity patterns in favour of earlier emergence in more forested habitats. However, a more shaded habitat may also reduce the negative effects of warmer climatic conditions (De Lombaerde et al., 2022; Neel et al., 2021;

Pincebourde et al., 2016; Pincebourde & Woods, 2020; Woods et al., 2015). Thus, we hypothesise that sites with higher forest cover buffered the effects of June 2022 heat waves on female condition, relative telomere length, parturition dates and reproductive allocation strategies. This buffering effect of forest cover could both explain delayed parturition dates (Rutschmann, Miles, Le Galliard, et al., 2016), higher body and muscular condition, higher reproductive investment and higher telomere length (McLennan et al., 2022) in populations with higher forest cover. Vegetation structure could also covary with prey abundance (arthropods: Lassau et al. 2005; Uetz 1979). In turn, greater prey abundance in populations with higher forest cover could explain the positive effect of forest cover on female body and muscular condition (e.g., Bodineau et al. 2024), telomere length (e.g., McLennan et al. 2022) and reproductive investment (e.g., Wang et al. 2017).

While previous experimental and correlational studies in the common lizard have highlighted the importance of free-standing water availability in the environment for optimal hydroregulation (Chabaud et al., 2022; Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017) and thermoregulation (Rozen-Rechels et al., 2021), free-standing water access was not the environmental variable with the greatest influence on the studied traits. In addition, none of the environmental factors studied explained the geographical variations in female SVL among populations. Larger-scale studies on the common lizard highlight that activity season length is the main driver of geographic variation in SVL in this species (Horváthová et al., 2013; Roitberg et al., 2020). Geographical differences in litter size were also not explained by the environmental variables studied and disappeared when we took female body size into account. Thus, geographic variations in litter size were driven by variations in female body size, which strongly constrains litter size in the common lizard (Pilorge et al., 1983). Furthermore,

we found no evidence of geographical variations in metabolic rates. Since phenotypic traits were measured after female parturition to avoid confounding effects of gestation stage on physiological and behavioural traits, it is likely that acclimation to rearing conditions eliminated or reduced population variations in some traits, especially flexible traits such as basal metabolic expenditure (Llewelyn et al., 2018).

5. Conclusion

Overall, our study of intraspecific variation in climate-relevant and reproductive traits in female common lizards highlights that local daytime and nighttime temperature conditions, along with forest cover, are key environmental factors determining geographic variation in cellular, morphological, physiological, behavioural, and reproductive traits. These results confirm the importance of considering intraspecific variation of climate-relevant and reproductive traits (Chardon et al., 2020; DeMarche et al., 2019), the combined effects of diurnal and nocturnal warming (Speights et al., 2017) as well as habitat features (Neel et al., 2021; Stark et al., 2023) when modelling species' vulnerability to climate change. Future studies should focus on evolutionary processes underlying these variations and the relative contribution of genetic adaptation, acclimatisation and behavioural adjustments to improve predictions of ectotherm responses to climate change.

Authors' contributions

Théo Bodineau, Luis M. San-Jose, Julien Cote, Jean-François Le Galliard, Sandrine Meylan and Pierre de Villemereuil conceived the ideas and designed the methodology; All authors collected the data; Théo Bodineau, Jean-François Le Galliard and Divina Beejmohun analysed the data with the help of Sandrine Meylan, Pierre de Villemereuil and Julien Cote; Théo Bodineau led the writing of the manuscript with the help of Jean-François Le Galliard, Sandrine Meylan, Pierre de Villemereuil and Julien Cote. All authors contributed critically to the paper and gave final approval for publication.

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Conflict of Interest

The authors declare no competing or financial interests.

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Supplementary information

Table S1: Description, sample number (*N*) and environmental characteristics of 14 geographical localities where reproductive females of the common lizard (*Zootoca vivipara*) were captured.

Population	Mountain Range	Department	Longitude	Latitude	<i>N</i>	Elevation (m)	Forest cover index	Water access	T _{min} (°C)	T _{mean} (°C)	T _{max} (°C)
BARN	Mont-Lozère	Lozère	3.755575	44.433189	15	1516.6	0.00	Permanent	7.41	11.85	16.37
BEL	Mont du Velay	Ardèche	4.024956	44.672442	15	1414.2	0.62	Temporary	7.82	12.23	17.17
BES	Margeride	Lozère	3.5080861	44.587647	15	1218.6	0.39	Permanent	6.92	13.12	19.55
BOB	Mont du Vivarais	Ardèche	4.227575	44.823414	15	1430	0.19	Permanent	6.82	12.09	17.59
BON	Mont d'Aubrac	Lozère	3.1279	44.560161	14	1341	0.00	Permanent	7.34	12.47	18.35
COM	Margeride	Lozère	3.5327722	44.667025	15	1399.4	0.21	Permanent	5.67	12.00	19.69
COP	Mont du Velay	Ardèche	4.0304972	44.655106	15	1371.2	0.04	Permanent	6.73	12.14	17.14
GIB	Mont-Lozère	Lozère	3.858919	44.384148	15	1431.9	0.00	Permanent	6.49	12.03	19.19
JOC	Mont du Vivarais	Ardèche	4.2110138	44.835183	10	1295.7	0.11	Permanent	6.23	12.55	21.42
LAJ	Margeride	Lozère	3.4308361	44.84475	15	1323	0.52	Temporary	6.92	13.40	21.90
MON	Mont du Velay	Ardèche	4.008155	44.511183	15	1047.8	0.13	Permanent	9.37	14.83	21.82
PEJ	Mont du Cantal	Cantal	2.84415	45.163931	15	1207	0.02	Permanent	6.52	13.01	19.64
PUY	Mont du Cantal	Cantal	2.6850277	45.107158	15	1431	0.01	Permanent	7.78	12.15	17.69
TIO	Mont d'Aubrac	Lozère	3.1070194	44.588447	15	1272.4	0.01	Permanent	4.86	13.28	23.55

Table S2: List of models tested to analyse geographic variation in female morphological, physiological, behavioural and reproductive traits.

List of tested models	
Fixed effects	Random effect
Y ~ 1	Population
Y ~ Forest cover	Population
Y ~ Water access	Population
Y ~ T _{min}	Population
Y ~ T _{max}	Population
Y ~ T _{min} + T _{max}	Population
Y ~ T _{min} + Water access	Population
Y ~ T _{max} + Water access	Population
Y ~ T _{min} + T _{max} + Water access	Population
Y ~ T _{min} + Forest cover	Population
Y ~ T _{max} + Forest cover	Population
Y ~ T _{min} + T _{max} + Forest cover	Population
Y ~ SVL	Population
Y ~ SVL + Forest cover	Population
Y ~ SVL + Water access	Population
Y ~ SVL + T _{min}	Population
Y ~ SVL + T _{max}	Population
Y ~ SVL + T _{min} + T _{max}	Population
Y ~ SVL + T _{min} + Water access	Population
Y ~ SVL + T _{max} + Water access	Population
Y ~ SVL + T _{min} + T _{max} + Water access	Population
Y ~ SVL + T _{min} + Forest cover	Population
Y ~ SVL + T _{max} + Forest cover	Population
Y ~ SVL + T _{min} + T _{max} + Forest cover	Population

Note: Models including SVL were not tested to analyse geographical variations in female SVL.

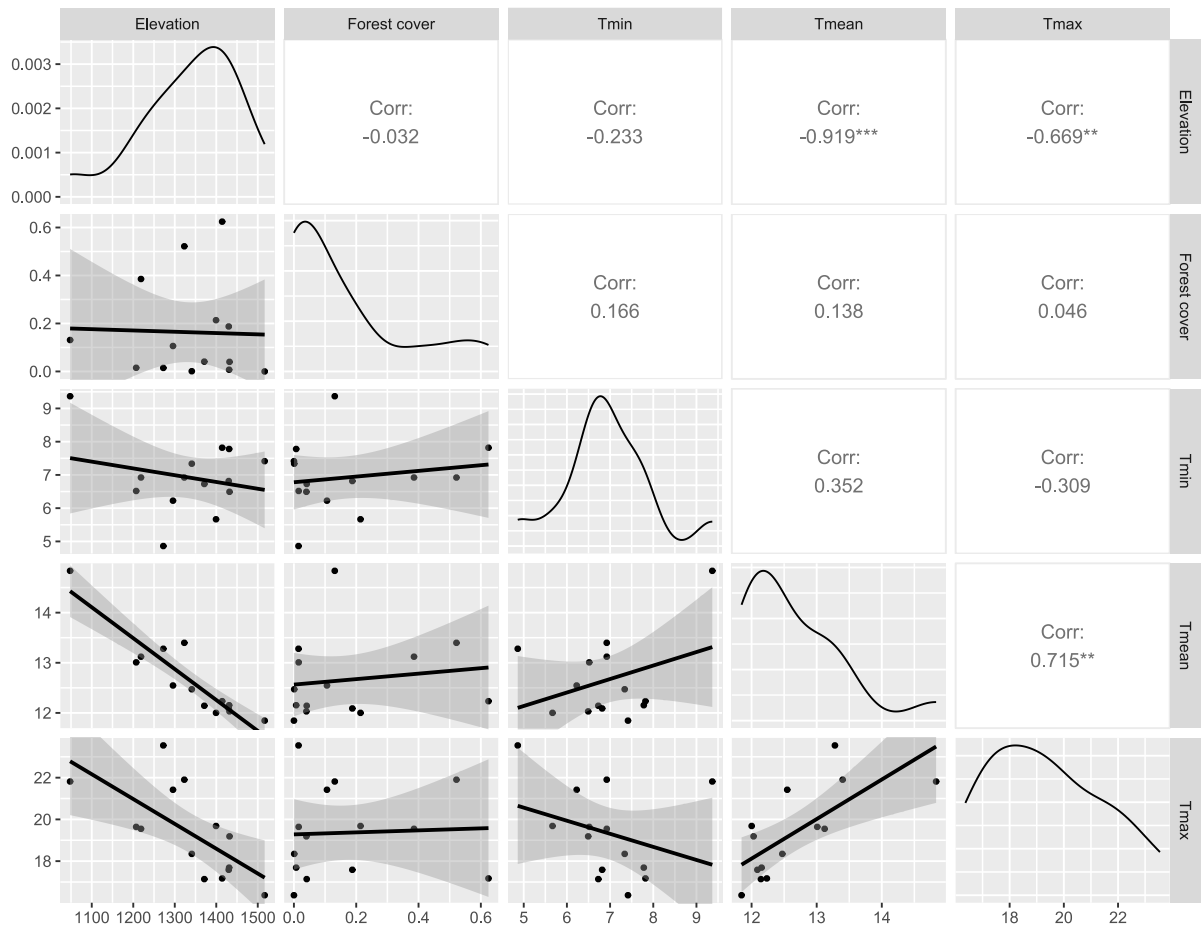


Figure S1: Scatterplot matrix of altitude (m), forest cover index, mean daily minimum temperature (T_{\min} ($^{\circ}\text{C}$)), mean daily mean temperature (T_{mean} ($^{\circ}\text{C}$)) and mean daily maximum temperature (T_{max} ($^{\circ}\text{C}$)) of studied populations. Lower panels show scatterplots for pairs of environmental variables in the original scale with the best linear regression line. The diagonal represents the distribution of each variable. The upper panel provides the Pearson correlation coefficients between pairs of variables. Elevation of our study sites was significantly correlated with T_{mean} and T_{max} . We therefore chose to study the effects of thermal conditions rather than altitude on female traits. In addition, since T_{mean} was significantly correlated with T_{max} , we chose to keep T_{min} as a climatic proxy related to nighttime temperatures and T_{max} as the climatic proxy related to daytime temperatures in our analysis.

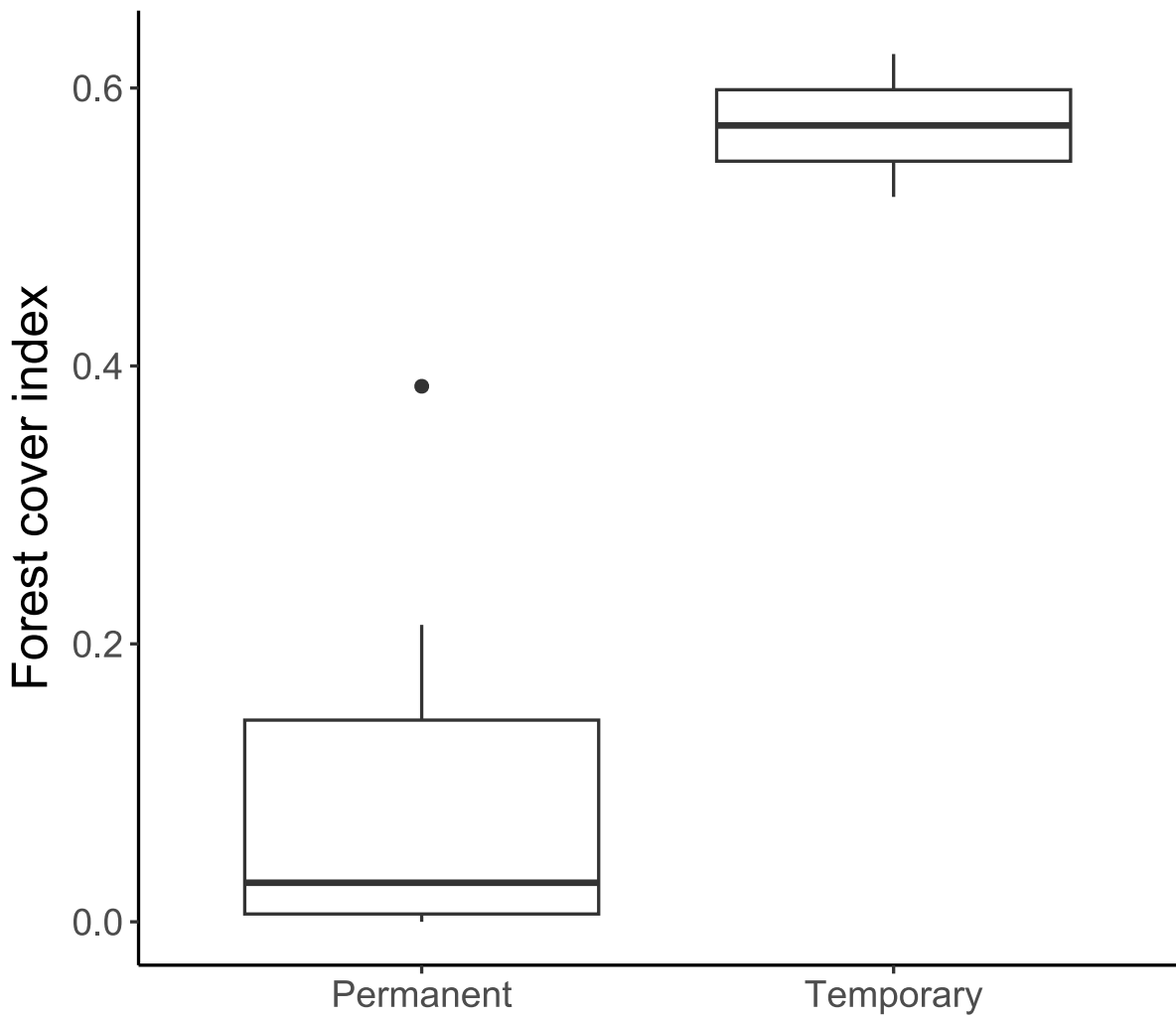


Figure S2: Relationship between the forest cover index and free-standing water access in sampled populations. Boxplots of the distribution of data are displayed. The forest cover index is significantly higher in populations with temporary access to free-standing water ($F_{1,12} = 29.1$, $p < 0.001$).

Chapitre 2 - Déterminants environnementaux des dates de parturition, héritabilité et sélection



Femelle gestante en position de thermorégulation dans une population naturelle de lézard vivipare sur les monts d'Aubrac. © Théo Bodineau

Article 2

High thermal plasticity, low heritability and constant directional selection on breeding phenology in a viviparous ectotherm

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Abstract

1. Shifting breeding phenology is a widespread response to global warming in ectothermic species such as reptiles. In turn, breeding phenology can have considerable impacts on reproductive success and population dynamics. Thus, understanding causes and consequences of plasticity and micro-evolution in breeding phenology is important for determining vulnerability to climate change.

2. Here, we study environmental and individual determinants of breeding phenology, its heritability and the temporal variation of selection on parturition date using a 31-year monitoring of a wild population of common lizards (*Zootoca vivipara*).

3. Mean daily maximum temperatures during the post-winter activity period and body size drove variation in parturition dates. On average, warmer temperatures advanced parturition dates and larger females gave birth earlier, but warmer temperatures also reduced size-related phenological variability.

4. Over 31 years, breeding phenology did not change towards earlier or later dates despite an increase of +0.6 °C per decade in mean daily maximum temperatures at our study site. Parturition dates were repeatable among females but weakly heritable, which suggests that inter-individual consistency of parturition dates may be related to non-heritable factors such as home range quality, nutritional condition or behaviour. In addition, we found evidence for a directional selection toward earlier parturition, without fluctuation in time.

5. This study highlights the strong interannual thermal plasticity coupled with a limited adaptive potential of breeding phenology in the common lizard. In future, warmer conditions, the interplay between such plasticity and a selection apparently independent from environmental fluctuations would thus essentially depend on the, yet unknown, cost of thermal plasticity.

Keywords: Adaptation, climate change, ectotherm, phenology, phenotypic plasticity, quantitative genetics, reproduction, selection.

1. Introduction

For many organisms living in seasonal environments, breeding phenology is closely related to life history traits that determine populations dynamics (e.g., annual growth, survival and reproductive success), and therefore to persistence in changing environments (McLean *et al.*, 2016; Iler *et al.*, 2021). Changes in breeding phenology related to warmer temperatures over the last decades have been widely reported and are now considered as a universal response climate warming in natural populations of plants and animals (reviewed in Walther *et al.*, 2002; Root *et al.*, 2003; Parmesan, 2006). However, such warming-induced phenological changes exhibit significant variation in both direction and magnitude across taxonomic groups (Thackeray *et al.*, 2016; Vitasse *et al.*, 2021), and their effects on individual fitness remain highly uncertain across taxa (Duputié *et al.*, 2015). While stabilising selection on breeding phenology is well documented in birds or mammals (e.g., de Villemereuil *et al.*, 2020), selection on breeding dates in other vertebrates has received less attention so far (Olsson & Shine, 1997; Wapstra *et al.*, 2010; Bogner *et al.*, 2016).

In squamates reptiles, and particularly in lizards, experimental and correlative studies on captive, semi-natural, or wild populations show widespread evidence for directional selection favouring earlier laying or parturition dates, with many populations characterised by a seasonal decrease in reproductive investment and number of viable offspring (Olsson & Shine, 1997; Mitchell *et al.*, 2018; Bodineau *et al.*, 2024). This seasonal decline in fitness is similar to the one observed in other animal taxa (e.g., birds: Öberg *et al.*, 2014, insects: Landa, 1992, mammals: Feder *et al.*, 2008). It has been explained by the existence of a covariation between breeding date and

environmental conditions favouring early breeding in seasonal climates ("Date hypothesis", (Hatchwell, 1991; Moreno, 1998)) and/or by a covariation between the quality of breeders and their breeding date ("Quality hypothesis", (Hatchwell, 1991; Brinkhof *et al.*, 1993)). For example, both nutritional state and body condition are known to influence the timing and success of reproduction (Price *et al.*, 1988; Verhulst & Nilsson, 2008). Yet, while some studies on birds and mammals report fluctuating selection on breeding date depending on climatic conditions or prey availability (Visser *et al.*, 1998, 2015; Husby *et al.*, 2011; Gienapp *et al.*, 2013; Gamelon *et al.*, 2018; Marrot *et al.*, 2018; de Villemereuil *et al.*, 2020), no study has quantified temporal changes in the strength of selection on breeding dates in reptiles so far.

Further, in reptiles, interannual variations in breeding phenology are mainly explained by the thermal plasticity of the reproductive cycle (e.g., Ljungström *et al.*, 2015). Life history traits of ectotherms are particularly sensitive to external thermal conditions because of the tight relationship that exists between environmental temperatures, essential biochemical processes (e.g., biochemical reaction kinetics, enzyme inactivation or hormone regulation see (Hochachka & Somero, 2002)) and behavioural activity patterns (Gunderson & Leal, 2015). That is, warmer temperatures during the reproductive cycle can advance spring emergence (Moss & MacLeod, 2022), follicular and embryonic development (Duvall, 1982; Noble *et al.*, 2018), and ultimately laying or parturition dates (Ljungström *et al.*, 2015; Rutschmann *et al.*, 2016b). One consequence of this profound influence of temperature on breeding traits is that reptiles breeding phenology is likely to be sensitive to thermal conditions throughout the entire reproductive cycle (i.e., from post-winter emergence to the end of gestation), rather than during a critical period during the reproductive cycle (e.g., Porlier *et al.*, 2012). Although the environmental cues and the time-window that

explained most of the variation of reproductive phenology has received much attention in birds (e.g., Drake & Martin, 2018; Andreasson *et al.*, 2023), few field studies have identified climatic determinants of laying or parturition dates in reptiles (Lourdais *et al.*, 2004).

In addition, studies in reptiles often report significant inter-individual variations in reproductive timing (Olsson & Shine, 1997; Wapstra *et al.*, 2010; Ljungström *et al.*, 2015; Cunningham *et al.*, 2020), but mechanisms underlying such inter-individual variations are not well understood. Body size and body condition are important determinant of individual phenology in lizards, with larger and females in better condition giving birth generally earlier than others (Bauwens & Verheyen, 1985; Olsson & Shine, 1997; Le Galliard *et al.*, 2010; Hall *et al.*, 2018). However, the role of genetics in shaping inter-individual variation in reproductive phenology remains largely unknown in reptile species compared with others vertebrates (reviewed in mammals: Boutin & Lane, 2014; birds: Charmantier & Gienapp, 2014). Although few study in lizard suggests that females show repeatable parturition dates among years (Wapstra *et al.*, 2010; Cunningham *et al.*, 2020), no study has reliably estimated the heritability of laying or parturition dates in wild squamates populations using quantitative genetic methods (Urban *et al.*, 2014). Given that laying or parturition dates can significantly impact individual fitness and population dynamics, understanding how reproductive phenology differs within and between individuals, as well as the capacity of this trait to respond to selection is crucial for predicting how ectothermic squamates will respond to climate changes.

Here, we quantified climatic and individual determinants of parturition date using a long-term mark-recapture data set (31 years) from a natural population of European common lizards (*Zootoca vivipara*, Lichenstein 1823) in France. We also investigated

the shape, strength and temporal variation of selection on parturition date. In line with earlier studies showing that cold climate conditions constrain activity and reproduction in this cool margin population (Huey, 1982; Chamaillé-Jammes *et al.*, 2006; Marquis *et al.*, 2008), mean daily maximum temperatures during the post-winter activity period (including emergence, mating and early gestation) should be the most influential climatic proxy of inter-annual variations in parturition dates. Additionally, larger females should give birth earlier than smaller females (Bauwens & Verheyen, 1985). We used a time-window approach to study thermal and individual drivers of parturition dates. Second, parturition dates should be repeatable with a low to moderate heritability since breeding phenology is known to be highly plastic (Olsson *et al.*, 2018). We quantified the repeatability and the heritability of parturition dates using animal model. Finally, there should be a directional selection towards earlier parturition dates (Olsson & Shine, 1997) that could fluctuate depending on the thermal conditions experienced by females during the reproductive cycle. Warmer environmental temperatures could provide a higher quality environment for thermoregulation, embryonic development management and prey availability, thus reducing the strength of selection on parturition date. We quantified the direction, shape and temporal variation of selection on parturition dates using the number of viable juveniles produced by the female as an annual measure of fitness.

2. Material and methods

2.1. Model species, study site, sampling and rearing conditions

Longitudinal data on reproduction were obtained from long-term mark-recapture monitoring conducted from 1989 to 2019 in a population of common lizards located near the Mas de la Barque (Mont-Lozère, France; 1420 m a.s.l., see details in Clobert *et al.* 2014). The European common lizard is a small lizard widely distributed in

northern Eurasia in highly seasonal, cool and humid habitats. In our study area, activity starts for adult males around mid-April and for adult females in early May. Mating may occur immediately after female emergence and vitellogenesis occurs on average during the first three weeks of activity (Bauwens & Verheyen, 1985). Reproductive mode is viviparous and parturition occurs after an average gestation period of ca. 2 months (i.e., between July and early August (Bauwens & Verheyen, 1985)). Females lay on average five non-calcified eggs (range from 1 to 12) including both nonviable offspring (fertilised or unfertilised eggs, undeveloped embryos and stillborns) and live offspring which hatch quickly after parturition.

Each year, lizards were captured in early-June and mid-July ca. 1 month before the mean parturition date of females in this population (mean capture date: 29th June \pm 12.5 SD). Variations in capture dates are mainly due to variations in weather conditions, which influence capture possibilities and efficiency. Lizards were identified or marked by toe-clipping, measured for body length (snout-vent length, SVL) and sampled for tail tip tissues (< 1 cm) for pedigree construction (see below). Immediately after being measured, all individuals were released at the capture location except gravid females which were transported to the laboratory nearby the field site and kept until parturition. We maintained females with *ad libitum* food and water in individual terrariums (18 × 11 × 12 cm) filled with sterilised peat as substrate, equipped with a shelter. Terrariums were lit automatically between 9:00 am to 12:00 pm and 2:00 pm to 5:00 pm by an incandescent heating bulb (25W) placed on one side of the terrarium to generate a thermal gradient. After parturition, the litter was characterised by recording the number of unfertilised eggs, undeveloped embryos, stillborn and live juveniles. Live juveniles were marked by toe-clipping and a tail tip tissue was collected (< 3 mm) to infer paternity (see below). All juveniles were released within three days

after birth, together with their mothers, at the mother's capture location. Note that the rearing site changed four times during the long-term monitoring due to logistical constraints (respectively in 1993, 1997 and 2002). Differences in rearing conditions were taken into account in the statistical analyses (see below).

2.2. Climate data collection

Local climatic conditions (1989 to 2019) were reconstructed using weather conditions recorded by the nearest, high-quality, long-term meteorological station, which is situated at a similar elevation but 50 km south of our study population (Meteo France, Mont Aigoual, ID: 30339001, 1.567 m a.s.l., 44°07'17" N, 3°34'53" E). To do so, data collected at Mont Aigoual between August 2022 and August 2023 were downscaled to local conditions using climatic data collected *in situ* with HOBO® Pro v2 U23-002 loggers (ONSET 188 Cape Cod, Massachusetts) installed in the shade in a solar radiation shield from over the same time period. Specifically, we used linear regressions to relate the mean daily minimum (T_{\min}), mean (T_{mean}) and maximum (T_{\max}) temperatures recorded in our study site and the ones recorded at the Mont Aigoual from August 2022 to August 2023 (N=356; $R^2= 0.82$ for T_{\min} , $R^2= 0.94$ for T_{mean} and $R^2= 0.96$ for T_{\max} ; Figure S2). We then used the regression coefficients from each linear regression to reconstruct historic T_{\min} , T_{mean} and T_{\max} in our study site from Mont Aigoual data recorded over the entire time series (1989 - 2019). This method provides a reliable reconstruction of the local climate at our study site (Le Galliard *et al.*, 2010).

2.3. Pedigree

The genetic pedigree of the population was reconstructed from DNA samples extracted from caudal tissue samples from all captured animals and juveniles using DNeasy Blood & Tissue (Qiagen) kit. We genotyped microsatellite markers at 8 loci (Richard *et*

al., 2012). The CERVUS software (Kalinowski *et al.*, 2007) was then used to infer paternity of each newborn based on probabilistic modelling of allele segregation. When the individual was not born in the laboratory, we assigned fictitious identities to unknown (i.e., uncaught) parents. As the depth of the pedigree was unsatisfactory before 2007, we carried out heritability analyses on a subset dataset between 2007 and 2019. Over this period, the pedigree had a maximum depth of 5 with an average of 1.60 generations.

2.4. Statistical analysis

Analyses were performed using R software version 4.2.0 (R Core Team, 2022). In all cases, we tested model fitting, model assumptions and we compared them using the Akaike information criterion corrected for small sample size (AICc).

2.4.1. Climatic and individual determinants of parturition dates

Analyses were performed on a dataset containing 2,119 female breeding events between 1989 and 2019. We estimated phenological trends in mean parturition dates from 1989 to 2019 with a linear model fitted with mean capture date, rearing site (to control for rearing site changes) and year as fixed effects. Then, we carried out a time-window analysis to determine whether there is a period during which this species is most strongly influenced by thermal conditions. We focused on the influence of environmental temperatures on parturition dates by generating 4-weeks time-windows at sliding one-week intervals. These periods were generated between 1st April (i.e., before likely post-winter emergence) and 30th June (i.e., between the middle and the end of female capture dates). We also generated a longer time-window including the entire post-winter activity period between 1st May and 30th June. For each time-window, we compared the effects of T_{\min} , T_{mean} and T_{\max} on parturition dates using linear mixed

models based on the *lme4* package (Bates *et al.*, 2015). Models included capture date, rearing site (to control for rearing site changes) and female body size as fixed effects. Individual identity and year were also included as random effects. This model selection led to retain $T_{\max \text{ May} - \text{ June}}$ as the best explanatory temperature proxy (see below). Since phenological advances caused by higher temperatures can be accompanied by a decrease in parturition dates variance (Massot *et al.* 2017), we characterised changes in parturition date variances as a function of $T_{\max \text{ May} - \text{ June}}$ using a power variance function “varPower” of the *nlme* package. To further explore the effects of $T_{\max \text{ May} - \text{ June}}$, we tested whether size-induced phenological differences were influenced by $T_{\max \text{ May} - \text{ June}}$ by incorporating an interactive effect of female body size and $T_{\max \text{ May} - \text{ June}}$.

2.4.2. Repeatability and heritability of parturition dates

We used the Bayesian R package *brms* with default priors (Bürkner, 2017) to estimate the repeatability and the heritability of parturition date. Number of iteration and length of burn-in period were determined so that the effective sample size is above 1000 for all parameters and the potential scale reduction factor is 1.01 or below, after graphically checking for convergence (Vehtari *et al.*, 2021). In general, studies in birds and mammals quantify the repeatability and heritability of the absolute (i.e., calendar) laying or parturition date, as the reproductive phenology of these species is first-order constrained by photoperiod (Paul *et al.*, 2007; Helm *et al.*, 2013). As the reproductive phenology of reptiles is primarily determined by thermal conditions which can fluctuate considerably each year (Van Dyke, 2014), we also calculated the repeatability and heritability of relative parturition date (i.e., the propensity of a female to give birth early or late relative to other females in the population, calculated as the difference with the mean parturition date of the year). To quantify repeatability, we fitted a linear mixed model including body size and capture date as fixed effects and individual identity and

the year as random effects. Models were run for 3000 iterations with a thinning interval of 1, after a burn-in of 1000. We calculated the absolute parturition date repeatability as the ratio between the individual identity variance and the total phenotypic variance (i.e., sum of all variance components in the model). We calculated the relative parturition date repeatability as the ratio between the individual identity variance and the total phenotypic variance minus the between-year variance. We further estimated the heritability of parturition date using univariate animal models that use the information on individuals' relatedness computed from the population pedigree (Thompson, 1976; Kruuk, 2004). We analysed parturition date as a Gaussian trait using a linear mixed model including female body size and capture date as fixed effects. In addition to the additive genetic effect, the female identity (permanent environment effect), the mother identity (maternal effect) and the year were fitted as random effects. The models were run for 10,000 iterations with a thinning interval of 5, after a burn-in of 1000. The heritability of absolute parturition date was calculated as the ratio between the additive genetic variance and the total phenotypic variance. The heritability of the relative parturition date was calculated as the ratio between the additive genetic variance and the total phenotypic variance minus the between-year variance respectively (de Villemereuil *et al.*, 2019). Absolute parturition date repeatability and heritability calculations are discussed but not presented in the results section. All derived estimates (e.g., repeatability or heritability) posterior distribution were computed using the full MCMC sample, thus accounting for the uncertainty in estimating variances in the model.

2.4.3. Form and strength of selection on parturition dates

In order to quantify the shape and strength of selection on reproductive phenology, we used the number of viable juveniles produced by the female as an annual measure of

female fitness. First, we investigated the shape of selection on parturition using zero-inflated Poisson mixed models with the *glmmTMB* package (Brooks *et al.*, 2017). We compared a null model (“No selection”) to models including linear (“Constant directional selection”) or quadratic effects of standardised parturition date (“Constant non-linear selection”) on the entire time series. Standardised parturition dates were calculated as the residuals of a multiple linear regression of the parturition date, from capture date and rearing site standardised (mean-centred and standardised to a variance of 1) over the entire time series. In all models tested, we included the female body size which strongly constrains litter size in this species (Pilorge *et al.*, 1983) and the rearing site as fixed effects. We also included a random effect of the year. Note that the individual identity was not included in the random part of the model to avoid numerical complications due to the collinearity with the additive genetic effect and relative scarcity of repeated measurements, and after checking that our heritability estimation was not influenced by its inclusion. Once the best model chosen (i.e., “Constant directional selection”, see results), we investigated the temporal fluctuation of directional selection gradients between years by adding to the previous model an interaction term between the standardised parturition date and the year in the random part of the model (“Fluctuating directional selection”). Third, since our analyses suggest the existence of constant directional selection (see results), we attempted to discriminate the relative contribution of parturition date and climate on fitness. To do so, we compared the “Constant directional selection” model to an alternative model (“Constant selection mediated by $T_{\max \text{ May – June}}$ ”) in which we replaced the standardised parturition date with $T_{\max \text{ May – June}}$ identified as the main thermal driver of parturition dates, and a model (“Constant selection mediated by parturition date and $T_{\max \text{ May –$

June”) including the combined effects of the standardised parturition date and $T_{\max \text{ May} - \text{ June}}$ June.

3. Results

3.1. Climatic and individual determinants of parturition dates

The average parturition date varied between the 10th July and the 10th August from 1989 to 2019. Mean daily maximum temperatures between the 1st May and 30th June time-window ($T_{\max \text{ May} - \text{ June}}$) were the temperatures explaining most of the inter-annual variation in parturition dates over the past 31 years (see available data). This suggests that the interannual variability of parturition dates in this population is mainly explained by T_{\max} during the entire post-winter activity period (i.e., between the vitellogenesis in May and mid-gestation in June) rather than by a more restricted time-window, or another temperature indices such as T_{mean} or T_{min} . On average, higher $T_{\max \text{ May} - \text{ June}}$ resulted in earlier parturition dates with a three to four days advancement per degree increase ($\beta = -3.55 \pm 0.53 \text{ SE}$; $F_{1,26.32} = 8.52$, $p = 0.004$; Figure 1). Additionally, model fitting improved when accounting for heterogeneous variance across $T_{\max \text{ May} - \text{ June}}$, with evidence that the variance of parturition dates decreased with warmer $T_{\max \text{ May} - \text{ June}}$ (LRT = 44.9, $df = 1$, $p < 0.0001$). Furthermore, parturition dates were significantly influenced by the interactive effect of $T_{\max \text{ May} - \text{ June}}$ and female body size ($\beta = 0.23 \pm 0.08 \text{ SE}$; $F_{1,1973.42} = 8.70$, $p = 0.004$; Figure 2). While larger females gave birth earlier than smaller females on average, the correlation with body size was attenuated as the $T_{\max \text{ May} - \text{ June}}$ increased. From 1989 to 2019, $T_{\max \text{ May} - \text{ June}}$ increased by around 1.9°C in our study site ($\beta = 0.06 \pm 0.03 \text{ SE}$; $F_{1,29} = 5.46$, $p = 0.03$; Figure S1a) but we found no significant trend for mean parturition dates ($F_{1,25} = 1.31$, $p = 0.26$; Figure S1b).

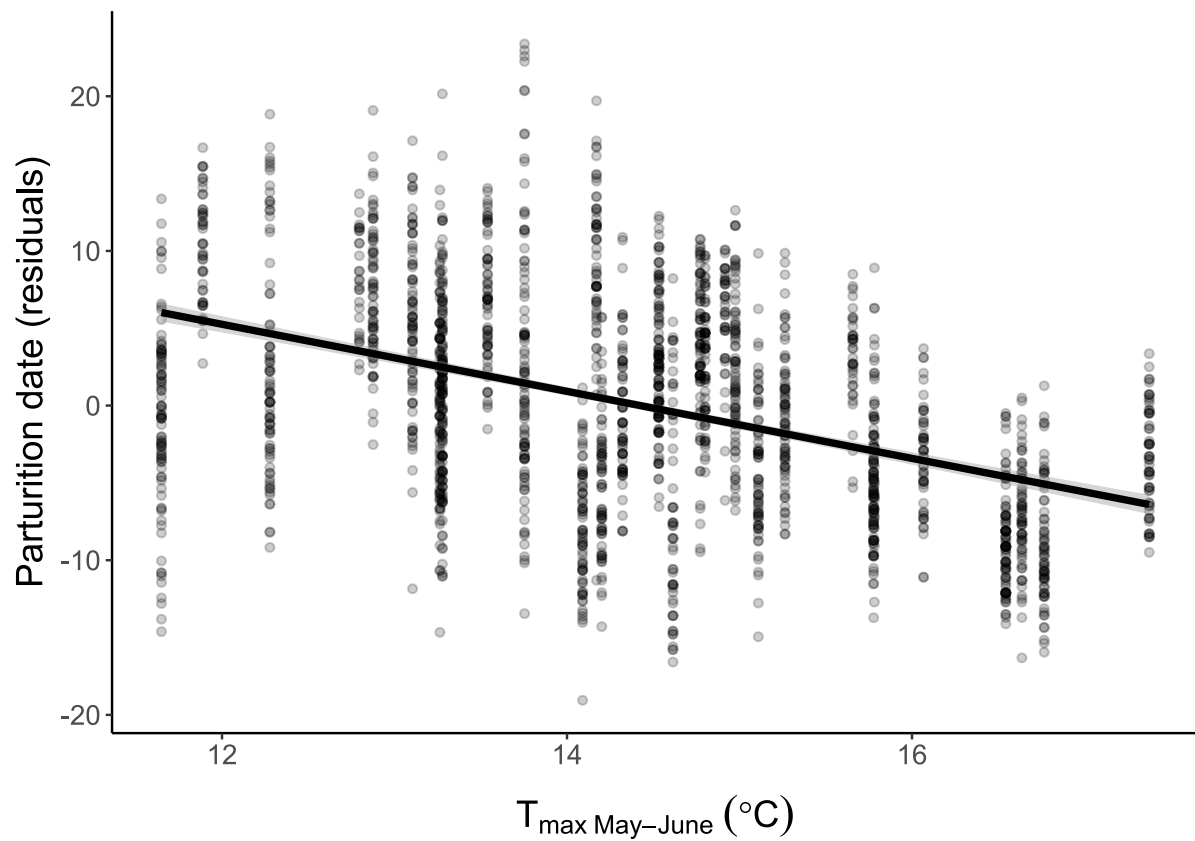


Figure 1: Relationship between female parturition date (residuals of a linear regression between female parturition date, capture date and rearing site) and mean daily maximum temperatures from the 1st May to the 30th June (T_{\max} May – June). Points represent individual data and regression lines are displayed with their 95% confidence bands.

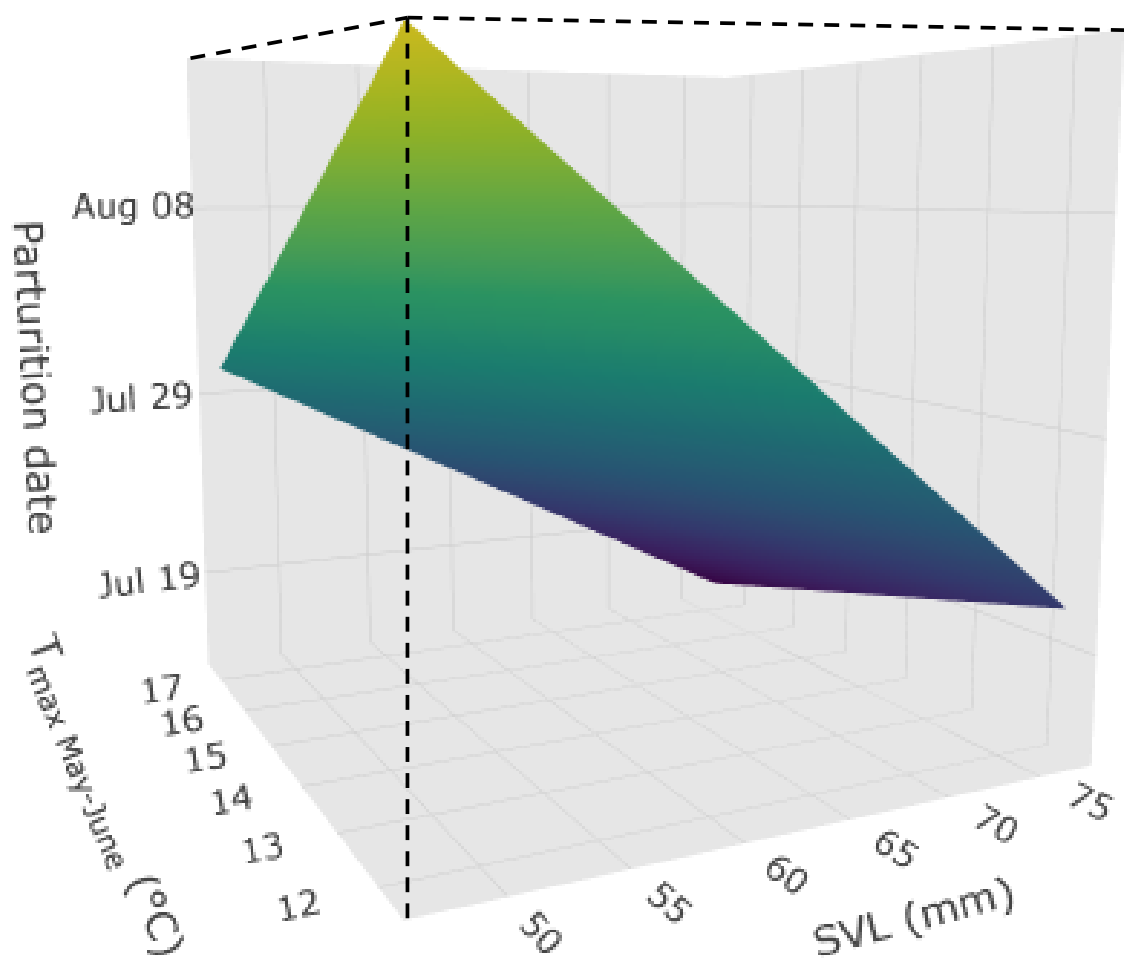


Figure 2: Parturition date as a function of female snout-vent-length (SVL) and mean daily maximum temperatures from the 1st May to the 30th June (T_{\max} May – June). The surface represents the interpolation of parturition date values for each female snout-vent-length and mean daily maximum temperature calculated from the best-selected model. The colour gradient highlights the values of predicted parturition date from late (yellow) to earlier (blue) parturition date.

3.2. Variance decomposition, repeatability and heritability of parturition dates

Parturition dates were highly variable between years, with year variance accounting for 76% [CI: 0.57 - 0.88] of the trait variance. Relative parturition dates of individual females were repeatable ($r = 0.31$ [CI: 0.22 - 0.39]; Table 1) suggesting that females differed consistently from one another in their breeding phenology. However, the heritability of the relative parturition date was low and heritability estimates showed large credible intervals ($h^2 = 15\%$ [CI: 0.09 - 33]; Table 1). The estimated variance of the permanent environment effect on relative parturition date was slightly higher than the additive genetic variance and accounted for 14% [CI: 0.11 - 31] of the total phenotypic variance. The maternal-effect variance explained a small amount (7% [CI: 0.02 - 20]) of the total phenotypic variance.

3.3. Form and strength of selection on parturition dates

We found a negative directional selection favouring an earlier parturition date (Table 2). Females who gave birth earlier produced more viable juveniles during the same year ($\beta = -0.05 \pm 0.02$ SE; $\chi^2_1 = 7.62$, $p = 0.006$; Figure 3). Additionally, the number of viable juveniles at birth was positively correlated with female body size ($\beta = 0.25 \pm 0.01$ SE; $\chi^2_1 = 356.7$, $p < 0.0001$). We found no evidence of a temporal fluctuation of the selection gradient during the study period, as the “Fluctuating directional selection” model was not selected (Table 2). Furthermore, when comparing the main or combined effects of parturition date and $T_{\max \text{ May - June}}$ on the number of viable juveniles produced, we found that the best model explaining inter-individual variations in fitness includes parturition date rather than the $T_{\max \text{ May - June}}$ or combined effects of both (Models “Constant selection mediated by $T_{\max \text{ May - June}}$ ” and “Constant selection mediated by parturition date and $T_{\max \text{ May - June}}$ ”; Table 2), suggesting that parturition date has a more direct impact on fitness than $T_{\max \text{ May - June}}$ per se.

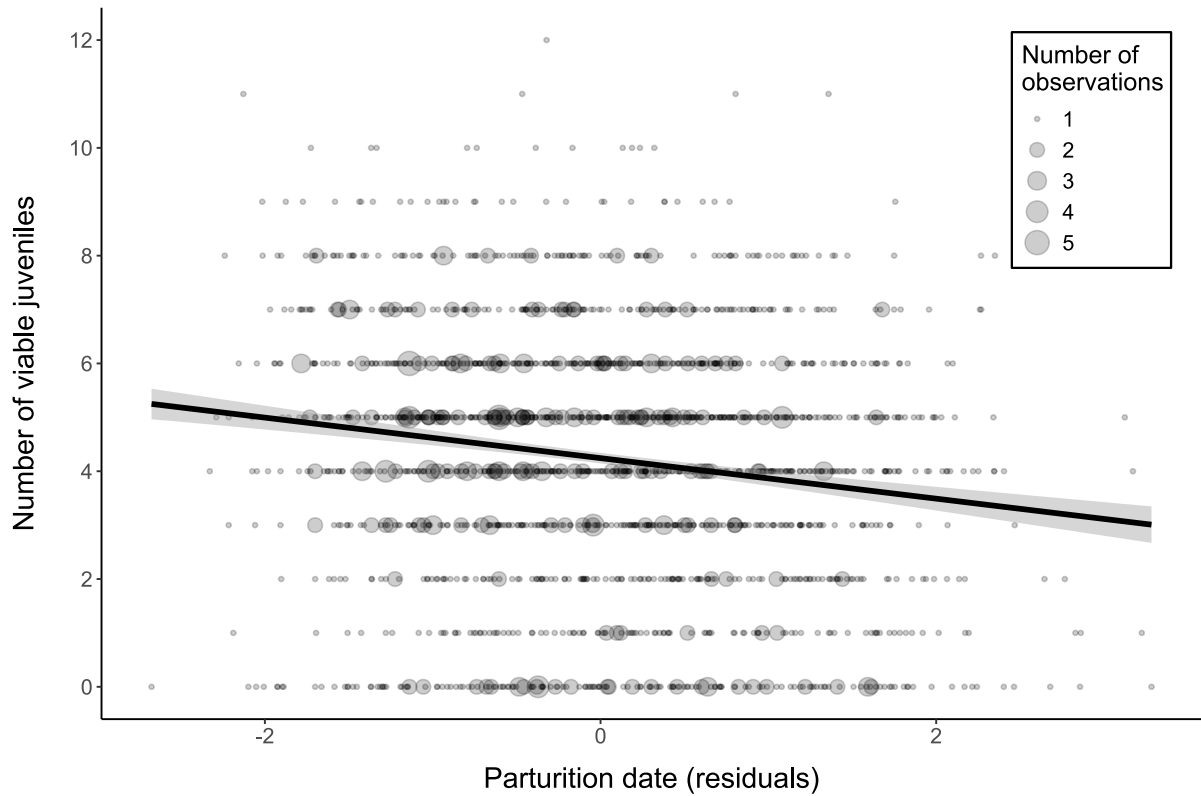


Figure 3: Standardised linear selection gradient for parturition date (solid lines) estimated from 31-year long-term monitoring of a natural population of common lizard (*Zootoca vivipara*). The parturition date corresponds to the standardised residuals of a multiple linear regression between the parturition date, capture date and rearing site. The linear regression is plotted with their 95% confidence limits (shaded areas) and the point size corresponds to the number of observations.

Table 1: Variance decomposition, repeatability and heritability estimates of female relative parturition date in a natural population of common lizards (*Zootoca vivipara*).

	Parameter	Posterior mean	Posterior median	95% credible interval
Repeatability	Individual identity variance	0.0793	0.0787	0.0543 - 0.108
	Fixed effects variance	0.0258	0.0253	0.0137 - 0.0406
	Year variance	0.728	0.676	0.375 - 1.38
	Residual variance	0.154	0.153	0.133 - 0.178
	Total phenotypic variance	0.987	0.936	0.632 - 1.64
	Repeatability of relative parturition date	0.305	0.305	0.220 - 0.389
Heritability	Additive genetic variance	0.037	0.0368	0.00022 - 0.0849
	Fixed effects variance	0.0296	0.0293	0.0177 - 0.0439
	Individual identity variance (permanent environment variance)	0.0358	0.034	0.000252 - 0.0856
	Mother identity (maternal effect variance)	0.0168	0.0117	0.0000336 - 0.0573
	Year variance	0.783	0.689	0.33 - 1.81
	Residual variance	0.131	0.132	0.0952 - 0.165
	Total phenotypic variance	1.03	0.94	0.579 – 2.06
	Heritability of relative parturition date	0.147	0.148	0.000898 - 0.33

Note: To estimate the repeatability and heritability of the relative parturition date, we subtracted the year variance from the total phenotypic variance. The repeatability of parturition dates has been estimated on the whole dataset from 1989 to 2019 and the heritability has been estimated on a subset of the dataset from 2007 to 2019.

Table 2: Natural selection on breeding phenology. AICc-based model selection comparing the influence of parturition date and mean daily maximum temperatures from the 1st May to the 30th June ($T_{\max \text{ May - June}}$) on the annual number of viable juveniles (i.e., annual reproductive success) produced by female common lizard (*Zootoca vivipara*). Body size and rearing site was always included in the model, which also accounts for random variation in the intercept (mean value) among years.

Hypothesis	Model parameterisation	k	AICc	Δ AICc	w_i	LL
No selection	Annual number of viable juveniles ~ SVL + rearing site + (1 Year)	7	8768.8	5.56	0.03	-4377.4
Constant directional selection	Annual number of viable juveniles ~ SVL + standardised parturition date + rearing site + (1 Year)	8	8763.2	0	0.43	-4373.6
Constant quadratic selection	Annual number of viable juveniles ~ SVL + standardised parturition date + parturition date ² + rearing site + (1 Year)	9	8765.1	1.86	0.17	-4373.5
Fluctuating directional selection	Annual number of viable juveniles ~ SVL + standardised parturition date + rearing site + (standardised parturition date Year)	10	8764.7	1.54	0.20	-4372.3
Constant selection mediated by $T_{\max \text{ May - June}}$	Annual number of viable juveniles ~ SVL + $T_{\max \text{ May - June}}$ + rearing site + (1 Year)	8	8770.4	7.18	0.01	-4377.2
Constant selection mediated by parturition date and $T_{\max \text{ May - June}}$	Annual number of viable juveniles ~ SVL + standardised parturition date + $T_{\max \text{ May - June}}$ + rearing site + (1 Year)	9	8765.2	1.96	0.16	-4373.5

Note: Random effects are indicated in brackets. SVL: snout-vent-length, $T_{\max \text{ May - June}}$: Mean daily maximum temperature between 1st May and 30th June, k: number of parameters, AICc: Akaike information criterion, Δ AICc: AIC difference between ranked models, w_i : AICc weight, LL: Log likelihood.

4. Discussion

In this study we quantified individual and environmental determinants of breeding phenology and analysed patterns of natural selection acting on parturition dates over a 31-year period in a wild population of a viviparous ectotherm. We found that inter-annual variations in parturition dates were mainly explained by mean daily maximum temperatures during the post-winter activity period. Higher mean daily maximum temperatures were correlated with earlier parturition dates as well as a reduced inter-individual variability of parturition dates. While we also found that larger females give birth earlier on average than smaller ones, the strength of this relationship decreased as mean daily maximum temperatures increased. In addition, there was a constant, positive directional selection towards earlier parturition dates regardless of the environmental conditions encountered during reproduction. Finally, parturition dates were repeatable but weakly heritable, suggesting a low capacity of the breeding phenology to respond to natural selection.

4.1. Influence of thermal environment and body size on breeding phenology

In line with several studies on lizards, we highlighted a significant plasticity in the breeding phenology of the common lizard with large interannual variations in parturition dates (Wapstra *et al.*, 2010; Olsson *et al.*, 2018). Interannual variation in parturition dates is largely due to thermal conditions during the post-winter activity period, from emergence to gestation, as temperature significantly affects all stages of the reproductive cycle (Duvall, 1982; Lutterschmidt, 2012). Maximum daily temperatures were the best thermal index to explain interannual variations in breeding phenology (proportion of annual variance explained = 63%), and warmer maximum daily temperatures advanced parturition dates, which is in agreement with previous studies in the common lizard (Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016b; Massot *et al.*,

2017). In general, daily maximum temperatures are correlated with insolation and are a better predictor of thermoregulatory opportunities than mean or minimum temperatures in populations where cold conditions limit behavioural activity (Huey, 1982; Marquis *et al.*, 2008). Although mean daily maximum temperatures in May-June increased by +0.6°C per decade at our study site between 1989 and 2019, we did not find an advance in mean parturition dates over this period. Massot *et al.* (2017) estimated an average advance in parturition date of 8.1 days per decade in natural populations of common lizards including our study site between 1989 and 2001. Although our estimates of phenological trends could be biased by changes in rearing sites that occurred during population monitoring, our results suggest that estimates of phenological trends in viviparous lizards are probably overestimated. Extreme thermal events could also significantly affect phenology and bias estimates of phenological trends in ectothermic species.

Moreover, as observed in many lizards species (Bauwens & Verheyen, 1985; Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016b; Hall & Warner, 2017), we found larger females to give birth earlier than smaller ones. But more interestingly, our models showed climate to interact with female body size to drive parturition dates, with size-induced phenological differences being more pronounced in colder post-emergence periods with lower daily maximum temperatures. Three non-exclusive hypotheses may explain the interactive effects of body size and mean daily maximum temperatures on parturition date. Firstly, body size can influence heat regulation capacity of females and consequently the parturition date. In general, larger individuals heat up and cool more slowly than smaller ones due to their stronger thermal inertia and several studies on lizards have highlighted that larger body size has a positive effect on body heat retention (Gvoždík, 2002; Gabirot *et al.*, 2013; Zamora-Camacho

et al., 2014). In highland populations where thermoregulation opportunities are limited, larger females with greater thermal inertia could maintain a body temperature that optimizes embryonic development for longer periods, enabling them to give birth earlier. The advantage of greater thermal inertia in larger females would be reduced in warmer years offering more thermoregulation opportunities, which could explain the reduction of size-induced parturition dates differences during warmer years. Secondly, size-induced differences in parturition dates may be linked to the fact that larger and older females are more competitive. For example, they could initiate their reproductive cycle earlier due to their body reserves or sexual selection processes (e.g., male preference for larger females during mating (Bauwens & Verheyen, 1985)), they could be more efficient in capturing prey or in mobilising energy during vitellogenesis and gestation (e.g., egg formation during vitellogenesis (Price, 2017)), and they could have privileged access to optimal thermoregulation sites (Rusch & Angilletta Jr, 2017). Warmer mean daily maximum temperatures could reduce some of these competitive advantages of larger females, if warmer temperatures increased invertebrate abundance (Robinet & Roques, 2010) or the abundance of high-quality basking sites. Thirdly, delayed breeding dates in smaller females may be the results of trade-offs between resource allocation to reproduction and growth, as seen in the common lizard (Bauwens & Verheyen, 1985). Since warmer environmental temperatures can in some cases increase insect density (Haridas *et al.*, 2016), increase lizard activity periods (Adolph & Porter, 1993) and the efficiency of prey acquisition and assimilation (Van Damme *et al.*, 1991), warmer years could reduce this trade-off and size-induced phenological differences among females (Rutschmann *et al.*, 2016a).

4.2. Repeatability and heritability of parturition dates

We quantified the repeatability of parturition dates and, for the first time, provided a measure of the heritability of this trait in a wild population of a reptile species. Relative parturition dates (i.e., the propensity of a female to give birth earlier or later than other females in the population) were repeatable ($r = 31\%$) and weakly heritable ($h^2 = 15\%$) in our study population. Heritability estimate for relative parturition date in the common lizard are comparable in magnitude to the heritability of laying or parturition date generally observed in birds and mammals ($h^2 = 0.13$ to 0.19 ; (Clements *et al.*, 2011; Charmantier & Gienapp, 2014)) and may even be slightly lower, as these studies assess the heritability of absolute breeding dates. As expected, given the high thermal plasticity of parturition dates, the repeatability and heritability values of absolute parturition dates (i.e., calendar parturition dates) were very low ($r = 0.09$ [0.04 - 0.14]; $h^2 = 4\%$ [0.02 - 10.8]). Regardless of the method used to estimate the heritability of parturition dates, approximately half of the inter-individual consistency of parturition dates was related to additive genetic effects, and half was related to non-heritable factors. The non-heritable part of the individual-level effects of parturition dates could be linked to female physiological or behavioural phenotype and/or female home range quality which could affect their parturition date. For example, the condition-dependent model of laying date in migratory birds predicts that females optimise their breeding phenology as a function of arrival body condition, arrival date, and the ability to gain in condition in breeding areas (Rowe *et al.*, 1994; Descamps *et al.*, 2011; Hennin *et al.*, 2016). Common lizards have a limited annual activity window and use resources stored or recently acquired during reproduction to fuel reproduction (Bleu *et al.*, 2013). Thus, females in better condition or better able to gain condition before reproduction may reproduce earlier. Earlier breeding also provides a longer period to recover energy

before winter and could allow earlier breeding the following year (Bodineau *et al.*, 2024). Furthermore, thermal physiology (e.g., thermal preference) and the quality of female home range (e.g., microclimate conditions, availability of thermoregulation sites, food availability) could influence key physiological processes in reproductive timing (e.g., follicular recruitment, embryonic development). Thus, thermal traits and the microhabitat may explain a significant part of the individual consistency of parturition date (Struelens *et al.*, 2018; Shutt *et al.*, 2022).

4.3. Directional selection drives parturition date in the common lizard

Reproductive phenology is a critical trait influencing annual fitness in many mammal and bird species (de Villemereuil *et al.*, 2020). In agreement with previous studies in lizards (Olsson & Shine, 1997; Mitchell *et al.*, 2018; Bodineau *et al.*, 2024), we found a directional selection for early parturition dates, characterised by a seasonal decrease in the number of viable juveniles produced with late parturition date. Further, although developmental thermal conditions can affect the quality of embryonic development and the viability of juveniles produced (Noble *et al.*, 2018; While *et al.*, 2018), inter-annual variations in annual reproductive success were correlated with the mean parturition date rather than with post-winter daily maximum temperatures. Two non-exclusive hypotheses have been formulated to explain the seasonal decline of fitness: the “*date hypothesis*” (Hatchwell, 1991; Moreno, 1998) and the “*quality hypothesis*” (Hatchwell, 1991; Brinkhof *et al.*, 1993). The “*date hypothesis*” predicts an environment-dependent selection occurring through seasonal changes in environmental conditions (e.g., food abundance, climatic conditions, abundance of available sexual partners or predators). Instead, the “*quality hypothesis*” predicts a seasonal decline in reproductive performance through differences in parental quality between early and late breeders (e.g., better physiological and nutritional condition, better territory quality) leading to an

apparent causal correlation between breeding timing and fitness (discussed in Verhulst & Nilsson, 2008; Harriman *et al.*, 2017; Pärt *et al.*, 2017).

The observed directional selection towards earlier parturition date between 1989 and 2019 suggests that a significant part of the selection pressure on parturition timing could be related to seasonal changes in environmental conditions (e.g., food abundance, climatic conditions, abundance of available sexual partners or predators). In addition, if inter-individual differences in condition or quality of breeding females (i.e., selection dependent on relative competition between individuals) strongly determined the relationship between parturition date and fitness, we would expect a temporal fluctuation in the selection gradient, as environmental temperatures or food availability should influence the intensity of competition to optimize their reproductive investment, the embryonic development and consequently, the number of viable juveniles produced (Rutschmann *et al.*, 2016a; Wang *et al.*, 2017). For example, numerous studies in birds have demonstrated that selection pressures on breeding phenology are altered by environmental conditions, especially annual temperature or prey availability (Husby *et al.*, 2011; Gienapp *et al.*, 2014; Chevin *et al.*, 2015; Visser *et al.*, 2015; Marrot *et al.*, 2018; de Villemereuil *et al.*, 2020; Le Vaillant *et al.*, 2021; Jantzen & Visser, 2023). Instead, our results suggest that the quality hypothesis contributes weakly to the seasonal decline of fitness, or that competition between individuals is constant and not influenced by environmental conditions in the common lizard.

In addition, the low heritability of parturition dates found in this study suggests slow and limited adaptive potential in reproductive phenology, hence limited adaptive potential to climate change through microevolutionary processes. That is, the consequences of temperature-induced phenological changes will depend on the cost-benefit balance of the thermal plasticity of breeding dates. Plastic response to global

warming toward earlier parturition dates could have positive effects on the number of viable juveniles produced (this study), and confer clear advantages for juveniles with increased survival, growth and recruitment (Olsson & Shine, 1997; Qualls & Andrews, 1999; Uller & Olsson, 2010; Wapstra *et al.*, 2010; Le Henanff *et al.*, 2013; Li *et al.*, 2018; Liu *et al.*, 2022). In contrast, the thermal acceleration of gestation beyond optimal environmental temperatures can challenge importantly homeostasis in breeding females given the increased energetic costs of reproduction at high temperatures (e.g., reserve depletion (Brusch IV *et al.*, 2023; Bodineau *et al.*, 2024)). Earlier investigations have observed a geographic correlation between demographic decline and a trend for earlier breeding in wild populations of common lizards (Dupoué *et al.*, 2022). Future studies must examine the long-term fitness consequences of early breeding dates for females as well as intergenerational consequences for juveniles. Additionally, we need more estimates of the heritability of breeding dates in other reptiles to improve our knowledge of the ability of breeding phenology to respond to selection in the context of climate change in these organisms.

Authors' contributions

Théo Bodineau, Pierre de Villemereuil, Jean-François Le Galliard and Sandrine Meylan conceived the ideas and designed the methodology; Pierre de Villemereuil, Alexis Rutschmann, Murielle Richard, Jean Clobert, Manuel Massot and Sandrine Meylan collected the data; Murielle Richard performed the molecular and statistical analyses necessary to build up the pedigree, with help from Alexis Rutschmann; Théo Bodineau and Pierre de Villemereuil analysed the data with the help of Jean-François Le Galliard and Sandrine Meylan; Théo Bodineau led the writing of the manuscript with the help of Pierre de Villemereuil, Jean-François Le Galliard and Sandrine Meylan. All authors contributed critically to the paper and gave final approval for publication.

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Conflict of Interest

The authors declare no competing or financial interests.

Ethical approval

Experiments were performed under the approval of Cuvier Experimentation Ethics Committee (APAFIS#15897-2018070615164391 v3 & APAFIS #34093-

2021112211094302 v4) in an animal breeding facility accredited with permit DDETSPP-SPAE-2022-262-001.

Data availability statement

Data are available at Zenodo with DOI: <https://doi.org/10.5281/zenodo.14022141>

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Supplementary information

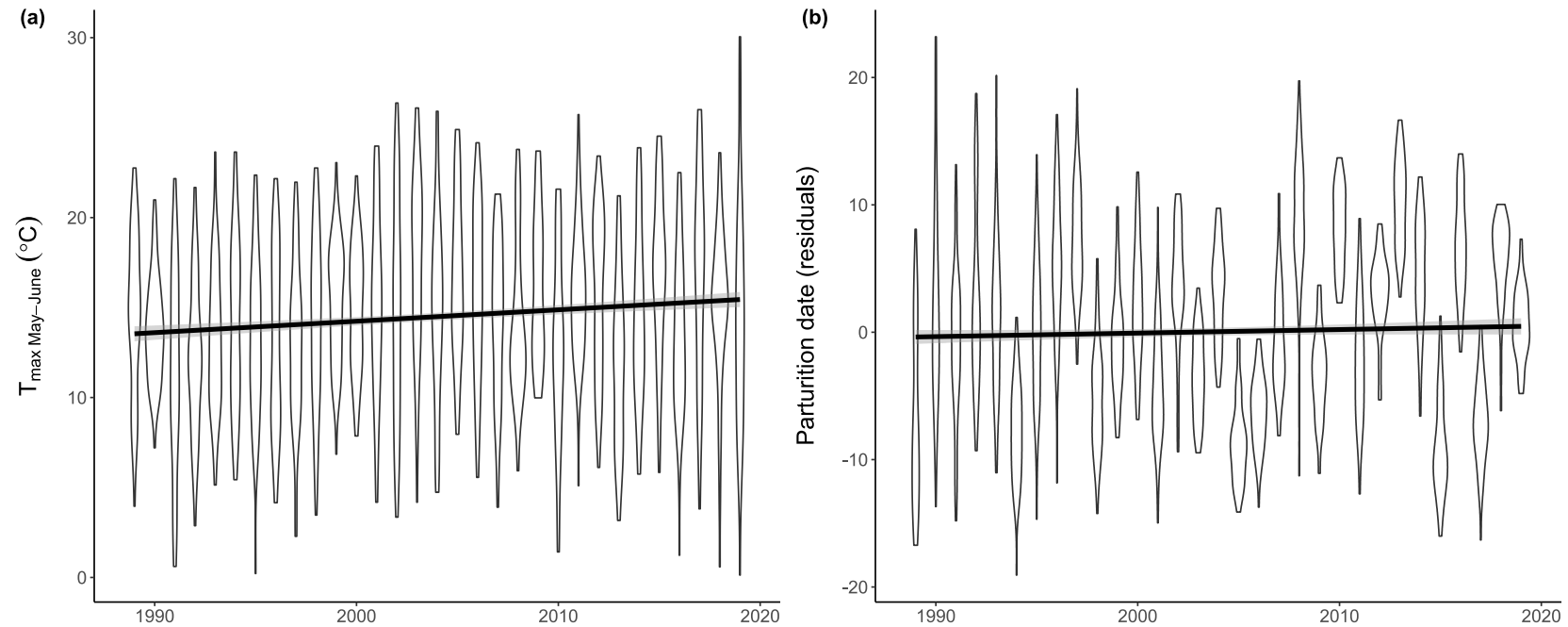


Figure S1: Violin plot of the temporal trend of (a) mean daily maximum temperature recorded from the 1st May to the 30th June (T_{\max} May – June) and (b) mean parturition date (residuals of a linear regression between female parturition date, capture date and rearing site) in our study population of common lizard (*Zootoca vivipara*) between 1989-2019. From 1989 to 2019, T_{\max} May – June increased by around 1.9°C in our study site ($\beta = 0.06 \pm 0.03$ SE; $F_{1,29} = 5.46$, $p = 0.03$) but mean parturition date did not change significantly ($F_{1,25} = 1.31$, $p = 0.26$). The black regression line is plotted with their 95% confidence limits (shaded areas).

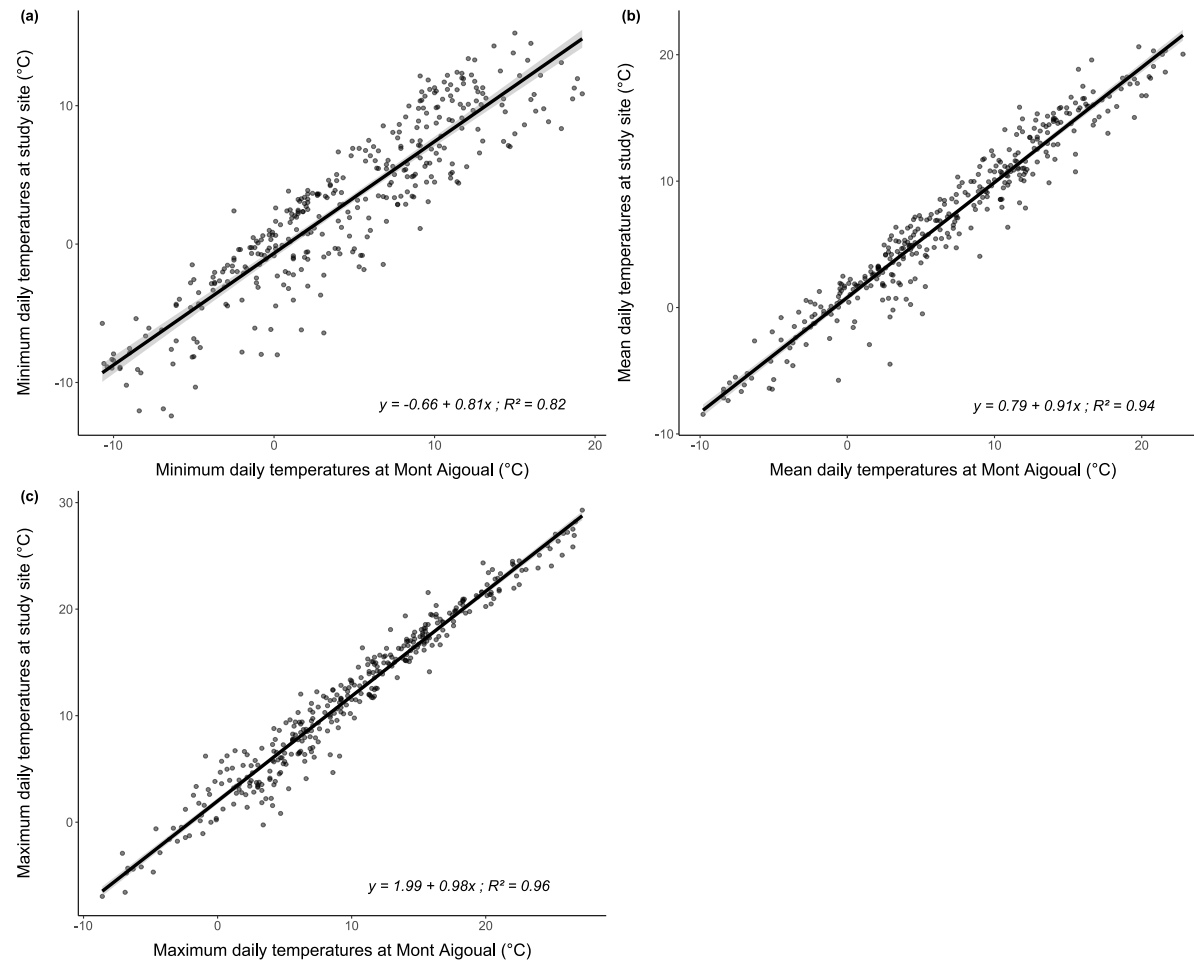


Figure S2: Linear regressions between (a) minimum, (b) mean and (c) maximum daily temperatures recorded in our study site and the ones recorded at Mont Aigoual from August 2022 to August 2023. The black regression line is plotted with their 95% confidence limits (shaded areas).

Chapitre 3 - Conséquences de la plasticité thermique de la gestation



Juvenile lézard vivipare dans un enclos semi-naturel du CEREAP Ecotron IDF. ©
Montaine Delmotte

Article 3

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

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Editor's choice

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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

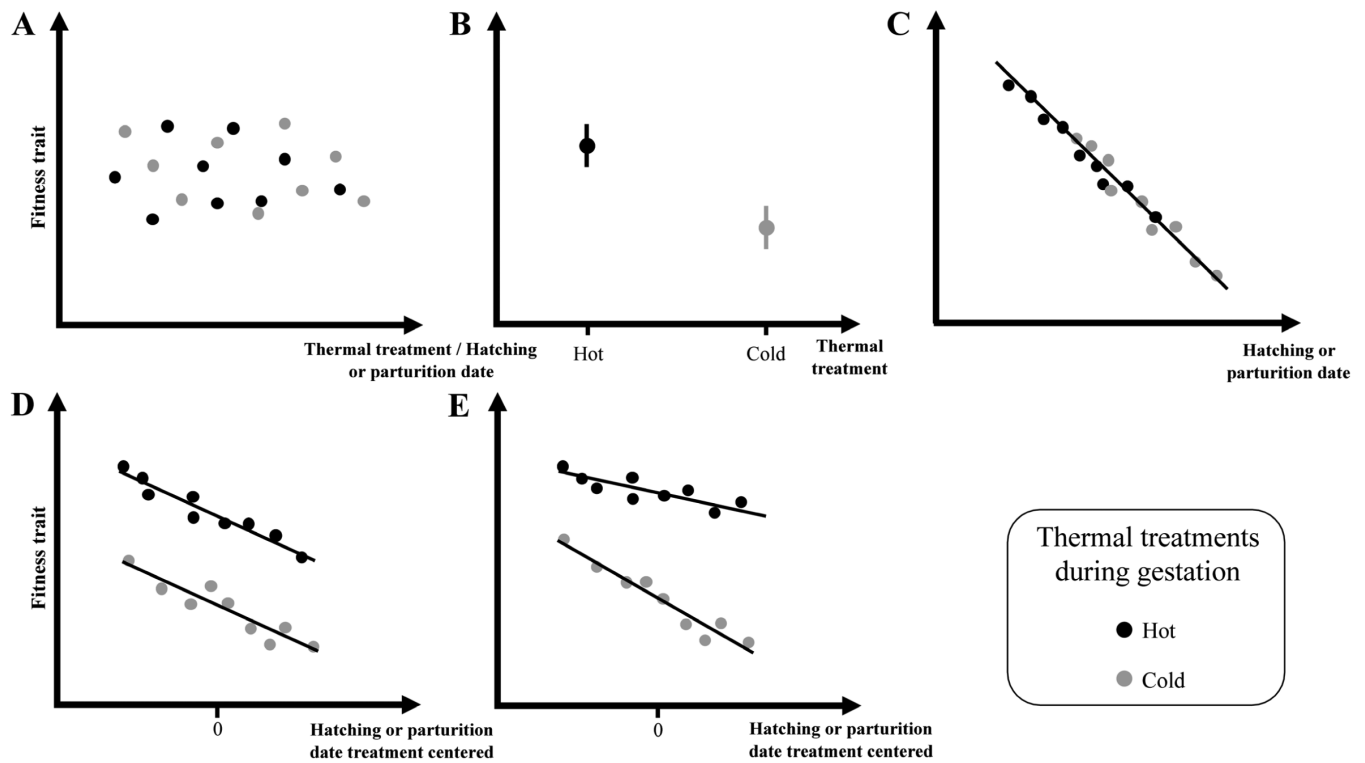


Figure 1. Hypothetical framework of the relationships between thermal treatment, parturition date (or hatching date) and fitness traits of females and the offspring. To test the effects of thermal treatments, parturition date, and combined effects of both on fitness traits, we built and compared the 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

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; Bruschi 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) = $[\ln(\text{SVL}) - \ln(\text{initial SVL})]/\text{days}$) 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.

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 ; $\chi_1^2 = 4.26$, $p = 0.03$). 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; $\chi_1^2 = 5.9$, $p = 0.02$), 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; $\chi_1^2 = 52.1$, $p < 0.001$).

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: $\chi_1^2 = 3.8$, $p = 0.05$; 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 ($\chi_1^2 = 5.1$, $p = 0.02$) 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 ($F_{1,72} = 7.9$,

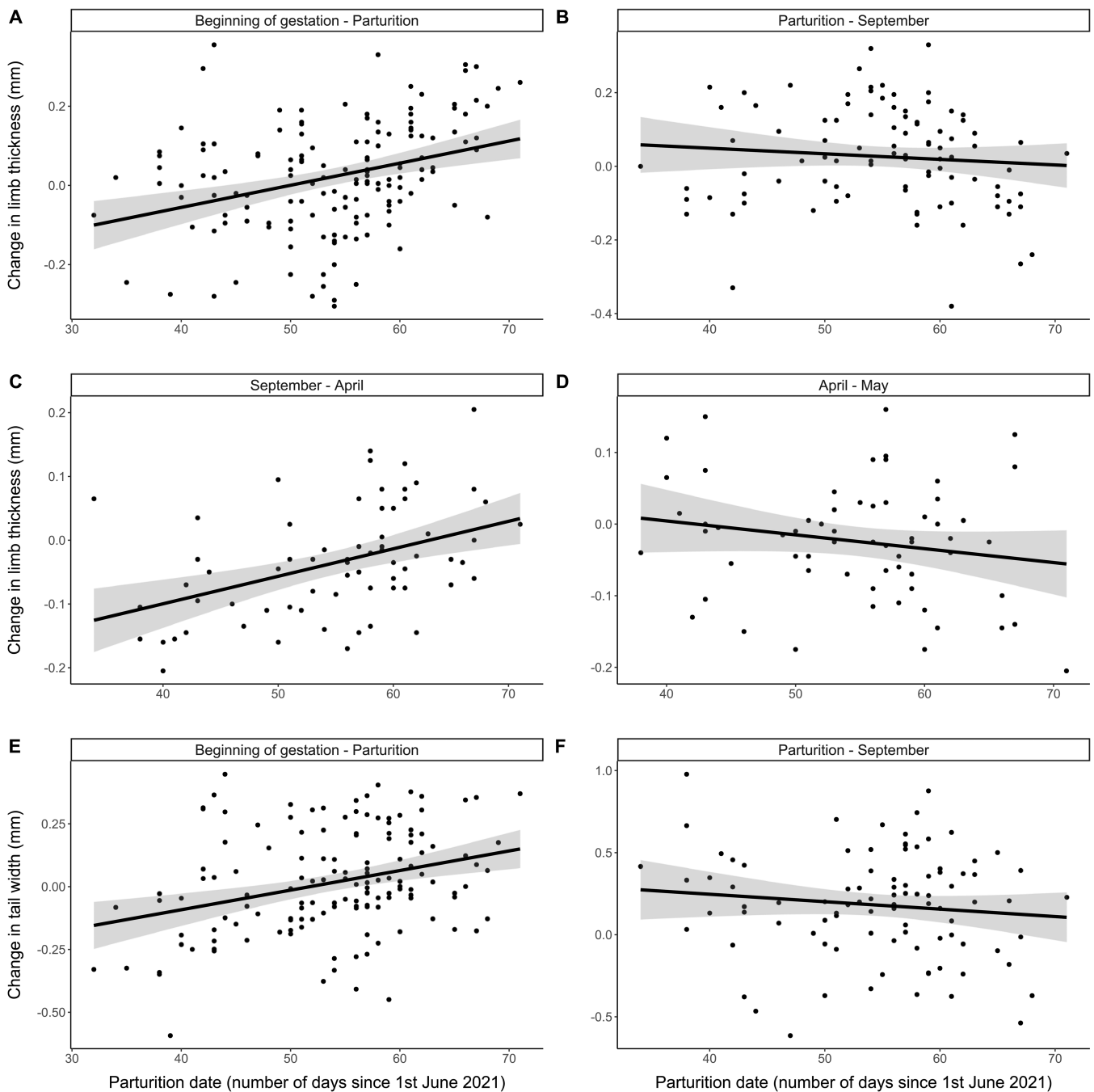


Figure 2. Effects of parturition date on intraindividual changes in limb thickness (A, B, C, D) and tail width (E, F) of breeding females *Zootoca vivipara*. Points represent raw data and a negative change indicates a decrease in the limb thickness or tail width over time. The linear regressions are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

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
Intra-generational	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
Inter-generational	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., Bruschi 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

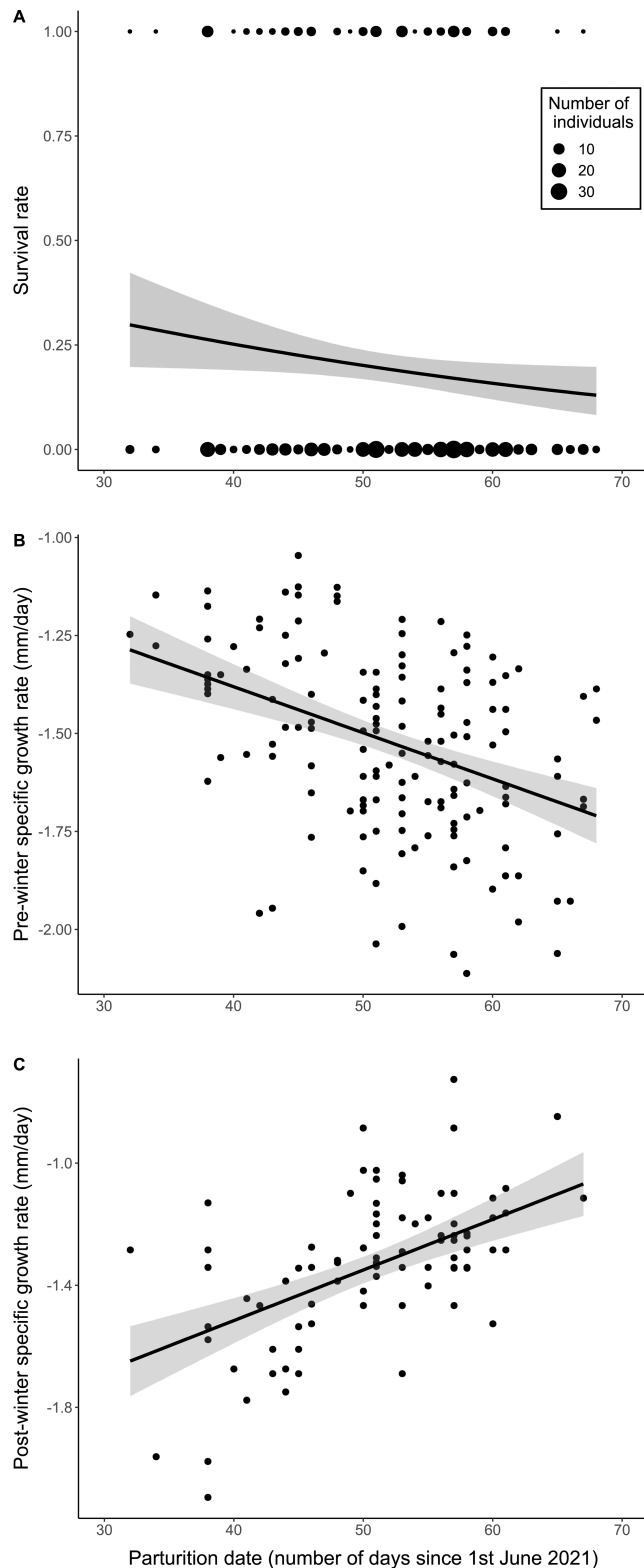


Figure 3. Effects of parturition date on juvenile survival probability (A), pre-winter specific-growth rate (B), and post-winter-specific growth rate (C). In A, solid line represents the average survival probability as a function of parturition date obtained from a logistic regression. The point size 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.

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

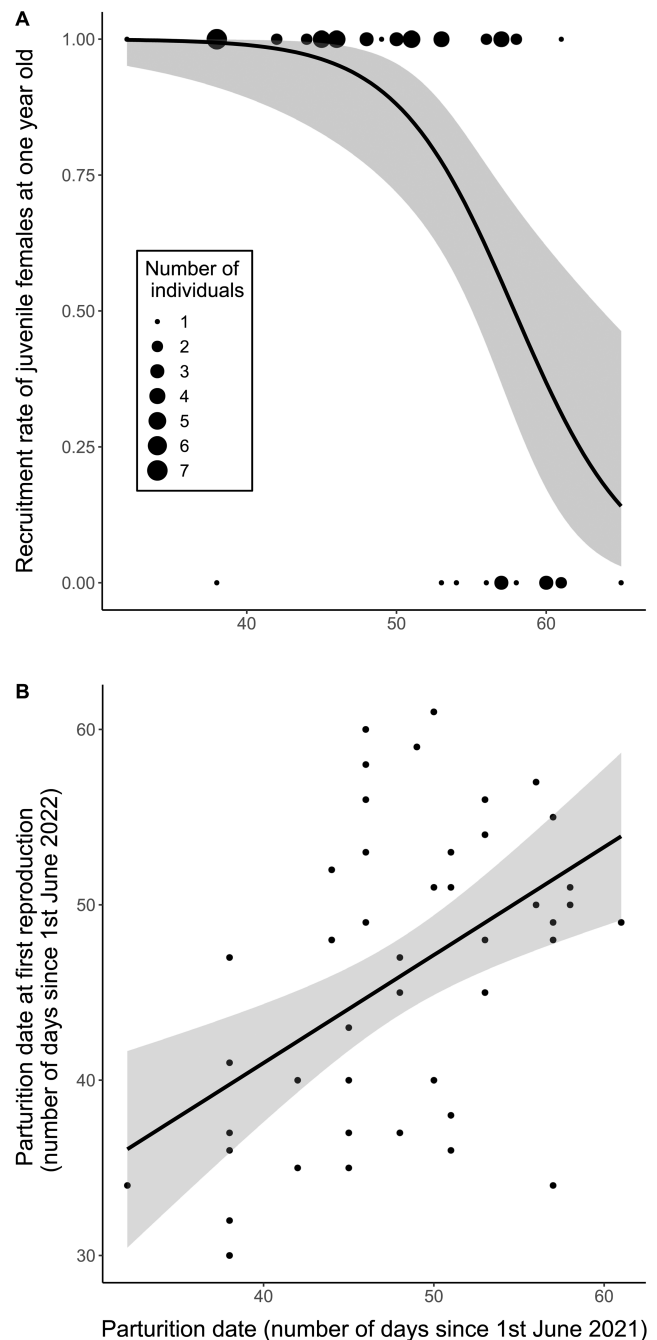


Figure 4. Effects of parturition date on recruitment rate (A) and parturition date (B) of juvenile females at 1 year old. In A, solid line represents the average recruitment of a given parturition date estimated from a logistic regression. The point size corresponds to the number of observations. In 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.

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,

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.

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 Decenci re (Investigation [supporting]), Simon Agostini (Investigation [supporting]), Jean-Fran ois 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/SPA/E/57.

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Supplementary information

Behavioural monitoring during gestation

During the first three weeks of the experiment (i.e., 1, 3, 8, 10, 15 and 17 days after the beginning of the manipulation of thermal regimes), we recorded activity and thermoregulatory behaviours of adult females with an instantaneous sampling every 30 minutes from 10 am to 4 pm local time (i.e., 13 readings during the day) to quantify the average thermoregulatory efforts of adult females in response to treatment and potential buffering effects of maternal thermoregulation behaviour. One naïve observer noted if lizards were hidden or visible and, if they were visible, the observer distinguished between two behaviours: basking (stationary position with flat body, extended limbs, and underneath the heat lamp) or not basking. Behavioural monitoring was only performed on adult females due to logistic constraints. To study basking behaviours, we counted the number of times each day out of 13 observations where females exhibited basking behaviour. We then analysed these count data as success-failure events with generalised linear mixed models (GLMM, Bates et al., 2014) assuming a binomial distribution. These models had a satisfactory fit to the data based on Pearson's chi-square goodness-of-fit tests. We fitted the GLMMs with scenarios A to B including the effect of time (i.e., the number of days since the beginning of manipulation). We found strong support for an effect of thermal treatment on basking behaviour of adult females (“thermal hypothesis”: 95% vs. (“null hypothesis”: 5%). Adult females exposed to the cold treatment showed higher basking rate during gestation than females exposed to hot treatment (0.39 ± 0.25 and 0.27 ± 0.21 respectively; $\chi^2_1 = 7.8$, $p < 0.01$).

Article 4

A multi-trait evaluation of patterns and fitness consequences of breeding phenology plasticity with nocturnal warming and food restriction in a lizard

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Abstract

1. Faced with climate warming, ectothermic species shift their breeding phenology, which is in part attributed to an acceleration of gestation or incubation in warmer environments. Thermal acceleration of gestation may have important fitness implications for breeding females and their offspring by impacting maternal homeostasis, embryonic development and hatching date, but these benefits and costs have been poorly documented. In addition, while climate change is characterised by a stronger trend for night-time than for daytime warming and concurrent alterations of food availability, few studies have quantified phenology-trait effects of increasing nocturnal temperatures and decreasing energy intake.

2. Here, we exposed female common lizards (*Zootoca vivipara*) to contrasted nocturnal temperatures and prey availability during gestation. We used a multi-trait approach by quantifying the functional impacts of nocturnal warming and food availability on maternal morphology, phenology, physiology and behaviour, current reproductive output and both females and offspring life-history traits.

3. Nocturnal warming advanced parturition dates, but food restriction further accelerated gestation and females muscle catabolism under moderate nocturnal warming.

4. Nocturnal warming and food restriction during gestation had negative effects on reproductive output and increased physiological imbalances in breeding females. Hot nocturnal temperatures down-regulated basal corticosterone levels and immunocompetence, while food restriction reduced antioxidant capacity of females. However, the thermal acceleration of gestation induced by nocturnal warming has

positive effects on offspring life history traits related to fitness such as endurance at birth and growth during the first few months of life.

5. By analysing multiple traits, our study provides an integrated understanding of the intra- and intergenerational effects of nocturnal warming and resource availability during ectotherm reproduction. Our results underline the importance of considering nocturnal warming and resource availability as factors causing increased physiological imbalances and negative effects on ectotherm reproduction. They also show the need to consider the benefits and costs of phenological advances for breeding females and their offspring in order to improve our understanding of the consequences of phenological changes in the context of climate change.

Keywords: ectotherm, food availability, nocturnal temperatures, performance, phenology, plasticity, reproductive costs, trade-off

1. Introduction

Terrestrial ectotherms are amongst the most affected organisms by global warming because their metabolism, behavioural activity and life history are highly dependent on the thermal conditions in the environment (Duffy et al., 2022; Kingsolver, 1995; Sinervo et al., 2010). Faced with climate change, terrestrial ectotherms show marked phenological changes with emergence and breeding dates advancing by several days to several weeks per decade due to climate warming (Cohen et al., 2018; Thackeray et al., 2016; Vitasse et al., 2021). Although genetic adaptation can explain these phenological advances, phenotypic plasticity is the favoured hypothesis for ectotherms (Ljungström et al., 2015) given the thermodynamic effects of temperature on essential biochemical processes (such as reaction kinetics, enzyme inactivation or hormone regulation) and behaviours (such as activity) that influence key events in the life history

such as spring emergence (Moss & MacLeod, 2022), reproduction timing, and gestation (for viviparous species) or incubation length (for oviparous species) by influencing the speed of embryonic development (Noble et al., 2018). In particular, warmer developmental temperatures lead to a thermal acceleration of embryonic development and earlier hatching dates in a wide range of insects, amphibians and reptiles (Bradford, 1990; Noble et al., 2018; Rebaudo & Rabhi, 2018). Understanding the fitness consequences of this thermal plasticity of breeding phenology is therefore essential to anticipate demographic changes and vulnerability of ectothermic species exposed to climate warming.

In reptiles, thermal conditions during embryonic development can significantly influence offspring phenotype, survival and ontogenic trajectories (Booth, 2006; Noble et al., 2018; While et al., 2015). Incubation temperatures affect embryonic energy expenditure and the degree of conversion of yolk to tissue, which may influence body condition at birth (Pettersen et al., 2024; Storm & Angilletta, 2007). In general, the effects of developmental temperature on embryo viability, post-hatching survival and offspring performance seem to follow a concave shape with lower performance values for offspring from colder and warmer incubation temperatures (Noble et al., 2018). In addition, earlier hatching dates induced by accelerated embryonic development at warmer temperatures can increase postnatal survival, growth and recruitment (Le Henanff et al., 2013; Li et al., 2018; Pearson & Warner, 2018; Uller & Olsson, 2010; Wapstra et al., 2010). Indeed, early hatching date can give the offspring a 'head start' thanks to more favourable environmental conditions (e.g., extended period before winter for growth and production of fat bodies, warmer temperatures and longer periods of activity in early summer, greater prey abundance) and to less competition between conspecifics early in life (reviewed in Warner & Shine, 2007).

Although warmer developmental temperatures and phenological advances may be generally beneficial to the offspring, the effects of accelerated breeding phenology on performance traits and fitness of females remain largely unknown. In reptiles, reproduction entails substantial changes in the mother's behaviour (e.g., activity budget, thermoregulatory behaviour, feeding), physiology and energy balance (Bleu et al., 2012; Shine, 1980), and therefore represents a critical life stage for energy and water balance especially in viviparous species (Brusch et al., 2020; Dupoué et al., 2015; Lourdais et al., 2013). In addition to the direct allocation of energy and nutrients in egg formation, viviparity induces additional reproductive costs for the mother such as reduced locomotor performance, increased risk of predation and increased metabolic rate and energy expenditure during gestation (Foucart et al., 2014; Jara et al., 2019; Le Galliard et al., 2003; Van Dyke & Beaupre, 2011). Thermal acceleration of gestation may reduce such costs by decreasing the gestation length but it could also lead to significant energy demands in viviparous species, affecting female body condition as well as the quality and output of reproduction (Brusch et al., 2020; Brusch IV et al., 2023). In addition, warmer temperatures during gestation could alter maternal homeostasis by affecting key physiological processes such as the immunocompetence, the regulation of basal corticosterone secretion (the major glucocorticoid in reptiles) via the hypothalamo-pituitary-adrenal (HPA) axis and the regulation of redox balance. For example, exposure to high temperatures or heat waves can lead to an increase in basal corticosterone levels (Dezetter et al., 2022; Racic et al., 2020), an increase in oxidative stress (Costantini, 2014; Han et al., 2020), as well as down-regulation of the immunocompetence (Butler et al., 2013; Sacchi et al., 2017; Stahlschmidt et al., 2017; Q. Zhang et al., 2023). These effects of temperature on maternal homeostasis appear to be quite variable across studies of

reptiles and have rarely been studied during gestation (Ballen et al., 2012; Dupoué et al., 2018, 2020; Jessop et al., 2016). In addition, these physiological changes might have a significant impact on a wide range of fitness-related traits (Burraco et al., 2020; Dupoué et al., 2020; Graham et al., 2011; Love et al., 2013; Q. Zhang et al., 2023), calling for multivariate studies investigating the behavioural, energetic and homeostatic consequences of the thermal plasticity of breeding phenology.

While recent climate change is characterised by a more rapid increase in nocturnal temperatures than daytime temperatures in most regions of the globe (Sadok & Jagadish, 2020; Vose et al., 2005; Zhong et al., 2023), few studies have quantified the effect of nocturnal warming on breeding phenology and fitness traits in ectotherms (reviewed in Rutschmann et al., 2024; Speights et al., 2017). High nocturnal temperatures are correlated with several physiological and life history traits of ectotherms such as basal corticosterone levels (Dupoué et al., 2018), evaporative water loss (Dupoué, Rutschmann, Le Galliard, Miles, et al., 2017), heating rates (Rutschmann et al., 2020), growth rates (Rutschmann et al., 2021) and with population decline (Dupoué, Rutschmann, Le Galliard, Clobert, et al., 2017). In viviparous reptiles, nocturnal warming should accelerate gestation but could also increase reliance of reproductive females on energy or water intake due to increased metabolic rates and water loss rates at high nocturnal temperatures (Brusch IV et al., 2023; Clarke & Zani, 2012; Moore et al., 2020; Wu et al., 2012; Zhao et al., 2014). Thus, the consequences of nocturnal warming on energy budget and reproductive output of ectotherms should depend on the thermoregulation strategies of pregnant females as well as on resource availability (Rutschmann et al., 2024). In diurnal, perfect thermoregulating species, it is predicted that reduced food intake shifts the optimal nocturnal temperature for net energy gain towards lower values, because declining energy intake paired with

increased energetic expenditure during resting phases makes ectotherms less energetically tolerant of heat and leads to a “metabolic meltdown” (Huey & Kingsolver, 2019; Rutschmann et al., 2024; Thomas et al., 2017). In addition, numerous field studies have documented concomitant changes in climate, primary production and prey abundance for many reptiles (Hallmann et al. 2017, Laws 2017, Lister and Garcia 2018), making it extremely relevant to examine thermal plasticity of breeding phenology under different food conditions during gestation in ectotherms.

Here, we investigated the effects of increasing nocturnal temperatures and decreasing energy intake on breeding females and life-history traits of their offspring in the viviparous common lizard (*Zootoca vivipara*, Lichenstein 1823). Using an experimental design, we exposed pregnant females to contrasted nocturnal temperatures (21°C, 16°C, 13°C) and prey availability (*ad libitum* food or moderate food restriction) during gestation. We quantified behavioural and physiological responses of females by recording their activity and thermoregulation behaviours and measuring multivariate indicators of body condition, immunocompetence and homeostasis (i.e., baseline corticosterone levels, oxidative damage and antioxidant capacity) throughout gestation. We also quantified reproductive output, offspring morphology and performance traits at birth and released females and juveniles into semi-natural enclosures to examine delayed effects of nocturnal temperature and food availability on mother and offspring fitness. We examined the following four related hypotheses and predictions. First, we hypothesised that nocturnal warming should accelerate gestation and that highest temperatures and food restriction should additively reduce maternal physiological condition, reproductive output, as well as their post-breeding condition and survival. Thus, warmest nights should decrease female immunocompetence, increase oxidative stress and baseline corticosterone levels.

Additionally, nocturnal warming and food restriction should decrease female energetic condition, reproductive investment and litter viability. Second, females should develop short-term behavioural strategies to mitigate the negative effects of too high nocturnal warming and food restriction. We predict a reduction in activity and shifts in thermoregulation behaviours to promote energy conservation during gestation in warmest and/or food restricted environments. Third, food restriction should negatively impact offspring body condition and performance at birth, while nocturnal warming should increase offspring performance as well as post-summer survival and growth due to earlier hatching date. Fourth, we predict synergetic effects of food restriction and temperature during gestation on maternal traits and reproductive output due to the lower thermal optimum of performances with restricted energy intake (Huey & Kingsolver, 2019).

2. Material and methods

2.1. Study species, sampling and rearing conditions

The European common lizard (*Zootoca vivipara*) is a small diurnal and terrestrial lizard widely distributed in northern Eurasia in highly seasonal, cool and humid habitats. In natural and our captive populations, the mating period begins shortly after the emergence of sexually mature females from overwintering (Bauwens & Verheyen, 1985). Mated females carry out vitellogenesis during two to three weeks between mid-April and May, which is followed by ovulation and egg fertilisation that mark the onset of gestation (Bauwens & Verheyen, 1985). Parturition occurs after an average gestation period of ca. two months and ranges between late June and early August depending on thermal conditions and individual characteristics (Rutschmann et al., 2016). Breeding females (N=138) used in this study were captured inside semi-natural

populations maintained in outdoor enclosures at CEREEP-Ecotron IleDeFrance (48°17'11.5" N, 2°40'45.6" E) after the mating season (i.e., between May 3rd and May 26th). Females were acclimated in individual terrariums (25 × 15 × 15 cm) filled with sterilised peat as substrate, equipped with a shelter, and installed in a temperature-controlled room before experiments (25°C during daytime from 8:30 a.m. to 6:00 p.m., 16°C at night from 6:00 p.m. to 8:30 a.m.). Terrariums were lit and heated automatically from 9:00 a.m. to 12:30 a.m. and from 1:30 p.m. to 4:30 p.m. by a UVB-enhanced neon tube (30 W) and a halogen heating bulb (25W) placed on one side of the terrarium to generate a thermal gradient relevant to this species. All lizards were acclimated for a minimum of one week before the experiments by providing food *ad libitum* (400 ± 25 mg of crickets *Acheta domestica* three times a week), water *ad libitum* and a humid environment (three water sprays per day). We inferred reproductive status of females by the presence of recent bite marks on the abdomen and determined the initial gestation stage of females (i.e., vitellogenic or ovulatory stage) and the ovulation date by ultrasonography (SonoSite M-Turbo, Inc., Bothell, WA, USA). Ovulation is detected by the change in the appearance of follicles from spherical and echolucent during vitellogenesis to highly echogenic ovulated eggs (Gilman & Wolf, 2007; see Supplementary figure S1). All females were captured during vitellogenesis or close to ovulation. Experiments were performed under the approval of Charles Darwin Animal Experimentation Ethics Committee (APAFIS 41678) in an animal breeding facility accredited with permit 17/DDPP/SPAE/57.

2.2. Experimental design

Using air-conditioned breeding rooms and heaters, we exposed pregnant females during all the gestation to contrasted nocturnal temperatures from 6:00 p.m. to 8:30 a.m. (see Supplementary figure S2; hot night (H): 21 ± 1.43°C, intermediate night (I):

16 ± 0.75°C, cold night (C): 13 ± 0.46 °C) and food availability conditions (control feeding treatment (F): *ad libitum* feeding with 400 ± 25 mg of crickets three times per week, moderate feeding restriction (FR): feeding with 200 ± 20 mg of crickets three times per week). Intermediate and warm nocturnal temperatures simulate moderate and strong nocturnal warming scenarios, while cold treatment nights simulate current thermal conditions encountered in cold populations of this species (Dupoué et al., 2022). On average, we started the experimental treatments at or shortly after ovulation. Ovulation date was negatively correlated with body condition at capture, such that females in better body condition at capture ovulated earlier (slope: -6.33 ± 1.25; $F_{1,122} = 26.46$, $p < 0.0001$) but it was not influenced by main effects of nocturnal temperatures ($F_{2,122} = 1.56$, $p = 0.21$) and food availability ($F_{1,122} = 0.36$, $p = 0.55$), or their interaction ($F_{2,120} = 0.70$, $p = 0.50$). Throughout the experiment, the females were maintained individually under the same daytime lighting and heating conditions as during acclimatisation. We equally distributed pregnant females of similar size, condition and vitellogenic stage into six experimental groups (N=23 per group) formed by the factorial combination of the nocturnal temperature and food treatments and randomly arranged them in rearing rooms. In addition, due to the important sample size and the time required for measurements, we formed three experimental batches of 46 females composed of a balanced number of females from each experimental group. Females from the same batch were measured for morphological, physiological and behavioural traits during the same day.

2.3. Morphological changes during gestation

Before the start of experimental treatments and two days after parturition, we quantified tail width and limb thickness of females, which are reliable proxies of energetic condition. In reptiles, decrease in tail width and limb thickness indicate muscle

catabolism and mobilisation of caudal energy reserves (Brusch et al., 2020; Brusch IV et al., 2023). We took digital pictures of the females ventrally using a flatbed scanner (CanoScan LiDE 700F, Canon) and measured tail width at the 7th subcaudal scale rows with ImageJ software (Schneider et al., 2012). At the same time, left hind limb thickness was measured using a spessimeter (ID-C1012BS, Mitutoyo, Japan). We then calculated intra-individual changes in limb thickness and tail width between the beginning of the experiment and parturition day.

2.4. Physiological changes during gestation

We monitored baseline corticosterone levels, oxidative stress and immunocompetence throughout gestation by taking three repeated individual measurements at the beginning of gestation before the start of treatments, during gestation approximately in mid to two-thirds of gestation as detected by regular ultrasound monitoring of some females (see below) and after parturition day. At each measurement session, females were bled using a standard protocol within 3 minutes of restraining the animal to avoid handling-induced stress effects (Meylan et al., 2003). Approximately 50 μ L of whole blood was collected from the post-orbital sinus and plasma was obtained by centrifugation at 11 000 rpm for 6 minutes of the blood samples, divided in two sub-samples and stored at -25°C until assay. Corticosterone level was measured on one sub-sample with a competitive enzyme-immunoassay method using corticosterone EIA (IDS Corticosterone EIA kit, ref AC-14F1, lot J54692, IDS EURL Paris, France) after 1:10 dilution (see details in Josserand et al., 2017; intra-plate repeatability: $F_{35,36} = 16.62$, $p < 0.0001$, $r = 0.89$). Furthermore, we measured the reactive oxygen metabolites (ROMs) in plasma as an index of oxidative damage with the d-ROMs colorimetric kit (MC003, lot NST03AA, Diacron International Italy), which measures the activity of organic hyperoxides (intra-plate repeatability: $F_{65,66} = 17.16$, $p < 0.0001$, $r =$

0.89). We further used OXY-absorbent test kits (MC435, lot NST38BA, Diacron International Italy) to measure the non-enzymatic antioxidant capacity (OXY) of diluted plasma samples (1:100) to neutralise an oxidant attack from hypochlorous acid (intra-plate repeatability: $F_{67,69} = 3.86$, $p < 0.0001$, $r = 0.59$; see details in Dupoué et al., 2020). In addition, we estimated immunocompetence using phytohaemagglutinin (PHA) induced skin-swelling test at least 2 days after the blood sampling. Local inflammation was assessed by skin swelling in response to the injection of a mitogen (i.e., 0.04 mL of a solution of PBS containing 2.5 mg/mL of PHA (Sigma-Aldrich; reference L8754)) in the right hind limb of the lizard as described by Meylan et al. (2013). The PHA swelling response includes both innate and adaptive components of the immune system in the common lizard (Mugabo et al., 2015), which may bias repeated measurements due to adaptive immunity after the first administration. We thus administered all females with a subcutaneous injection of PHA in the right hind limb during the acclimatisation phase (ca. seven days before our first initial measurement) in order to elicit adaptive components. Skin swelling was calculated at the beginning, during gestation and at parturition as the absolute difference in the right limb thickness measured with a spessimeter (ID-C1012BS, Mitutoyo, Japan; to the nearest 0.01 mm) before and 12 h after the PHA injection (see details in Meylan et al., 2013).

2.5. Activity, body temperature and food consumption

We recorded once a week behavioural activity and surface body temperature of adult females with an instantaneous sampling every 45 minutes from 9:30 to 11:45 and from 14:00 to 15:30 local time (i.e., 7 readings during the day). One naïve observer noted if lizards were active (i.e., visible and outside the shelter) or inactive (hidden or under the shelter). If they were not hidden, surface body temperature was recorded using an

infrared thermometer (Raytek, Raynger MX2). In the middle of each behavioural record, we also noted the room temperature using a digital thermometer. To estimate the food consumption of pregnant females, at the end of each week (i.e., on Friday), we counted and weighed any uneaten crickets and removed them.

2.6. Reproductive monitoring and offspring phenotype

From acclimation to parturition, we monitored the females' gestation stage using ultrasound scans (SonoSite M-Turbo, Inc., Bothell, WA, USA) at least once a week. After parturition, each female was weighed and the litter was characterised by recording the number of unfertilised 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). We further calculated reproductive investment as the difference between the body mass of females before and after the parturition. All live juveniles were marked by toe-clipping. The following day, we measured their endurance capacity in a circular racetrack maintained at 30.7 °C (\pm 0.9 SD) with a heat lamp (see details in Le Galliard & Ferrière, 2008). Juveniles warmed up at 30°C before the measurement in a climatic chamber. During endurance tests, lizards were stimulated to run at a constant speed (ca. 0.66 km.h⁻¹) and motivated to continue after each stop with soft brush taps behind the tail until the lizard showed signs of exhaustion, determined by the loss of its ability to right itself after strong tail stimulations (Le Galliard et al., 2003; Sorci et al., 1995). Endurance was calculated as the running time until exhaustion (to the nearest second). Juveniles from the same litter were released in the evening after endurance measurements into one of fifteen outdoor enclosures chosen pseudo-randomly in order to standardise the density, sex ratio and treatment frequency of juveniles among enclosures. Females were released into the

same enclosure as their juveniles after all the measurements had been taken (on average 4 days after parturition).

2.7. Monitoring of survival, growth and condition during post-reproductive season

In September 2023, all surviving offspring and females were recaptured in outdoor enclosures and measured for SVL and body mass in order to assess survival and growth during the post-reproductive summer season. We measured left hind limb thickness and tail width of adult females following the same method described above to estimate long-term effects of treatments on body condition. We calculated the specific growth rate of juveniles before wintering ($SGR = [\ln(SVL) - \ln(\text{initial SVL})]/\text{days}$) using established methods (Liu et al., 2022).

2.8. Replication statement

Manipulated factors	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Nocturnal temperatures (cold, intermediate, hot) and food availability (ad libitum, moderate food restriction)	Individual females Individual juveniles	Individual females	23 females of each nocturnal temperature/food availability combination

2.9. Statistical analyses

Analyses were performed with R software version 4.2.0 (R Core Team, 2022). For each analysis, we built a full model, checked its assumptions and performed a goodness-of-fit test when relevant. Non-significant effects were then eliminated using

a stepwise model selection procedure starting from the full model. We analysed maternal phenological, morphological and physiological traits during gestation using mixed models including a random effect of the capture enclosure to account for potential differences among the enclosure from where the female was captured and a fixed effect of the experimental batch since these measurements were carried out successively for each experimental batch. We analysed ovulation date of females using linear mixed models (LMMs) including the body condition of females at capture (i.e., residuals of the mass-over-size regression) and the two-way interaction between nocturnal temperatures and food availability as fixed effects. We analysed the parturition date of females with LMMs including the fixed effect of the individual-centred ovulation date and the two-way interaction between nocturnal temperatures and food availability. To study intra-individual changes in limb thickness and tail width during gestation, we used LMMs including fixed effects of the initial limb thickness or tail width at capture, individual-centred ovulation date and the two-way interaction of nocturnal temperatures and food availability. We analysed repeated measurements of PHA swelling response, baseline corticosterone, ROMs and OXY levels using LMMs including fixed effect of individual-centred ovulation date and the three-way interaction between measurement session (factor with 3 levels: at the beginning, during gestation, after parturition), nocturnal temperatures and food availability. We also added a random effect of individual identity to controlled for inter-individual variability. For baseline corticosterone, ROMs and OXY levels analyses, we corrected the inter-plate variability of the assays by adding a fixed plate effect to the models. Female litter size and viability were analysed with generalised linear mixed models (GLMMs) assuming Poisson and binomial distribution respectively, and we used LMMs to study female reproductive investment and post-partum body mass. These models included female

SVL and interactive effects of nocturnal temperatures and food availability as fixed effects. In all analyses described above (except the ovulation date analysis), we added a fixed effect of individual-centred ovulation date because ovulation date, which marks the onset of gestation, can be correlated with parturition date and female quality (Bauwens & Verheyen, 1985) and because the experimental treatments and physiological measurements started or were carried out not at the same time of the reproductive cycle for each female.

We analysed repeated measurement of maternal behaviours during gestation using mixed models including a random effect of individual identity to control for inter-individual variability and a fixed effect of the experimental batch. We analysed surface body temperatures throughout the gestation (which is linearly linked to internal body temperature; see Figure S3) using LMMs including fixed effects of the breeding room temperatures, the gestation stage (calculated as the number of days between the ovulation date and the date of measurement, divided by the number of days between ovulation date and parturition date) and the two-way interaction between nocturnal temperatures and food availability and the experimental batch. To ensure a Gaussian distribution of the residuals, we performed a Box-Cox transformation of raw surface body temperatures. To study activity behaviours, we counted the number of times each day out of 7 observations where females were active and then analysed these counts data as success-failure events with GLMMs assuming a binomial distribution including fixed effects of the gestation stage, the two-way interaction between nocturnal temperatures and food availability and the experimental batch. We calculated the ratio of crickets consumed per week (calculated as the mass of crickets supplied minus the mass of crickets not consumed, divided by the mass of crickets

supplied) with LMMs including the two-way interaction between nocturnal temperatures and food availability and the gestation stage as fixed effect.

To analysed offspring SVL, body mass and endurance at birth, we used LMMs with the interactive effects of maternal treatments (nocturnal temperatures and food availability), sex, individual-centred ovulation date of the mother and offspring SVL (except for SVL analyses) as fixed effects and a random effect of female identity. For endurance analyses, we also added the number of stimulation and the running distance as fixed effects.

We analysed delayed effects of experimental treatments on both female and offspring morphology and survival using mixed models including the release enclosure as random effect. Post-summer juvenile SVL, juvenile specific growth rate and female body condition in September were analysed with LMMs including the two-way interaction of maternal treatments during gestation, sex (except for female body condition analysis) and SVL (except for juvenile SVL and specific growth rate analysis). Female intra-individual changes in limb thickness and tail width between parturition to September were analysed with LMMs including the fixed effect of the limb thickness or tail width at parturition and the two-way interaction of nocturnal temperatures and food availability. For juvenile and female survival analyses, we fitted GLMMs assuming a binomial distribution and included the two-way interaction of maternal treatments during gestation and sex (only for juvenile survival analyses). In all juvenile post-summer traits analyses, we included a random effect of individual identity of the mother in the models.

3. Results

Parturition date was positively correlated with ovulation date (slope: 0.64 ± 0.05 ; $F_{1,102.9} = 175.38$, $p < 0.0001$) and was significantly affected by the interactive effects of nocturnal temperatures and food availability ($F_{2,106.3} = 6.72$, $p = 0.002$). Females that ovulated early had earlier parturition dates and nocturnal warming shortened gestation time regardless of food, except for females exposed to intermediate nights which gave birth earlier when food was restricted (Figure 1).

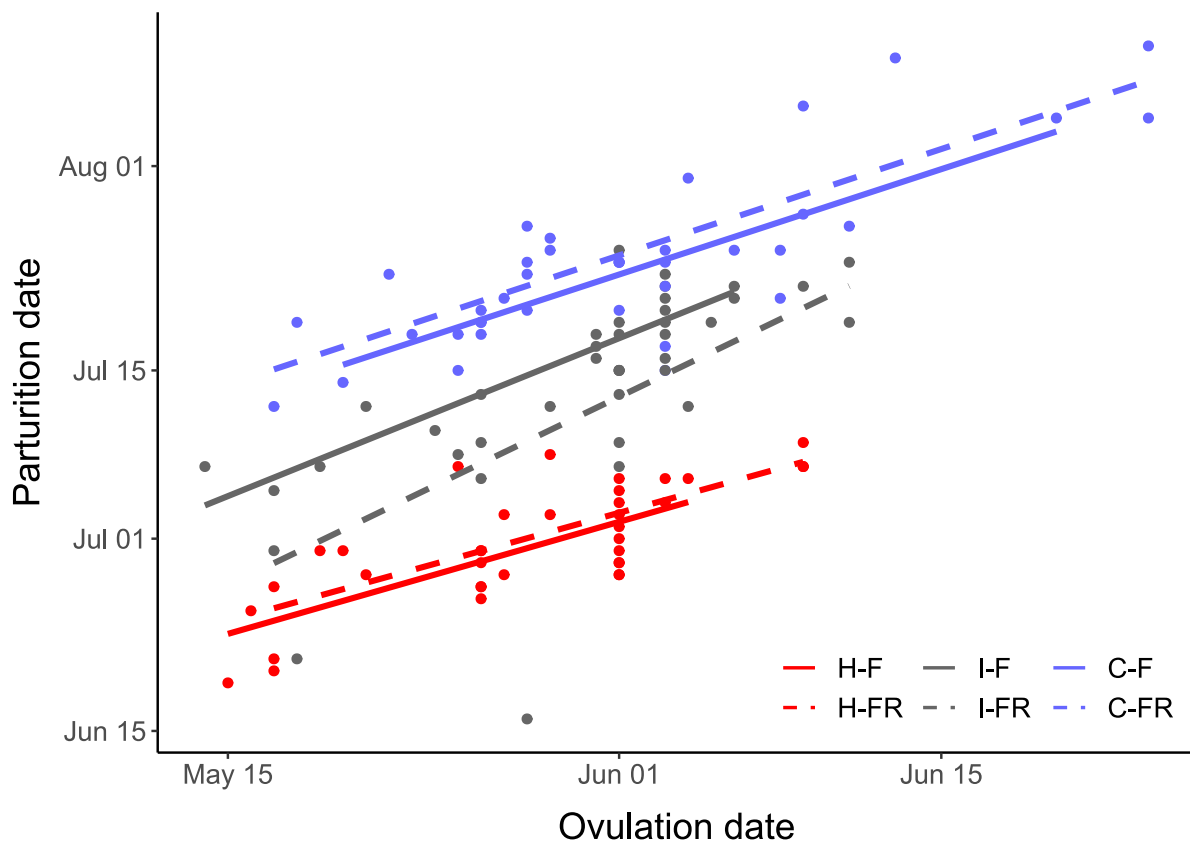


Figure 1: Relationship between parturition and ovulation dates of breeding females *Zootoca vivipara* as a function of nocturnal temperatures (H: hot (red); I: intermediate (grey); C: cold (blue)) and food availability treatments (F: ad libitum food (solid line); FR: food restricted (dashed line)). Confidence intervals were not displayed to improve visibility. Points represent individual values.

3.1. Morphological changes during gestation

Female limb thickness changes during gestation were positively correlated with ovulation date (slope: 0.002 ± 0.001 ; $F_{1,113.5} = 6.07$, $p = 0.02$) and influenced by the interactive effects of nocturnal temperatures and food availability ($F_{2,117.1} = 3.78$, $p = 0.03$). In *ad libitum* feeding conditions, only females exposed to warm nights showed a decrease in leg thickness, while the limb thickness of the other groups tended to increase slightly during gestation (Figure 2a). Under food restriction conditions, females from warm and intermediate nights lost limb thickness during gestation, whereas limb thickness was stable in cold night conditions. In addition, female tail width changes during gestation were affected by additive effects of nocturnal temperatures ($F_{2,118} = 5.84$, $p = 0.004$) and food availability ($F_{1,118} = 6.78$, $p = 0.01$) but not by their interaction ($F_{2,115.8} = 2.07$, $p = 0.13$) and by ovulation date ($F_{1,117} = 0.91$, $p = 0.34$). On average, tail thickness increased during gestation, but to a lesser extent in food restricted females and in hot nocturnal conditions (Figure 2b). Finally, post-partum body condition was influenced by nocturnal temperatures ($F_{2,122} = 6.41$, $p = 0.002$) and food availability ($F_{1,122} = 19.41$, $p < 0.0001$) but not by their interaction ($F_{2,120} = 1.72$, $p = 0.18$) and by ovulation date ($F_{1,119} = 2.39$, $p = 0.12$). Hot and intermediate nocturnal temperatures as well as food restriction during gestation reduced post-partum female body condition (Figure 2c).

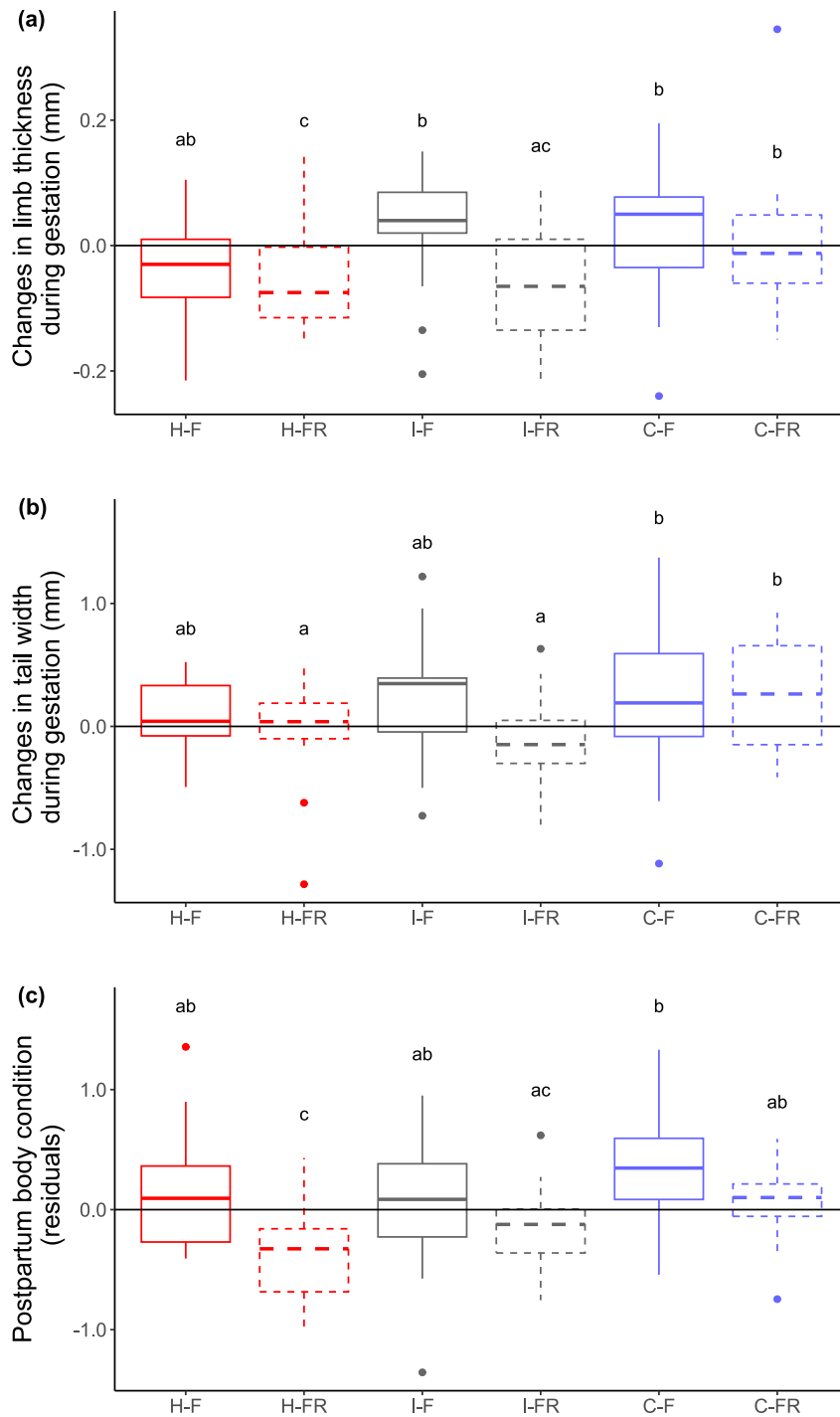


Figure 2: Intra-individual changes in (a) limb thickness and (b) tail width and postpartum body condition of females (c) as a function of nocturnal temperatures (H: hot (red); I: intermediate (grey); C: cold (blue)) and food availability treatments (F: ad libitum food (solid line); FR: food restricted (dashed line)). In (a) and (b), a negative change indicates a decrease in the limb thickness or tail width. Body condition of females after parturition are residuals of a linear regression between female body mass and SVL. Boxplots of the distribution of data are displayed and different letters indicate significant differences between groups ($p < 0.05$; Tukey's HSD post hoc test).

3.2. Physiological response to nocturnal temperatures and food availability

The skin swelling response was affected by the interaction between gestation stage and nocturnal temperatures ($F_{4,247.7} = 2.39$, $p = 0.05$) independently of food availability ($F_{2,245.7} = 1.77$, $p = 0.17$) and ovulation date ($F_{1,123.8} = 0.34$, $p = 0.56$). Skin swelling response increased on average during gestation for females exposed to intermediate and cold nocturnal temperatures but decreased under hot nocturnal temperatures (Figure 3a). Baseline corticosterone levels of females were also significantly affected by the interaction between the gestation stage and nocturnal temperatures ($F_{2,245.8} = 3.01$, $p = 0.02$) but not by food availability ($F_{1,243.9} = 0.32$, $p = 0.73$) and ovulation date ($F_{1,123.9} = 2.58$, $p = 0.11$). Baseline corticosterone levels rose during early gestation regardless of treatments and subsequently declined after parturition, except for females exposed to cold nocturnal temperatures that maintained high corticosterone levels after parturition (Figure 3b). Regarding oxidative stress markers, OXY levels were influenced by the interaction between gestation stage and food availability ($F_{2,244.6} = 6.15$, $p = 0.002$) but not by nocturnal temperatures ($F_{4,240.5} = 1.34$, $p = 0.26$) and ovulation date ($F_{1,118.1} = 0.05$, $p = 0.82$). On average, OXY levels increased during gestation for well-fed females but decreased for food restricted females (Figure 3c). We found no significant effects of nocturnal temperatures ($F_{4,207.6} = 1.03$, $p = 0.39$), food availability ($F_{2,208.1} = 2.61$, $p = 0.08$) and ovulation date ($F_{1,126.5} = 2.32$, $p = 0.13$) on ROMs levels. We did not detect any interactive effect of nocturnal temperatures and food availability on maternal physiological parameters described above (all $p > 0.05$).

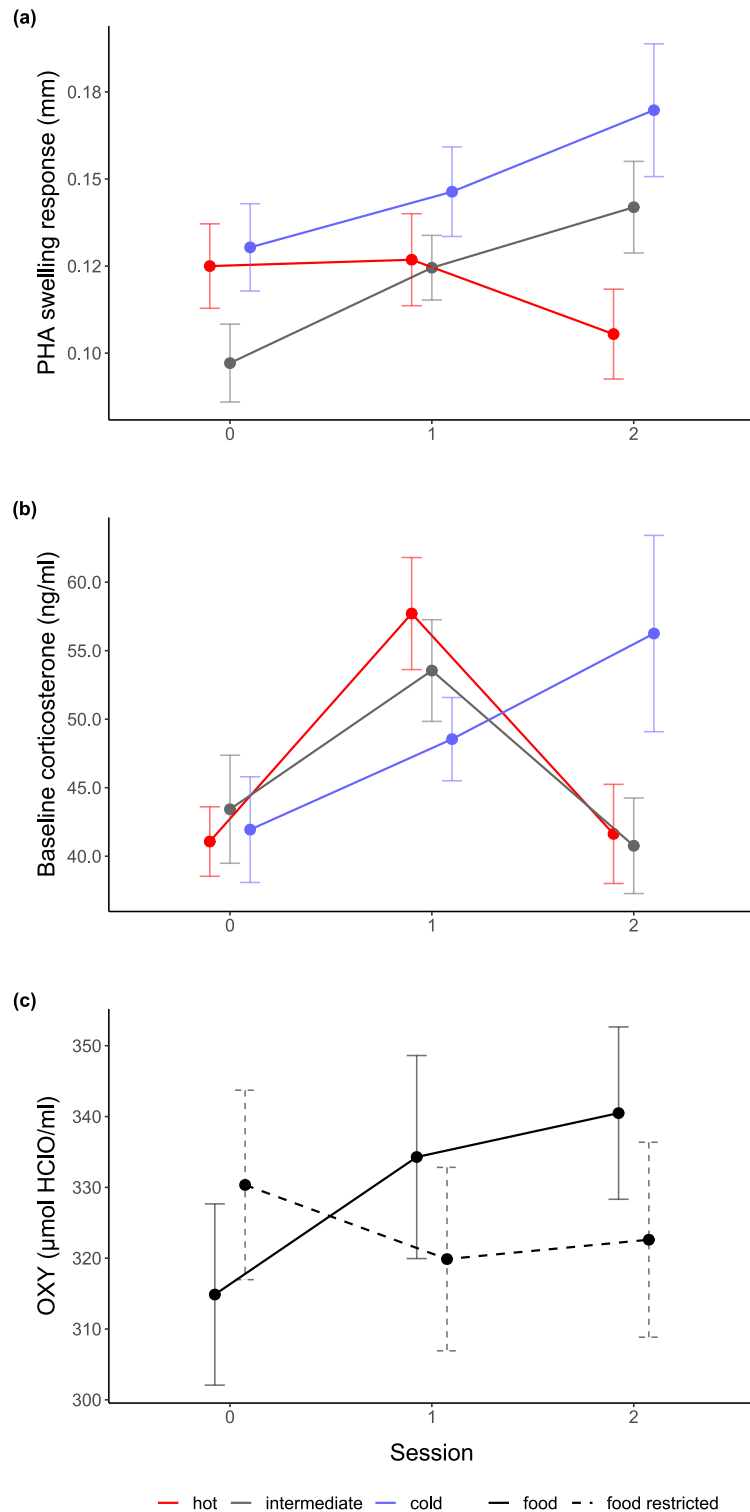


Figure 3: Effects of nocturnal temperatures (hot (red); intermediate (grey); cold (blue)) and food availability treatments (ad libitum food (solid black line); food restricted (dashed black line)) on (a) PHA swelling response, (b) baseline corticosterone and (c) OXY levels of breeding females throughout gestation (0: beginning of gestation; 1: mid-gestation; 2: after parturition). Points are mean values \pm SE.

3.3. Feeding, activity and surface body temperature of females

Surface body temperatures of females were influenced by the gestation stage ($F_{1,4335.2} = 8.33$, $p = 0.004$) and nocturnal temperatures ($F_{2,113.1} = 58.4$, $p < 0.0001$), but not by food availability ($F_{1,118.2} = 0.02$, $p = 0.90$) and interaction of food and nocturnal temperatures ($F_{2,112.8} = 0.49$, $p = 0.61$). On average, the surface body temperature of females increased during early gestation and then fell following a concave curve (Figure S4a). Females had slightly higher daytime body temperatures when they were exposed to warmer nocturnal temperatures (hot: 26.56 ± 3.18 °C; intermediate: 26.06 ± 3.09 °C; cold: 25.16 ± 2.84 °C). In addition, we found significant effects of the gestation stage ($\chi^2_1 = 24.4$, $p < 0.0001$) and the interaction between nocturnal temperatures and food availability on behavioural activity ($\chi^2_2 = 5.89$, $p = 0.05$). On average, activity levels of pregnant females decreased during gestation (Figure S4b). Activity patterns of *ad libitum* fed females did not change with nocturnal temperatures, whereas food restricted females showed higher daytime activity when they were exposed to warm nights compared with cold nights. The ratio of cricket consumed during gestation was significantly affected by the gestation stage ($F_{1,568.4} = 11.55$, $p < 0.001$) and by the interaction between nocturnal temperature and food availability ($F_{2,129.8} = 15.55$, $p < 0.0001$). On average, food consumption decreased during gestation (Figure S4c). Food restricted females consumed almost all crickets independently of nocturnal temperatures, while fed females exposed to hot nights consumed a higher ratio of cricket than fed females exposed to intermediate or cold nights.

3.4. Reproductive output

Litter size was not affected by nocturnal temperatures ($\chi^2_2 = 2.91$, $p = 0.23$) and food availability ($\chi^2_1 = 0.0002$, $p = 0.99$) but increased with SVL (slope: 0.04 ± 0.01 , $\chi^2_1 = 12.01$, $p < 0.001$) and decreased slightly with ovulation date (slope: -0.01 ± 0.005 , $\chi^2_1 = 4.25$, $p = 0.04$). We detected significant additive effects of nocturnal temperatures ($F_{2,116.5} = 10.36$, $p < 0.0001$), food availability ($F_{2,120.6} = 8.80$, $p = 0.003$) and ovulation date (slope: -0.03 ± 0.01 ; $F_{1,115.2} = 34.02$, $p < 0.0001$) on reproductive investment after accounting for a positive effect of female SVL ($F_{1,120.8} = 10.59$, $p = 0.001$). Females exposed to hot nights had a lower reproductive investment (hot: 1.74 ± 0.65 g; intermediate: 2.14 ± 0.59 g; cold: 2.14 ± 0.74 g), as well as food-restricted females (food ad libitum: 2.16 ± 0.59 g; food restricted: 1.83 ± 0.74 g) and females which ovulated later. We also found additive effects of nocturnal temperatures ($\chi^2_2 = 12.2$, $p = 0.002$), food availability ($\chi^2_1 = 12.90$, $p = 0.0003$) and ovulation date (slope: -0.33 ± 0.01 ; $\chi^2_1 = 82.96$, $p < 0.0001$) on litter viability. The proportion of viable offspring in the litter was higher among females who ovulated early, in females exposed to intermediate nocturnal temperatures compared with hot and cold nights (hot: 0.59 ± 0.42 ; intermediate: 0.74 ± 0.35 ; cold: 0.58 ± 0.35), and in well fed females (food ad libitum: 0.70 ± 0.35 ; food restricted: 0.56 ± 0.40 g). We did not detect any interactive effect of nocturnal temperatures and food availability on female reproductive parameters (all $p > 0.05$).

3.5. Offspring phenotype at birth

Juvenile SVL was not influenced by nocturnal temperatures ($F_{2,91} = 0.59$, $p = 0.56$), food availability ($F_{1,90.6} = 0.22$, $p = 0.64$) and ovulation date ($F_{1,91.9} = 2.26$, $p = 0.14$). However, juvenile body condition was influenced by food availability ($F_{1,87.5} = 3.79$, $p =$

0.05) but not by nocturnal temperatures ($F_{2,85.6} = 0.18$, $p = 0.84$) and ovulation date ($F_{1,86} = 1.01$, $p = 0.32$). Juveniles born from food restricted females were slightly less corpulent than juveniles from well-fed females (Figure 4a). In addition, nocturnal temperatures ($F_{2,85.7} = 4.48$, $p = 0.01$) unlike food availability ($F_{1,86.6} = 1.81$, $p = 0.18$) affected offspring endurance. Juveniles born from females exposed to hot nights had a higher endurance capacity than juveniles from females exposed to cold nights (Figure 4b). We did not detect any interactive effect of nocturnal temperatures and food availability on the traits of juveniles at birth (all $p > 0.05$).

3.6. Delayed effect on survival and phenotype of juveniles and females

Of 135 living females and 508 juveniles born in the laboratory and released in the field, we recaptured 119 juveniles and 97 females in September 2023 (estimated survival rates: 72% for adult females and 23 % for juveniles). Nocturnal temperatures and food availability did not affect post-summer juvenile survival ($\chi^2_2 = 0.92$, $p = 0.63$; $\chi^2_1 = 0.26$, $p = 0.61$ respectively) and juvenile specific growth rate ($F_{2,47.5} = 0.91$, $p = 0.41$; $F_{1,44.7} = 0.83$, $p = 0.37$ respectively) after correcting for sex effects ($\chi^2_2 = 0.92$, $p = 0.63$; $F_{1,107.6} = 4.03$, $p = 0.05$ respectively). However, the post-summer SVL of juveniles was influenced by nocturnal temperatures ($F_{2,53.8} = 25.9$, $p < 0.0001$) but not by food availability ($F_{1,54.1} = 0.43$, $p = 0.52$) after correcting for sex effects ($F_{1,100.5} = 9.25$, $p = 0.002$). Juveniles from females exposed to warm nights were larger in September than juveniles from females exposed to cold nights (Figure 4c). Nocturnal temperatures and food availability did not affect post-summer female survival ($\chi^2_2 = 0.31$, $p = 0.86$; $\chi^2_1 = 0.66$, $p = 0.41$ respectively), nor limb thickness change ($F_{2,81.4} = 0.62$, $p = 0.54$; $F_{1,87.3} = 0.64$, $p = 0.42$ respectively) nor tail width change ($F_{2,82.7} = 0.06$, $p = 0.94$; $F_{1,90.8} = 2.35$, $p = 0.13$). Nevertheless, we found a negative effect of food restriction on female body condition in September ($F_{1,87.5} = 9.24$, $p = 0.003$; contrast = -0.27 ± 0.08 g)

independently on nocturnal temperatures ($F_{2,82.6} = 0.87$, $p = 0.42$). We detected no interactive effects of nocturnal temperatures and food availability on the survival and phenotype of females and juveniles in September (all $p > 0.05$).

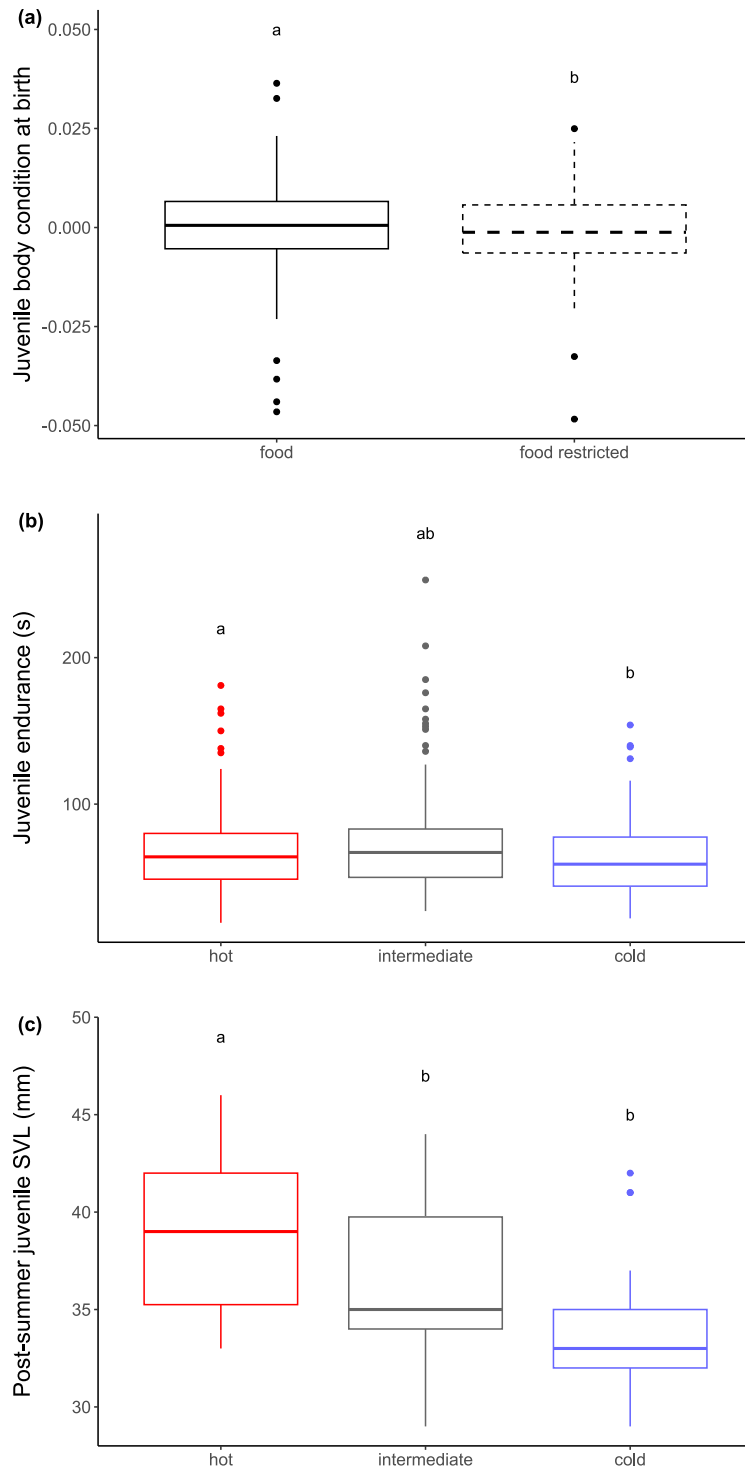


Figure 4: Effects of nocturnal temperatures (hot (red); intermediate (grey); cold (blue)) and food availability treatments (ad libitum food (solid line); food restricted (dashed line)) on (a) juvenile body condition at birth, (b) juvenile endurance and (c) post-summer juvenile SVL. Juvenile body condition at birth are residuals of a linear regression between juvenile mass and juvenile SVL. Boxplots of the distribution of data are displayed and different letters indicate significant differences between groups ($p < 0.05$; Tukey's HSD post hoc test).

4. Discussion

To improve our understanding of thermal plasticity of breeding phenology in viviparous ectotherms, we examined the combined effects of nocturnal warming and prey availability during gestation on parturition dates and multivariate indicators of condition, reproduction, offspring phenotype at birth and maternal and juvenile fitness. Nocturnal warming shortened strongly average gestation time in line with several previous studies of lizards (Brusch IV et al., 2023; Clarke & Zani, 2012; Moore et al., 2020) and the general thermal plasticity of gestation in reptiles (reviewed in Noble et al., 2018). Furthermore, exposure to warmest nights and food restriction had negative additive effects on reproduction and increased the costs of reproduction as shown by changes in the immune system and energy balance of pregnant females. In contrast, moderate nocturnal warming increased litter viability and thermal acceleration of gestation was beneficial to the offspring by enhancing their performance at birth and allowing for a longer growth period and size advantage throughout early life.

4.1. Nocturnal temperatures and food availability interact to drive breeding phenology

As expected, parturition date was positively correlated with ovulation date and exposure to hot nights (+8°C) accelerated gestation strongly by around 39% compared to cold nights. These results are in line with previous research in oviparous and viviparous reptiles showing that higher nocturnal temperatures and earlier ovulation dates both lead to earlier parturition or hatching dates (Bauwens & Verheyen, 1985; Brusch IV et al., 2023; Clarke & Zani, 2012; Lorigoux et al., 2013; Moore et al., 2020). In addition, nocturnal temperatures and food availability had unexpected interactive effects on parturition dates. Under cold and hot nocturnal conditions, food availability did not influence breeding phenology, but food-restricted females gave birth earlier

than well-fed females under intermediate nocturnal temperatures. Changes in parturition dates due to resource availability have been demonstrated in birds where some species might cue on food availability to decide where and when to reproduce (reviewed in Martin, 1987; Robb et al., 2008). To our knowledge, no study has demonstrated an effect of resource availability alone or in interaction with temperature on the breeding phenology of reptiles. We did not expect a strong relationship between breeding phenology and energetic status in the common lizard because food is unlikely to influence directly the speed of embryonic development *in utero*. However, the effects of energetic status could be the consequence of subtle behavioural modifications in response to food availability and nocturnal temperatures. For example, under hot and intermediate nights, food-restricted females were more active than well-fed females, whereas females exposed to cold nights showed similar activity patterns. Even if the mean body temperatures of the females were influenced solely by nocturnal temperatures, an increase in activity behaviour could subtly affect the speed of embryonic development. These behavioural adjustments could generate earlier parturition dates under intermediate temperatures but not under hot nights since females exposed to hot nights might already be at their phenological limit (Brusch IV et al., 2023). This *a posteriori* explanation would require further testing with a more careful examination of the relationship between environmental temperatures, food availability and body temperature of pregnant females.

4.2. Ovulation date, nocturnal temperatures and prey availability drive reproductive output

The ovulation date (which marks the start of gestation) was negatively correlated with body condition during vitellogenesis and further influenced reproductive traits. Females that ovulated early in the season had higher fecundity, reproductive investment and

litter viability, which is consistent with the pattern of seasonal decline in reproductive investment and suggests that early ovulation covaries with individual quality or condition in the common lizard like in many other taxa (e.g. Dawson, 2008; Green & Rothstein, 1993; Mitchell et al., 2018; Olsson & Shine, 1997; Verhulst et al., 1995). Nocturnal warming and food restriction also strongly influenced reproductive investment and litter viability but had no effect on fecundity probably because litter size is set before the start of the experiment in this lecithotrophic species (Bauwens & Verheyen, 1985). The common lizard uses mixed capital and income reproductive strategies (Bleu et al., 2013), where reproductive investment and reproductive success may depend on both stored resources and resources recently acquired during vitellogenesis or gestation (Bonnet et al., 1998). Higher energy expenditure induced by hot nights and lower food intake due to food restriction both reduced the amount of energy available to fuel reproduction, thus reducing reproductive investment and embryo viability. These results are consistent with previous studies in viviparous lizards reporting negative effects of too high nocturnal warming or too low food availability during gestation on reproductive investment (Brusch IV et al., 2023; Wang et al., 2017). Nevertheless, nocturnal temperatures had non-linear effects on litter viability such that moderate nocturnal warming increased litter viability in line with the general pattern of a concave curve between offspring viability and developmental temperatures across studies of squamate reptiles (Noble et al., 2018). For example, too cold or too hot developmental temperatures often increase embryonic mortality and developmental abnormalities (Cui et al., 2022; Ji et al., 2002; Qualls, 1999).

4.3. High nocturnal temperatures and food restriction disrupt maternal homeostasis

Breeding phenology plasticity due to nocturnal warming was associated with significant alterations of key physiological traits such as immunocompetence and basal

corticosterone levels. High nocturnal warming led to a decrease in immunocompetence relative to cold and intermediate nocturnal conditions like in other reptile species (Butler et al., 2013; Sacchi et al., 2017; Stahlschmidt et al., 2017). Our current study cannot provide a detailed mechanistic understanding of the effects of temperature on the immune system as the PHA swelling response includes several innate and adaptive components (Demas et al., 2011; Mugabo et al., 2015). Immune suppression at high temperatures could be due to direct effects of temperature on the activity of phagocytic and cytotoxic cells of the innate and adaptive immunity (Rios & Zimmerman, 2015) or to indirect effects of high temperatures on the amount of energy that can be allocated to the immune system. However, in the second case we would have predicted a negative effect of food restriction on immunocompetence, as seen in multi-ocellated racerunner for example (Wang et al., 2017), which we did not observe. Furthermore, while corticosterone levels tend to increase during gestation in several viviparous squamate species (Lorioux et al., 2016; Taylor et al., 2004), this pattern was only visible in females exposed to cold nights, whereas intermediate and hot night temperatures down-regulated basal corticosterone levels late in gestation, contrary to our initial predictions. A down-regulation of circulating corticosterone levels in response to warming is consistent with the negative relationship between basal corticosterone levels and minimum daily temperatures observed in natural populations and could constitute an energy conservation mechanism in response to chronic exposure to high temperatures (Dupoué et al., 2018). Finally, nocturnal temperatures had no significant effect on the oxidative balance of females (i.e., oxidative damage and antioxidant capacity). Although environmental temperatures can modulate oxidative stress or antioxidant responses in reptiles (Dupoué et al., 2020; Han et al., 2020), previous studies on the common lizard also reported no nocturnal warming effect on oxidative balance

(Brusch et al., 2020; Rutschmann et al., 2021). This could be explained by the ability of females to buffer the effects of nocturnal warming through physiological or behavioural adjustments or might be explained by the use of global instead of more specific markers of oxidative stress (Rutschmann et al., 2024). In contrast, food restriction reduced the non-enzymatic antioxidant capacity of females, probably because food provides antioxidant compounds and because the production of antioxidant molecules requires energy (reviewed in Costantini, 2014).

4.4. Temperature and food effects on the energetic costs of reproduction

In ectotherms, activity behaviours, thermoregulation and environmental temperatures drive the net energy budget which depends on a balance between inputs from food intake and assimilation and outputs from energy expenditure at rest and during activity (Dillon et al., 2010; Levy et al., 2017; Rutschmann et al., 2024). On average, females reduced their cricket consumption, activity and mean body temperature as gestation progressed. Decreases in activity, selected body temperatures and food intake during gestation are common in viviparous reptiles, and these behavioural adjustments are either the direct consequences of mechanical constraints imposed by the eggs volume in the abdomen, which reduce locomotor capacities, or potential tactics to limit predation and protect embryos from high temperatures (Le Galliard et al., 2003; Moore et al., 2020). In line with a previous study, *ad libitum* fed females exposed to hot nights increased their cricket consumption probably because hot nocturnal temperatures improved digestion rates or to compensate energetic imbalances induced by hot nocturnal temperatures (Brusch IV et al., 2023). Nevertheless, while some reptiles may reduce their mean body temperature or activity during chronic exposure to fasting or heat waves in order to promote energy conservation (Angilletta Jr., 2009), common lizards exposed to hot nights had slightly higher daytime surface body temperatures

and higher activity rates under low prey availability. Increased activity and body temperatures in energetically challenging environments could be short-term responses to promote energy intake, as higher body temperatures favour food intake and digestive efficiency (Van Damme et al., 1991), but these responses do not constitute effective energy conservation strategies against chronic exposure to high nocturnal temperatures or low prey availability. High nocturnal temperatures and food restriction thus challenged the net energy gain of breeding females: we found that the warmest nocturnal temperatures and a low prey availability led both to body condition loss, muscle loss and mobilisation of caudal energy reserves (Bodineau et al., 2024; Bruschi et al., 2023). Muscle catabolism and utilisation of caudal lipid reserves stored as triglycerides in the tail (Avery, 1974; Price, 2017) is common in reptiles during reproduction and could be accentuated under food and thermal constraints to cover energy and amino acid requirements when energy expenditure increases or when food intake is insufficient (Bodineau et al., 2024; Bruschi et al., 2020). Interestingly, muscle loss was seen at intermediate nocturnal temperatures under food restriction but only at high nighttime temperatures under *ad libitum* food, suggesting that a lower optimal nocturnal temperature with restricted prey availability. Thus, in line with theoretical studies, reduced prey availability could accentuate the metabolic costs of nocturnal warming on female condition (Huey & Kingsolver, 2019; Rutschmann et al., 2024; Thomas et al., 2017). Yet, this shift in optimal temperatures was not seen on other components of body condition and energetics, such as caudal lipid mobilisation and overall body condition. We suggest that the combined effects of nocturnal warming and food deprivation may affect differently the different metabolic pathways (e.g., lipids and amino acids regulation) underlying body condition.

4.5. Intergenerational and delayed effects of temperatures and food availability

Thermal regimes did not influence juvenile morphology at birth, in accordance with a previous study in the common lizard (Brusch et al., 2020), but juveniles from mothers exposed to hot nocturnal temperatures had a higher endurance capacity at birth. In reptiles, developmental temperatures are important determinants of offspring fitness-related traits but these effects often vary in magnitude and direction between species and the underlying mechanisms are still poorly understood (reviewed in Booth, 2006; Noble et al., 2018; While et al., 2018). For example, some studies show positive effects of warmer developmental temperatures or increased maternal thermoregulatory opportunities on juvenile body condition and locomotor performance at birth (Li et al., 2018; Pearson & Warner, 2018; H. Zhang et al., 2013) while others show the opposite (Braña & Ji, 2000; Dayananda et al., 2017; Swain & Jones, 2000) or no effect (Beltrán et al., 2020; Brusch et al., 2020). Here, hot nocturnal temperatures increased juvenile endurance suggesting a positive effect of nocturnal warming on the intrinsic quality of neonates. Mechanisms underlying the effects of thermal regimes on offspring locomotor performance could include beneficial effects of warmer developmental temperatures or reduced gestation length on the development of musculoskeletal or brain function in embryos (Booth, 2017; While et al., 2009) or different thermal performance curves between juveniles from different thermal treatments as we tested the endurance at a single temperature (Pearson & Warner, 2018). In addition, we found a negative effect of low prey availability during gestation on juvenile body condition at birth. In viviparous reptiles, maternal effects mediated by food availability during gestation are variable and depend on the degree of placental nutrient support during embryogenesis (Botterill-James et al., 2019; Itonaga et al., 2012; Massot & Clobert, 1995; Swain & Jones, 2000; Wang et al., 2017). Since the common lizard is a

lecitotrophic species without placental exchange structure (Stewart et al., 2004), the negative effects of maternal food restriction on juvenile body condition may be related to behavioural or physiological changes caused by maternal food restriction or to the production of premature offspring under food restriction conditions (Itonaga et al., 2012).

We found no delayed effect of nocturnal warming on post-summer survival of adult females or on their condition-related traits (i.e., body condition, limb thickness and tail width). We only found a negative effect of food restriction on females post-summer body condition, which suggests long-lasting effects of food restriction after parturition. Yet, our results indicate that thermal acceleration of gestation induced by nocturnal warming had beneficial effects on the ontogenic trajectories of the offspring since the post-summer body size of juveniles was greater when females were exposed to warmer nocturnal temperatures. The effects of developmental temperatures on post-summer growth could be explained by differences in the offspring quality (e.g., foraging skills) and/or reflect the advantage of an early birth date which confers a longer growth period before winter (Adolph & Porter, 1993; Bodineau et al., 2024; Pearson & Warner, 2018; Warner & Shine, 2007). In fact, when we replaced the effect of nocturnal thermal treatment with juvenile birth date, we found a negative correlation between birth date and post-summer SVL (slope: -0.25 ± 0.02 ; $F_{1,46.5} = 112.71$, $p < 0.0001$). Thus, contrary to our predictions and some previous studies, high developmental temperatures did not improve post-summer juvenile growth rates or survival (Liu et al., 2022; Sun et al., 2018; Warner & Shine, 2007). This suggests that any advantage of warmer developmental temperatures or early birth in the common lizard is solely a consequence of growth period extension before wintering rather than from more advantageous growing conditions early in the season (i.e., more favourable

temperatures, longer days, weaker competition between conspecifics (Bodineau et al., 2024)).

5. Conclusion

We examined for the first time the combined impacts of nocturnal warming and prey availability during gestation on breeding phenology and multivariate indicators of female homeostasis, reproductive output and offspring quality in a viviparous ectotherm. Overall, our results suggest that nocturnal temperatures and prey availability drive reproductive output in viviparous ectotherms and that the acceleration of gestation induced by nocturnal warming has contrasting intragenerational and intergenerational effects. Nocturnal warming had beneficial effects on juvenile locomotor performance at birth and size advantage through growth, potentially via the impact of higher developmental temperatures and the advantage of being born early. Yet, nocturnal warming also increased immediate reproductive costs for females. Low prey availability further challenged the energy imbalance induced by nocturnal warming. Females showed limited, even sometimes counterproductive, behavioural strategies to counteract the higher energy expenditure induced by the hottest nocturnal temperatures, which suggests that diurnal reptiles may have difficulty in behaviourally buffering nocturnal warming (Rutschmann et al., 2024). Overall, our study highlights the existence of a potential mother-juvenile conflict concerning the thermal acceleration of gestation and demonstrates the importance to consider both benefits and costs of phenological acceleration in the context of climate change.

Authors' contributions

Théo Bodineau, Jean-François Le Galliard, Sandrine Meylan and Pierre de Villemereuil conceived the ideas and designed methodology; Théo Bodineau, Jean-François Le Galliard, Sandrine Meylan, Simon Agostini, and Beatriz Decenci re participated to lizard captures and breeding; Mat o Millet performed the endurance assays; Th o Bodineau and Baptiste Lemaire carried out physiological assays; Th o Bodineau collected and analysed the data with the help of Jean-François Le Galliard, Sandrine Meylan and Pierre de Villemereuil; Th o Bodineau led the writing of the manuscript with the help of Jean-François Le Galliard, Sandrine Meylan and Pierre de Villemereuil. All authors contributed critically to the paper and gave final approval for publication.

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Conflict of Interest

The authors declare no competing or financial interests.

Statement on inclusion

Our study brings together authors from the same countries, including a Senior Researcher, a Professor, a Lecturer, a PhD student, engineers and a master's student. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset.

Data availability statement

Data and scripts are available at Zenodo with DOI: <https://doi.org/10.5281/zenodo.11197883>

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Supplementary information

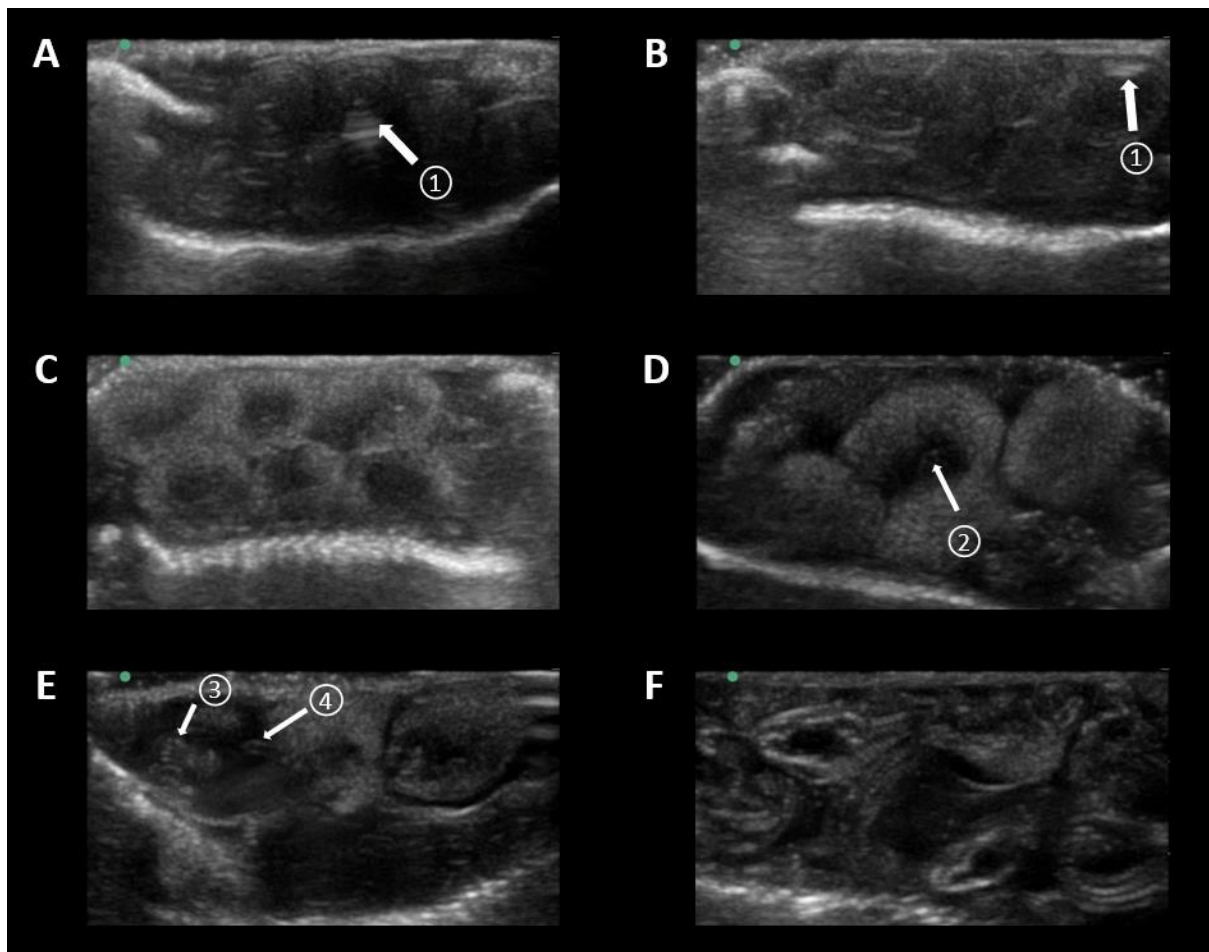


Figure S1: Longitudinal ultrasound scans of the thoracoabdominal region of a reproductive female *Zootoca vivipara* throughout the reproductive cycle. A., B. Vitellogenic stage characterised by follicles with concentric circles (1), which are spherical in shape and progressively echolucent during vitellogenesis (appearing dark in A) to echogenic at the end of vitellogenesis (appearing light in B). C. Ovulated and fertilised eggs with the appearance of the embryonic disc (echolucent zone) surrounded by the yolk (echogenic zone). D. Beginning of embryonic development. The embryo is visible in the echolucent zone (2). E. Developing embryos. Forelimbs (3) and tail (4) are visible. F. Embryo at the end of development. These scans were taken 13 days before ovulation (A), at the time of ovulation (B), 33 days (C), 29 days (D), 22 days (E) and 2 days (F) before parturition.

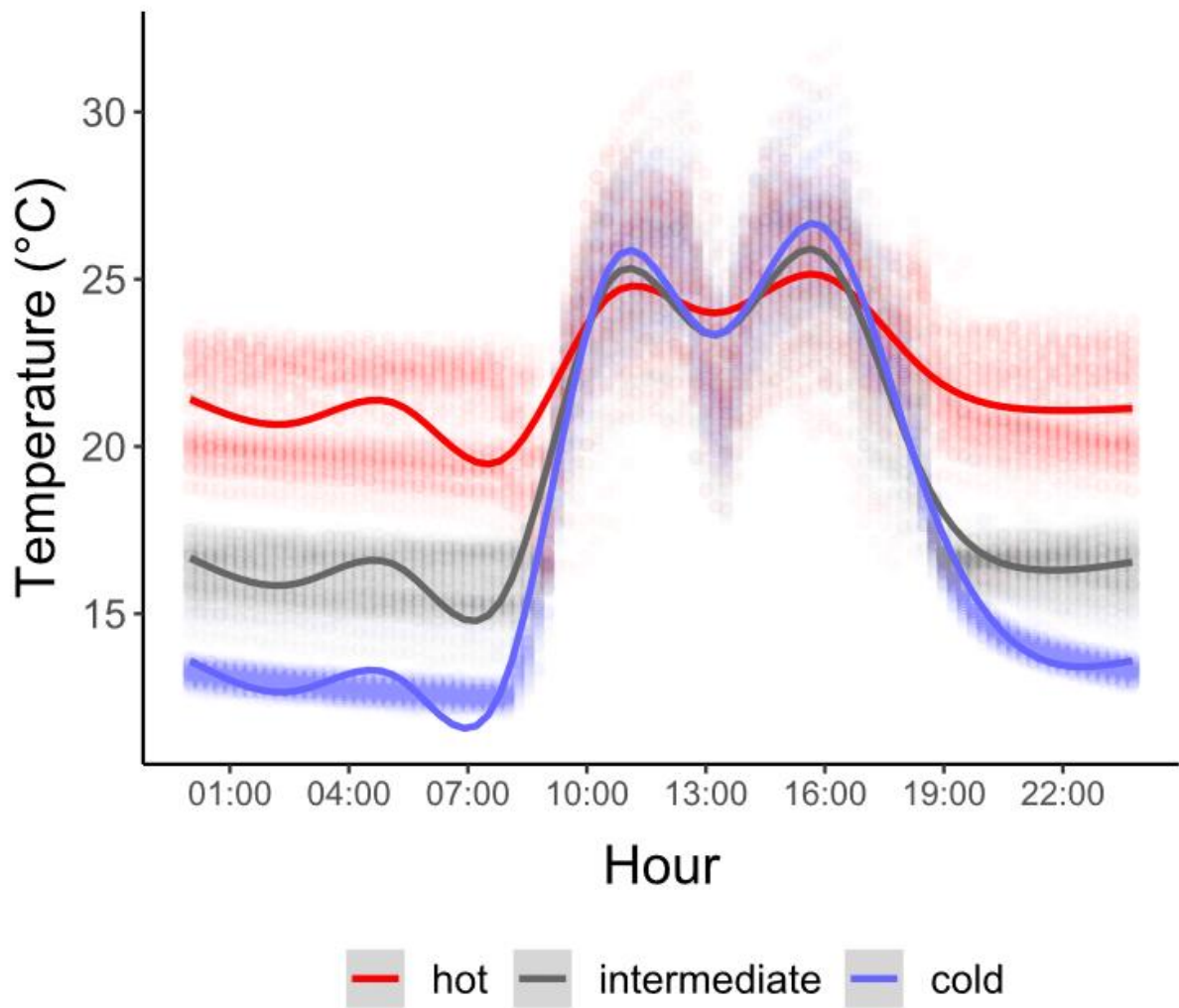


Figure S2: Average daily variation of temperature in the rearing rooms during the experiment as a function of nocturnal thermal treatment (hot night (red), intermediate night (grey) and cold night (blue)). Jittered points correspond to raw values and solid lines are predictions from a generalised additive model.

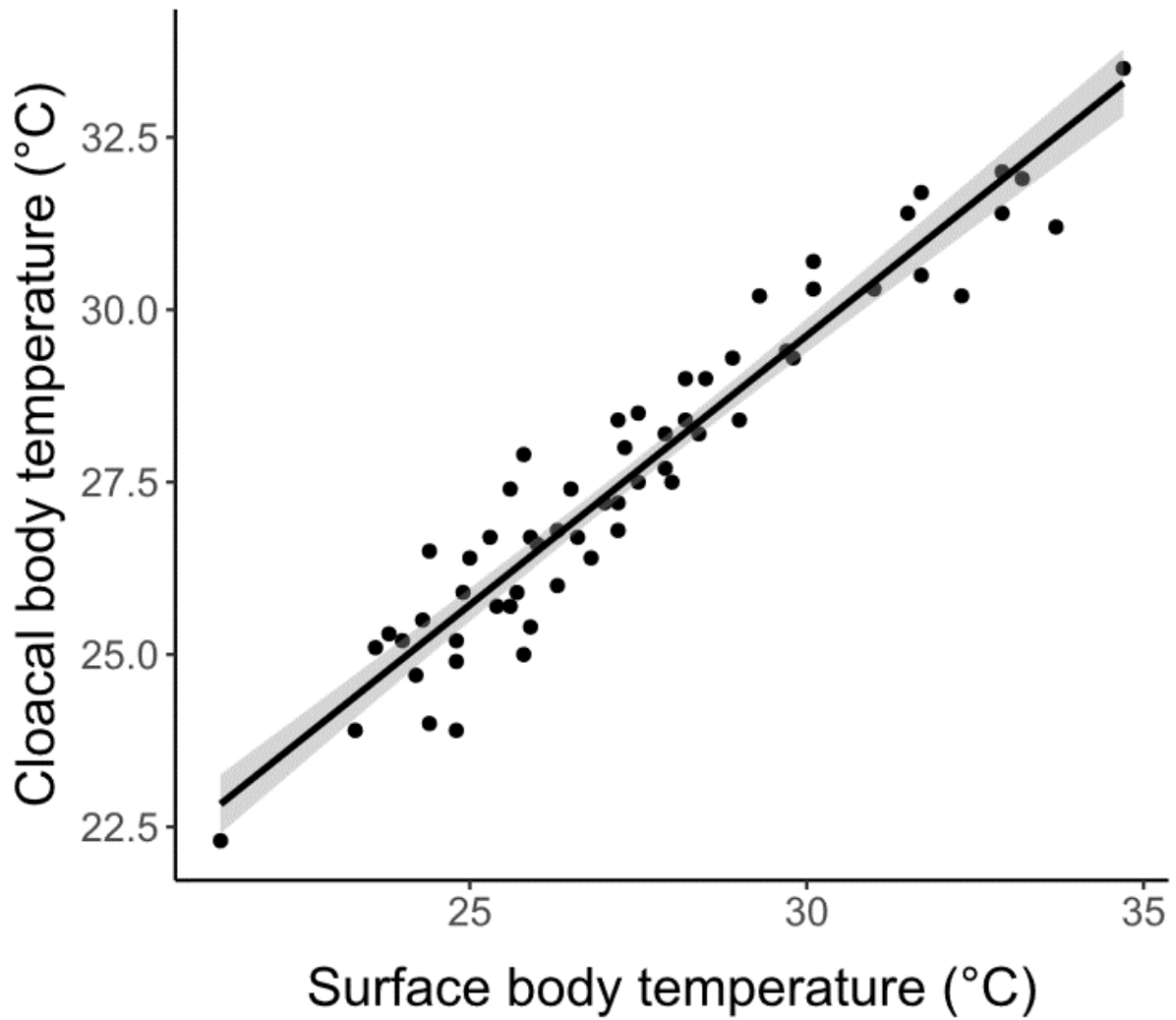


Figure S3: Relationship between cloacal body temperature and surface body temperature. Surface body temperatures (T_{IR}) and cloacal temperatures (T_b) were measured consecutively for each individual using an infrared thermometer (Raytek, Raynger MX2) and a K-type thermocouple (HI 935005N, Hanna). The linear regression (with 95% confidence interval) is plotted against raw data. Cloacal temperatures were strongly correlated with surface temperatures ($N=60$, $T_b = 6.20 (\pm 0.86) + 0.78 (\pm 0.03) \times T_{IR}$, $R^2 = 0.91$).

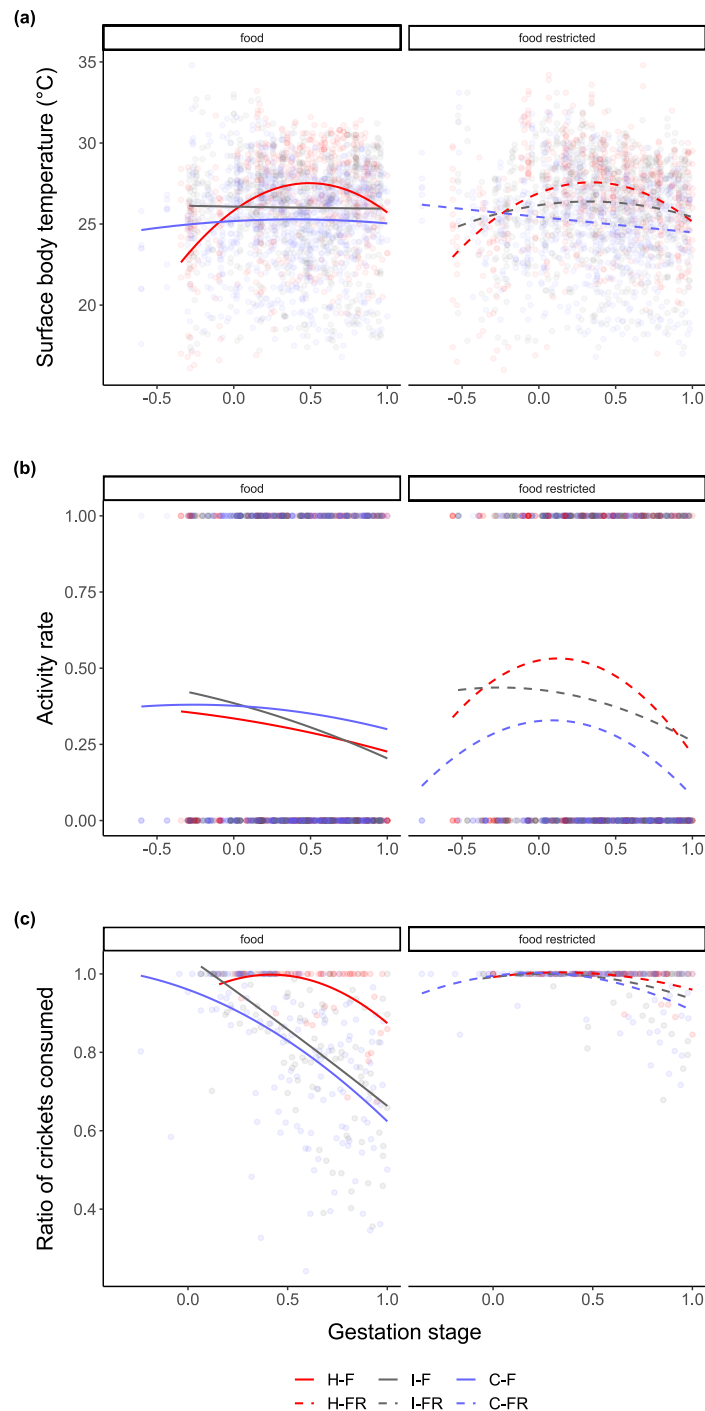


Figure S4: Effects of nocturnal temperatures (H: hot (red); I: intermediate (grey); C: cold (blue)) and food availability (F: ad libitum food (solid line); FR: food restricted (dashed line)) on (a) female surface body temperature, (b) female activity rate and (c) female crickets' consumption throughout gestation. The gestation stage represents the advancement of gestation from ovulation (0) to parturition (1). Points represent raw data of surface body temperature, activity and ratio of crickets consumed. The solid lines represent the average surface body temperature, activity rate or ratio of crickets consumed adjusted with a quadratic gestation stage effect.

DISCUSSION GÉNÉRALE ET PERSPECTIVES



1. Déterminants de la phénologie de la reproduction

1.1 Déterminants environnementaux des dates de parturition

Les **Articles 1 et 2** nous ont permis de quantifier les déterminants environnementaux majeurs des dates de parturition en milieu naturel (voir Figure 14 ci-après). Dans l'**Article 2**, nous avons mis en évidence une forte variation interannuelle des dates de parturition dans une population naturelle de lézard vivipare conformément à des études précédentes chez des reptiles et cette espèce (Ljungström *et al.*, 2015; Massot *et al.*, 2017; Cunningham *et al.*, 2020). Les variations interannuelles des dates de parturition sont explicables par la plasticité thermique des évènements du cycle reproductif (e.g., émergence post-hivernale (Moss & MacLeod, 2022), initiation de la reproduction (Van Dyke, 2014), période de gestation et d'incubation (Noble *et al.*, 2018)). D'une part, les températures environnementales peuvent influencer la phénologie reproductive en affectant les fenêtres d'activités potentielles des ectothermes (Gunderson & Leal, 2015) nécessaires aux activités essentielles pour la reproduction comme les accouplements, la capture et l'assimilation des proies ainsi que la thermorégulation comportementale. Sur notre site d'étude dans le Parc National des Cévennes, nous montrons que les températures maximales journalières durant la période d'activité post-hivernale sont le principal déterminant thermique des dates de parturition (**Article 2**). Les températures maximales journalières sont fortement corrélées à l'insolation et constituent généralement le meilleur prédicteur climatique des opportunités de thermorégulation pendant les périodes d'activité diurnes (Huey, 1982; Marquis *et al.*, 2008). Ces résultats suggèrent que les effets de la température sur les patrons d'activité et les opportunités de thermorégulation sont certainement les plus influents sur les dates de reproduction en milieu naturel. D'autre part, les

conditions thermiques de l'environnement peuvent affecter les dates de reproduction via des effets directs et « passifs » de la température sur les processus biochimiques et métaboliques essentiels déterminant les activités reproductrices et le développement embryonnaire (Hochachka & Somero, 2002a). Par exemple, l'exposition à des conditions chaudes durant les phases d'inactivités nocturnes en laboratoire entraîne une accélération « passive » de la gestation chez le lézard vivipare (**Article 4** ; (Brusch IV *et al.*, 2023)). Les conditions thermiques auxquelles sont exposés les œufs dans le nid déterminent aussi fortement la durée de l'incubation et la date d'éclosion chez les reptiles ovipares (Noble *et al.*, 2018). Compte tenu du réchauffement diurne et nocturne asymétrique dans la plupart des régions du globe (Karl *et al.*, 1991; Easterling *et al.*, 1997; Vose *et al.*, 2005; Davy *et al.*, 2017), des analyses complémentaires en milieu naturel seraient nécessaires afin de quantifier la contribution relative de la température durant les phases d'activité et d'inactivité sur la plasticité thermique de la phénologie chez les squamates. À notre connaissance, aucune étude n'a quantifié les effets des températures nocturnes sur la phénologie des squamates en milieu naturel (Rutschmann *et al.*, 2024). Puisque de nombreux squamates utilisent des terriers ou s'enterrent durant les phases d'inactivité et sont donc exposés à un microclimat souterrain pouvant largement différer du climat de surface (Beck & Jennings, 2003; Moore *et al.*, 2018; Enriquez-Urzelai & Gvoždík, 2024), les effets des températures nocturnes sur la phénologie constatés en laboratoire (**Article 4**, Clarke & Zani, 2012; Brusch IV *et al.*, 2023) devraient impliquer des paramètres microclimatiques spécifiques des microhabitats nocturnes. La décorrélation de ces effets de ceux des conditions diurnes nécessiteraient donc des analyses plus poussées que dans notre étude.

Dans l'**Article 1**, nous avons mis en évidence des variations géographiques des dates de parturition le long d'un gradient environnemental dans le Massif central. Les variations géographiques des dates de parturition étaient déterminées par la couverture forestière et les femelles des populations avec une couverture forestière plus faible poussaient plus tôt. La couverture forestière peut tamponner les conditions macroclimatiques (Woods *et al.*, 2015; Pincebourde *et al.*, 2016; Pincebourde & Woods, 2020; Neel *et al.*, 2021; De Lombaerde *et al.*, 2022), fortement contraindre la thermorégulation comportementale durant la gestation en générant des zones d'ombre (Sears *et al.*, 2016) et retarder les dates de parturition (Rutschmann *et al.*, 2016b). Contrairement aux résultats de l'**Article 2** et à des études précédentes chez le lézard vivipare (Rutschmann *et al.*, 2016b; Massot *et al.*, 2017), les variations géographiques des dates de parturition n'étaient pas déterminées par les conditions thermiques locales au sein des populations. Nous interprétons cette absence de corrélation entre les températures environnementales et les dates de parturition des femelles comme une potentielle conséquence de la vague de chaleur exceptionnelle survenue au cours de l'année d'échantillonnage (juin 2022). Cette vague de chaleur, caractérisée par des anomalies de température de +3-4°C au-dessus des moyennes saisonnières et un excès d'insolation, a potentiellement augmenté les possibilités de thermorégulation, même dans les populations habituellement plus froides, ce qui a réduit des différences phénologiques entre les populations. D'autre part, les profils thermiques diurnes et nocturnes opposés dans certaines populations échantillonnées (chaudes la journée mais fraîches la nuit) peuvent aussi avoir contribué à réduire les différences de températures moyennées sur la journée.

1.2 Déterminants individuels des dates de parturition

Puisque plusieurs études sur les squamates faisaient état de variations interindividuelles significatives dans les périodes de reproduction (e.g., Olsson & Shine, 1997; Wapstra *et al.*, 2010; Cunningham *et al.*, 2020), nous avons caractérisé les facteurs individuels sous-tendant les variations interindividuelles des dates de parturition en milieu naturel (**Article 2**).

Conformément à des travaux précédents sur les lézards, nous mettons en évidence que la taille corporelle est un déterminant important des dates de parturition (Bauwens & Verheyen, 1985; Olsson & Shine, 1997; Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016b; Hall *et al.*, 2018). Les femelles de grande taille présentent des dates de reproduction plus précoces que les femelles plus petites. Bien que nos travaux ne fournissent pas d'explications mécanistiques aux différences phénologiques induites par la taille, nous avons émis trois hypothèses non exclusives : (1) la taille corporelle peut influencer la capacité de rétention de chaleur des femelles, (2) les femelles plus grandes et plus âgées peuvent être plus compétitives (e.g., lors des accouplements, pour acquérir des ressources nutritives ou pour avoir accès à des sites de thermorégulation optimaux), et (3) les dates de reproduction retardées chez les femelles plus petites peuvent être le résultat de compromis entre l'allocation des ressources vers la reproduction et vers la croissance. Nous mettons également en évidence que les différences phénologiques induites par la taille dépendent du climat et qu'elles sont réduites lorsque les températures maximales quotidiennes durant la période d'activité post-hivernale sont plus élevées.

De plus, la décomposition de la variance des dates de parturition dans l'**Article 2** nous a permis de déterminer que les dates de parturition relatives à l'année de reproduction étaient répétables ($r = 0.31$ [CI: 0.22 - 0.39]) et qu'environ la moitié de la

cohérence interindividuelle des dates de parturition était liée à des facteurs non héréditaires autres que la taille corporelle. D'une part, les différences interindividuelles dans le calendrier de reproduction pourraient être liées à des variations de l'état énergétique des femelles reproductrices. Par exemple, la condition corporelle est connue pour influencer le moment de la reproduction chez les oiseaux (Rowe *et al.*, 1994; Verhulst & Nilsson, 2008; Hennin *et al.*, 2016). Puisque les femelles utilisent les ressources stockées ou récemment acquises durant la reproduction pour alimenter l'effort reproducteur chez le lézard vivipare (Bleu *et al.*, 2013), les femelles en meilleure condition ou plus à même d'acquérir des ressources énergétiques avant la reproduction pourraient se reproduire plus tôt. En ce sens, nous montrons dans l'**Article 4** que les dates d'ovulation (qui marquent le début de la gestation et qui sont fortement corrélées à la date de parturition) sont négativement corrélées à la condition corporelle des femelles au début du cycle reproductif. En outre, des différences interindividuelles dans les stratégies thermorégulatrices (par exemple, la préférence thermique des femelles durant la gestation) ainsi que des différences de qualité du domaine vital des femelles (par exemple, les conditions microclimatiques, la disponibilité des sites de thermorégulation et la disponibilité de la nourriture) pourraient expliquer une part importante de la cohérence individuelle de la date de parturition (Wapstra *et al.*, 2010; Struelens *et al.*, 2018; Greiser *et al.*, 2022; Shutt *et al.*, 2022). Les données sur les comportements de thermorégulation au cours de la gestation collectées lors de l'expérimentation 5 pourraient nous permettre de déterminer dans quelle mesure les stratégies thermorégulatrices des femelles gestantes influencent la date de parturition. De plus, une étude plus fine des effets de la qualité thermique du domaine vital sur la phénologie individuelle serait envisageable via l'utilisation de photographie aérienne à haute résolution spatiale, une cartographie des types de

microhabitats (e.g., herbe, callune, roche, bois) et des données thermiques propres à chaque type de microhabitat. Ces données sont disponibles dans notre population d'étude (ROB – **Article 2**) mais n'ont pas pu être exploitées par manque de temps.

Principaux déterminants des dates de parturition *in natura*

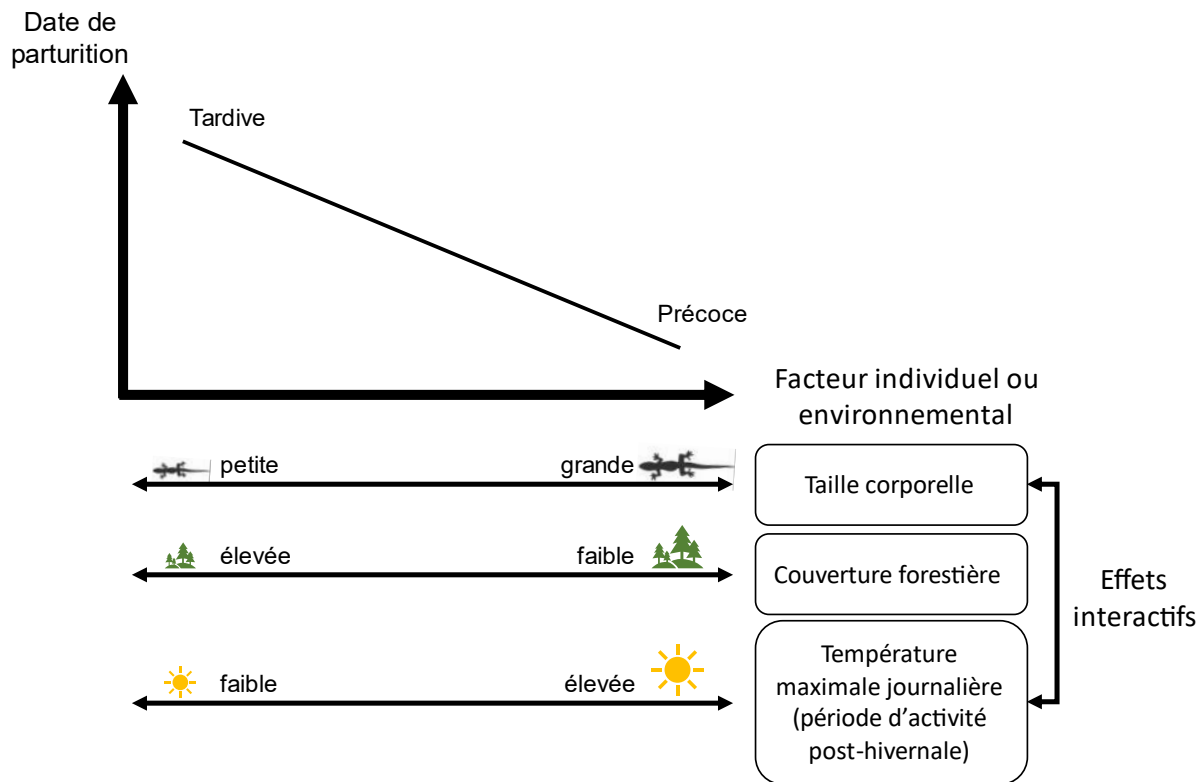


Figure 14 : Principaux déterminants des dates de parturition dans les populations naturelles de lézard vivipare (*Zootoca vivipara*) échantillonnées dans le Massif central.

2. Sélection naturelle sur les dates de parturition

2.1 Forme et fluctuation temporelle de la sélection naturelle

Nos résultats mettent en évidence l'existence d'une sélection directionnelle vers des dates de parturition précoces sans date de parturition optimale apparente. En effet, notre étude de la sélection sur les dates de parturition en milieu naturel (**Article 2**) ainsi que notre manipulation expérimentale des dates de parturition (**Article 3**)

démontrent que les femelles avec des dates de parturition précoces produisent plus de jeunes viables. Ces résultats confortent donc l'existence d'une sélection directionnelle négative sur les dates de reproduction déjà suggérée par des travaux sur d'autres lézards ovipares ou vivipares (Olsson & Shine, 1997; Mitchell *et al.*, 2018). De plus, la force de la sélection sur les dates de parturition estimée via le nombre de jeunes viables produits est constante en milieu naturel (**Article 2**).

La théorie du « match-mismatch » (Cushing, 1990) postule que les individus reproducteurs devraient faire correspondre la phase de leur cycle reproductif la plus coûteuse en énergie (e.g., l'élevage des jeunes chez les oiseaux) avec le pic de disponibilité des proies dans l'environnement afin de maximiser le succès reproducteur (Figure 15). Bien que ce cadre théorique ne soit pas toujours soutenu dans les études de terrain (Kharouba & Wolkovich, 2023), on constate généralement chez les oiseaux et les mammifères une sélection non linéaire sur la date de reproduction caractérisée par l'existence d'une date de ponte ou de parturition optimale correspondant plus ou moins au pic de disponibilité des ressources alimentaires (de Villemereuil *et al.*, 2020). Des études plus poussées chez les oiseaux insectivores mettent également en évidence une fluctuation temporelle de l'intensité de la sélection sur la phénologie de la reproduction (Gienapp *et al.*, 2014; de Villemereuil *et al.*, 2020). Par exemple, une inadéquation entre la phénologie reproductive des mésanges bleue (*Cyanistes caeruleus*) ou charbonnière (*Parus major*) et la phénologie de leurs proies pendant la reproduction (des chenilles) peut accentuer la sélection s'opérant sur la date de reproduction (Van Noordwijk *et al.*, 1995; Visser *et al.*, 1998; Charmantier *et al.*, 2008; Husby *et al.*, 2011; Reed *et al.*, 2013; Jantzen & Visser, 2023).

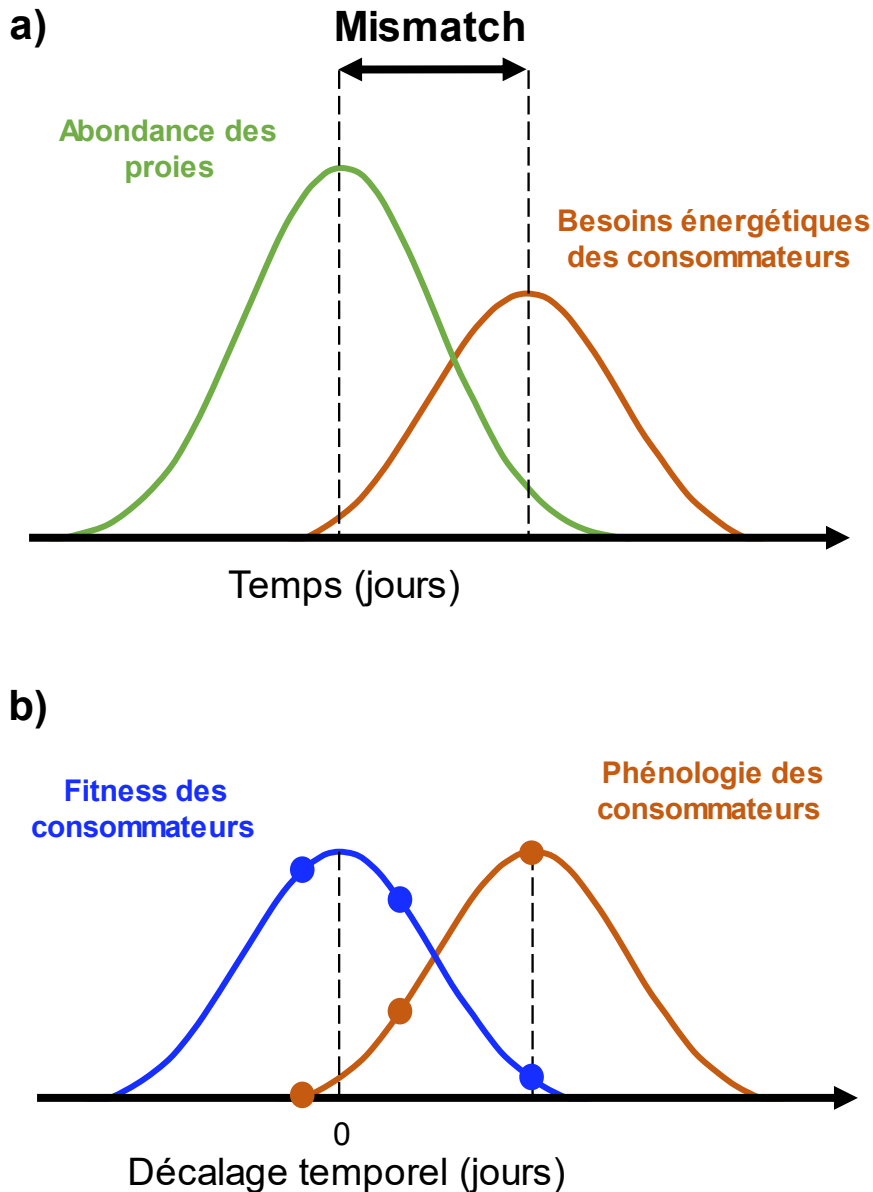


Figure 15 : Cadre conceptuel de l'hypothèse du « match – mismatch ». Les courbes marron représentent les demandes énergétiques (a) ou la phénologie (b) des consommateurs et la courbe verte représente l'abondance des proies. (b) La courbe bleue représente la relation entre la fitness et le décalage temporel entre l'abondance maximale des proies et la phénologie des consommateurs. Un « match » se produit lorsque la demande énergétique maximale du consommateur (ou de la population) se produit au même moment que la disponibilité maximale des ressources (i.e., décalage temporel égal à 0). (a) Un mismatch se produit lorsque le moment du cycle annuel où les besoins énergétiques du consommateur (ou de la population) sont les plus élevés ne correspond pas à la période où l'abondance des ressources est maximale. (b) Un décalage temporel entre la phénologie (i.e., date où les besoins énergétiques sont maximaux) du consommateur (points) ou de la population (ligne pointillée) entraînera une diminution de la fitness et une sélection en faveur d'une phénologie plus précoce (comme illustré ici) ou plus tardive. Modifié d'après Visser & Gienapp, 2019.

À notre connaissance, la théorie du « match-mismatch » n'a jamais été testée chez les reptiles squamates comme chez les oiseaux et nous avons peu de connaissances sur la fluctuation saisonnière des ressources alimentaires chez les reptiles insectivores (Hall *et al.*, 2018). Néanmoins, la sélection directionnelle sur les dates de parturition ou de ponte chez les lézards ainsi que l'absence de fluctuation temporelle du gradient de sélection que nous avons mis en évidence dans l'**Article 2** semblent suggérer que ce cadre théorique ne soit pas applicable au lézard vivipare et potentiellement à d'autres espèces de squamates. Premièrement, l'investissement reproductif chez les reptiles vivipares s'effectue sur une période relativement longue durant la vitellogenèse (où les ressources acquises sont dirigées vers la formation des œufs) et la gestation (où les ressources énergétiques permettent de soutenir les dépenses métaboliques liées à la croissance embryonnaire) ce qui pourrait remettre en question l'existence d'une période courte et critique durant laquelle l'adéquation du cycle reproductif avec la phénologie des proies influence fortement le succès reproducteur. Deuxièmement, le lézard vivipare présente un régime alimentaire varié (insectes, arachnides, annélides, crustacés (Avery, 1966)) ce qui pourrait lui permettre de s'adapter aux ressources disponibles au cours de la saison de reproduction. Enfin, les décalages phénologiques entre les arthropodes et les reptiles sont probablement moins importants que dans des systèmes proies-prédateurs impliquant des proies ectothermes et un prédateur endotherme (e.g., modèle chenille-mésange) compte tenu de la sensibilité thermique du métabolisme plus proche entre les reptiles insectivores et leurs proies (Gillooly *et al.*, 2001) qu'entre les oiseaux et leurs proies.

Afin de compléter nos analyses de la sélection en milieu naturel, il serait intéressant de quantifier la forme, l'intensité et les fluctuations temporelles de la sélection sur une autre composante de la fitness comme le recrutement des juvéniles.

En général, des dates de ponte précoces favorisent les juvéniles en termes de croissance, de survie et de recrutement (**Article 3** ; Le Galliard *et al.*, 2010; Uller & Olsson, 2010; Wapstra *et al.*, 2010; Le Henanff *et al.*, 2013; Li *et al.*, 2018; Pearson & Warner, 2018) car une date de naissance précoce est associée à une période de croissance préhivernale plus longue, des températures généralement plus chaudes et une compétition plus faible. Néanmoins, la forme de la sélection n'a généralement pas été explicitement testée et les effets d'une date de naissance précoce sur la survie sont variables (effet positif d'une date de naissance précoce: **Article 3**; Olsson & Shine, 1997; Wapstra *et al.*, 2010; Le Henanff *et al.*, 2013 ou absence d'effet sur la survie : Uller & Olsson, 2010; Sun *et al.*, 2018). En l'état actuel de nos connaissances, nous nous attendons à une sélection directionnelle négative où les dates de naissance précoces augmentent le recrutement des juvéniles. L'intensité de la sélection pourrait fluctuer en fonction de la longueur de la période d'activité préhivernale (i.e., la période entre la date de parturition moyenne de la population et le début de la brumation (i.e., léthargie hivernale)) et des conditions météorologiques. Plus spécifiquement, les avantages à naître tôt pourraient être accrus lors des années où la phénologie moyenne des femelles est tardive ou lorsque les conditions climatiques sont défavorables (e.g., températures plus faibles, plus fortes précipitations). Une hypothèse alternative serait l'existence d'une sélection non linéaire avec une date de naissance optimale pour les jeunes si les conditions environnementales (e.g., température, nourriture) sont défavorables en début et en fin de saison de reproduction.

2.2 Mécanismes sous-jacents au déclin saisonnier du succès reproductif

Deux hypothèses non exclusives pourraient expliquer la sélection directionnelle négative sur les dates de parturition. D'une part, le déclin saisonnier du nombre de

jeunes viables produit par les femelles pourrait être dû à une modification saisonnière des conditions environnementales affectant négativement les femelles se reproduisant plus tardivement (« hypothèse de la date »; Hatchwell, 1991; Moreno, 1998). Deuxièmement, le déclin saisonnier du nombre de jeunes viables pourrait aussi être lié à des différences de qualité parentale entre les reproducteurs précoces et tardifs (« hypothèse de qualité », (Hatchwell, 1991; Brinkhof *et al.*, 1993)). L'implication de ces hypothèses au déclin saisonnier du succès reproducteur a reçu peu d'attention chez les squamates comparativement aux oiseaux (Verhulst & Nilsson, 2008). Nos travaux ne permettent pas de séparer clairement la contribution de ces deux hypothèses, mais elles sont probablement toutes deux impliquées dans le déclin saisonnier du succès reproductif des femelles. La sélection constante vers des dates de parturition précoce (**Article 2**) pourrait indiquer une contribution importante des effets de la date en soi (hypothèse de la date). Au contraire, nous montrons dans l'**Article 4** une corrélation négative entre la date d'ovulation des femelles et le nombre de jeunes viables produits malgré la forte modification des dates de parturition induite par nos traitements thermiques nocturnes ce qui soutient l'hypothèse de la qualité. De futures études devraient tenter de mieux comprendre les effets de la qualité et de la date en soi sur la fitness des femelles.

2.3 Changements phénologiques et mécanismes sous-jacents

Plusieurs études chez les reptiles ont mis en évidence des avancées phénologiques significatives des dates d'émergence ou de reproduction (Ovaskainen *et al.*, 2013; Rugiero *et al.*, 2013; Massot *et al.*, 2017; Prodon *et al.*, 2017, 2020). Dans l'**Article 2**, nous ne mettons pas en évidence d'avancée phénologique entre 1989 et 2019 malgré l'augmentation des températures journalières maximales au mois de mai-juin (le paramètre thermique le plus influent sur les dates de parturition) sur notre site d'étude.

Nos résultats vont à l'encontre d'une étude précédente qui estimait une avancée moyenne des dates de parturition de 8.1 jours par décennie dans des populations naturelles de lézard vivipare incluant notre site d'étude entre 1989 et 2001 (Massot *et al.*, 2017). Nos résultats divergents pourraient être liés à des changements non linéaires du climat et des dates de reproduction sur notre période d'étude. Par exemple, des études mettent en évidence une pause dans l'augmentation des températures moyennes en Eurasie entre 1998 et 2012 (Li *et al.*, 2015) ainsi qu'une stabilisation voir une inversion de la tendance à l'avancement des dates d'émergence chez des amphibiens et des reptiles méditerranéens pendant cette période (Prodon *et al.*, 2017). Nos estimations des tendances phénologiques des dates de parturition pourraient également être biaisées à cause d'événements climatiques extrêmes (e.g., vagues de chaleur durant l'été 2003, 2005 et 2006) et des changements de conditions d'élevage qui ont eu lieu au cours du suivi longitudinal.

Les changements phénologiques observés chez les reptiles au cours des dernières décennies peuvent être liés à deux mécanismes non exclusifs : (1) la plasticité phénotypique (i.e., propriété des génotypes individuels à produire des phénotypes différents lorsqu'ils sont exposés à des conditions environnementales différentes (Pigliucci *et al.*, 2006)) qui permet généralement une réponse rapide aux changements environnementaux et (2) la microévolution (i.e., changement des fréquences alléliques au cours des générations au sein d'une ou de plusieurs populations reliées par un flux de gènes (Nunes *et al.*, 2013)) qui nécessite une variation génétique additive du trait phénologique conférant un avantage sélectif. La contribution de ces deux mécanismes aux modifications des dates de reproduction chez les animaux a surtout été étudiée chez les oiseaux et les mammifères pour lesquels les changements phénologiques semblent être davantage liés à des réponses

plastiques plutôt que des réponses évolutives (Gienapp *et al.*, 2008; Boutin & Lane, 2014; Charmantier & Gienapp, 2014; Biquet *et al.*, 2022). Chez les reptiles, on suppose que les changements des événements phénologiques sont principalement dus à la plasticité phénotypique compte tenu de la plasticité thermique de leur cycle reproductif, mais nous avons peu de connaissance sur l'héritabilité des traits phénologiques (Urban *et al.*, 2014).

Alors que plusieurs études chez les squamates suggéraient que les dates de la reproduction étaient répétables (Wapstra *et al.*, 2010; Cunningham *et al.*, 2020), un des apports majeurs de l'**Article 2** est une première estimation de l'héritabilité des dates de parturition chez une espèce squamate en milieu naturel (Urban *et al.*, 2014). Nous montrons que les dates de parturition relatives (i.e., la propension d'une femelle à mettre bas précocement ou tardivement par rapport aux autres femelles de la population pendant une année donnée) sont faiblement héritables ($h^2=15\%$ [CI: 0.09 - 33]) chez le lézard vivipare. L'héritabilité de la date de parturition relative chez cette espèce est du même ordre de grandeur que l'héritabilité de la date de ponte ou de parturition généralement observée chez des oiseaux et des mammifères ($h^2 = 13$ à 19% ; (Clements *et al.*, 2011; Charmantier & Gienapp, 2014)) voir légèrement plus faible compte tenu de nos méthodes de calculs de l'héritabilité de la date de parturition relative (et non absolue comme généralement estimée chez les oiseaux et les mammifères). Elle est cependant plus élevée que l'héritabilité de la date de nidification estimée chez une espèce de tortue ($h^2= 0\%$, McGaugh *et al.*, 2009). Ainsi, bien que les dates de parturition soient soumises à la sélection, nos analyses suggèrent (1) une capacité existante, mais limitée, du lézard vivipare de répondre à la sélection, (2) que l'avancement des dates de parturition mis en évidence par une étude précédente chez le lézard vivipare semble être majoritairement le résultat de la plasticité phénotypique

(Massot *et al.*, 2017) et (3) que les conséquences des changements phénologiques induits par les changements climatiques devraient donc dépendre des limites et des conséquences de la plasticité thermique des dates de reproduction sur les individus reproducteurs et leur progéniture.

3. Coûts et bénéfices de la plasticité thermique de la gestation

3.1 L'accélération thermique de la gestation et la restriction nutritive altèrent l'homéostasie maternelle

Chez les reptiles vivipares, la gestation est une période critique pour les femelles compte tenu de l'augmentation des taux métaboliques et des dépenses énergétiques causée par le développement embryonnaire (Foucart *et al.*, 2014). Nos travaux expérimentaux (**Articles 3 et 4**) montrent que des dates de parturition précoces, l'accélération thermique de la gestation causée par le réchauffement nocturne, et une faible disponibilité des proies durant la gestation entraînent une augmentation des coûts énergétiques immédiats de la reproduction et des altérations physiologiques pour les femelles gestantes.

Les femelles qui mettaient bas précocement, qui étaient exposées à des températures nocturnes élevées pendant la gestation ou qui étaient restreintes en nourriture présentaient une condition corporelle, musculaire et des réserves lipidiques caudales plus faibles après la reproduction. Nous avons également mis en évidence des effets interactifs des températures nocturnes et de la disponibilité de la nourriture sur le catabolisme musculaire qui permet de répondre aux besoins en énergie et en acides aminés lorsque les apports alimentaires sont insuffisants ou lorsque la dépense énergétique est élevée (Brusch *et al.*, 2020; Bodineau *et al.*, 2024 (**Article 5**)). En effet,

une faible disponibilité des proies durant la gestation a accentué les effets négatifs du réchauffement nocturne sur la condition musculaire des femelles (**Article 4**). Le réchauffement nocturne durant la gestation a également entraîné des changements physiologiques majeurs chez les femelles reproductrices. L'exposition à des températures nocturnes élevées diminuait l'immunocompétence des femelles comme constaté chez d'autres espèces de reptiles (Butler *et al.*, 2013; Sacchi *et al.*, 2017; Stahlschmidt *et al.*, 2017b) ainsi que les niveaux de corticostérone basaux (i.e., l'hormone glucocorticoïde majoritaire chez les reptiles) que nous interprétons comme un mécanisme de conservation d'énergie en réponse à l'exposition chronique à des températures élevées (Dupoué *et al.*, 2018). En revanche, bien que les températures environnementales puissent moduler l'équilibre oxydatif (c'est-à-dire les dommages oxydatifs et la capacité antioxydante) chez les reptiles (Dupoué *et al.*, 2020b; Han *et al.*, 2020b), nous n'avons pas mis en évidence d'effet des températures nocturnes sur l'équilibre oxydatif des femelles gestantes conformément à des études précédentes chez le lézard vivipare (Brusch *et al.*, 2020; Rutschmann *et al.*, 2021). Malgré les effets négatifs des dates de parturition précoces et des températures nocturnes plus chaudes sur la condition énergétique et l'immunocompétence des femelles, nous n'avons pas constaté d'effets différés de la date de parturition ou des conditions thermiques durant la gestation sur la survie pré- ou post-hivernale des femelles adultes (**Articles 3 et 4**).

En milieu naturel, nous n'avons cependant pas détecté d'effets des conditions thermiques locales sur la condition corporelle post-partum des femelles gestantes (**Article 1**). Ceci suggère que les coûts énergétiques d'une exposition chronique à des conditions thermiques diurnes ou nocturnes plus chaudes pourraient être plus facilement tamponnés en milieu naturel via la sélection de microhabitats, l'utilisation

de refuges et de terrier souterrains ou l'augmentation de la prise alimentaire si les ressources nutritives sont suffisamment abondantes (Moore *et al.*, 2018; Huey & Kingsolver, 2019). En revanche, les femelles des populations exposées à des températures journalières maximales ou nocturnes plus élevées présentaient une longueur relative des télomères plus faible. Ces résultats s'ajoutent à une série d'études corrélatives et expérimentales ayant mis en évidence un lien entre les conditions thermiques environnementales et la dynamique des télomères chez les ectothermes (e.g., Debes *et al.*, 2016; Dupoué *et al.*, 2017; Olsson *et al.*, 2018; Axelsson *et al.*, 2020; Friesen *et al.*, 2022; Zhang *et al.*, 2023a). Nos travaux suggèrent que des conditions thermiques diurnes et nocturnes plus chaudes peuvent entraîner une diminution de la longueur des télomères chez les femelles lézard vivipare (Burraco *et al.*, 2020). Deux hypothèses non exclusives peuvent expliquer la covariation apparente entre la longueur des télomères des femelles et les conditions thermiques locales. D'une part, cette relation peut refléter les effets des conditions thermiques annuelles vécues par les femelles au cours de la reproduction. Par exemple, une exposition expérimentale à une vague de chaleur aigüe (une semaine) réduit la longueur relative des télomères chez une espèce d'agame désertique (Zhang *et al.*, 2018) et on observe des ajustements saisonniers de la longueur des télomères chez le lézard agile (Axelsson *et al.*, 2020). D'autre part, cette relation peut refléter des effets transgénérationnels des conditions thermiques via une accumulation du raccourcissement télomérique au cours des générations si la longueur des télomères est héritée des parents (« hypothèse de la boucle du vieillissement » développée chez le lézard vivipare (Dupoué *et al.*, 2022)).

3.2 Effet des conditions thermiques, des dates de parturition et de la restriction nutritive sur les traits reproductifs et la progéniture

Au travers des **Articles 3 et 4**, nous avons déterminé dans quelle mesure les conditions thermiques, la date de parturition et la disponibilité des proies durant la gestation influencent les traits reproductifs et les traits phénotypiques des juvéniles à la naissance. Le réchauffement nocturne et la restriction alimentaire durant la gestation ont additivement influencé l'investissement reproductif et la viabilité de la portée sans affecter la fécondité (i.e., la taille de la portée) qui est déterminée au début du cycle reproductif lors de la vitellogenèse (Bauwens & Verheyen, 1985). Conformément à des études précédentes chez des lézards vivipares (Wang *et al.*, 2017; Bruschi *et al.*, 2023), l'augmentation des dépenses énergétiques sous des températures nocturnes élevées ainsi qu'une faible disponibilité des proies a réduit l'investissement reproductif et le nombre de jeunes viables à la naissance. Les températures nocturnes ont eu des effets non linéaires sur la viabilité des portées, de sorte qu'un réchauffement nocturne modéré a augmenté la viabilité des portées, conformément au schéma général d'une courbe concave entre la viabilité de la progéniture et les températures de développement chez les reptiles squamates (Noble *et al.*, 2018). En milieu naturel, nous retrouvons également une diminution du nombre de juvéniles viables produit par les femelles issues des populations exposées à des nuits plus chaudes (**Article 1**). Enfin, nous mettons en évidence un effet positif des dates de parturition précoce sur le nombre de jeunes viables produit dans l'**Article 3**.

Concernant la progéniture, nous n'avons pas mis en évidence d'effets des conditions thermiques développementales en soi sur la taille et la condition corporelle des juvéniles à la naissance (**Articles 3 et 4**), mais les juvéniles nés tôt étaient plus grands que les juvéniles nés plus tardivement ce qui conforte les résultats d'études précédentes rapportant des effets positifs d'une date d'éclosion plus précoce sur la

taille corporelle des juvéniles (Olsson & Shine, 1997; Wapstra *et al.*, 2010; Sun *et al.*, 2018). Les effets de la date de parturition sur la taille des juvéniles à la naissance peuvent résulter des effets maternels liés à la quantité d'énergie allouée à la production de vitellus ou à des comportements maternels de thermorégulation, conformément à l'hypothèse de la qualité (Olsson & Shine, 1997). Dans l'**Article 4**, les juvéniles issus des femelles exposées à des nuits chaudes présentaient une endurance plus importante à la naissance. Les effets des conditions thermiques développementales sur la fitness de la progéniture peuvent être liés aux effets des températures développementales en soi (i.e., hypothèse thermique présentée dans l'**Article 3**) sur les processus d'allocation du jaune vers la croissance somatique ou la maintenance (Shine & Harlow, 1993; Wapstra, 2000) et sur le développement des fonctions neuromusculaires lors du développement embryonnaire (While *et al.*, 2009; Booth, 2017). Néanmoins, les effets des températures développementales sur les performances de la progéniture varient souvent en ampleur et en direction entre les espèces et les mécanismes sous-jacents sont encore mal compris (Booth, 2006; Noble *et al.*, 2018; While *et al.*, 2018).

Enfin, la restriction alimentaire durant la gestation entraînait la production de juvéniles moins corpulents à la naissance sans affecter leur croissance préhivernale ou leur survie. Les effets de la restriction nutritive sur la corpulence des juvéniles sont probablement liés aux effets du manque de nourriture sur la physiologie ou les comportements maternels compte tenu de l'absence d'échanges nutritifs entre la mère et les embryons chez le lézard vivipare (Stewart *et al.*, 2004).

3.3 Effets bénéfiques d'une date de naissance précoce sur les traits d'histoire de vie des juvéniles

Nous mettons en évidence dans l'**Article 3** que les traits d'histoire de vie des juvéniles sont principalement déterminés par la date de parturition en soi, plutôt que par des effets persistants des conditions thermiques développementales sur la qualité de progéniture produite (i.e., hypothèse thermique présentée dans l'**Article 3**), ce qui conforte les résultats d'une étude précédente chez un lézard ovipare (Sun *et al.*, 2018). Les juvéniles nés tôt présentent une survie, des taux de croissance et une probabilité de se reproduire à l'âge d'un an plus importante. Les effets dominants de la date de naissance par rapport aux effets des conditions thermiques développementales en soi sont également soutenus par l'**Article 4** où l'accélération thermique de la gestation induite par le réchauffement nocturne entraîne des dates de naissance plus précoces qui favorisent la croissance de la progéniture sans toutefois influencer leur taux de croissance et de survie. Puisque la phénologie initiale des femelles a été largement modifiée par nos traitements thermiques nocturnes (**Article 4**; Figure 1), nous faisons l'hypothèse que les effets de la date de naissance sur les traits d'histoire de vie des juvéniles sont majoritairement liés à des mécanismes postnataux liés aux changements saisonniers des conditions climatiques, de la disponibilité de la nourriture et de la compétition entre conspécifique (hypothèse de la date) plutôt qu'à des mécanismes prénataux liés à la covariation entre la date de parturition et la qualité des femelles (hypothèse de la qualité). Indépendamment des mécanismes impliqués, des dates de parturition plus précoces ont des effets bénéfiques sur les juvéniles durant les premiers mois de vie chez le lézard vivipare.

3.4 Conflit mère-progéniture concernant l'optimisation de la date de parturition

Dans l'ensemble, nos approches expérimentales ont permis de mettre en évidence un compromis entre les femelles et leur progéniture concernant l'optimisation des dates de parturition et la plasticité thermique de la gestation. Alors que des dates de parturition précoces et une accélération thermique de la gestation altèrent l'homéostasie maternelle probablement via la réduction de l'étalement de l'effort reproducteur, elle confère à la progéniture des avantages évidents en termes de croissance voir de survie et de recrutement chez le lézard vivipare. Des études complémentaires seront nécessaires afin de comprendre si les avantages à naître tôt ne sont pas contrecarrés par des coûts futurs causés par les effets d'une croissance accrue au début de la vie et d'un âge de reproduction plus précoce sur la longévité (Massot *et al.*, 2011; Bestion *et al.*, 2015; Burraco *et al.*, 2020). De plus, étendre l'étude de la balance coût-bénéfice de la plasticité thermique de la phénologie de la reproduction aux squamates ovipares permettrait de mieux comprendre et de prédire les conséquences des changements phénologiques chez les squamates. Chez les espèces ovipares, les coûts de l'accélération thermique de la phénologie de la reproduction pourraient diminuer pour les femelles qui ne subissent pas les coûts reproductifs imposés par le développement embryonnaire in utero (Foucart *et al.*, 2014). Au contraire, les conditions thermiques développementales pourraient avoir des effets importants sur la progéniture (Noble *et al.*, 2018) car elles ne sont pas tamponnées par les effets maternels durant le développement embryonnaire (e.g., comportement thermorégulateur (Beltrán *et al.*, 2021)).

4. Réponses comportementales, physiologiques et importance de l'habitat dans l'atténuation des effets des changements climatiques

Alors que nos approches expérimentales en laboratoire nous ont permis de mieux comprendre les liens de cause à effet entre les conditions thermiques, la phénologie et leurs conséquences intra- et intergénérationnelles, un des objectifs de cette thèse était d'évaluer la variation géographique des traits fonctionnels ainsi que les facteurs environnementaux responsables de ces variations en milieu naturel. Nos analyses mettent en évidence que des traits physiologiques et comportementaux liés à la régulation de l'équilibre thermique, hydrique et énergétique covariaient avec les conditions climatiques diurnes et nocturnes locales (**Article 1**). Les femelles provenant des populations exposées à des températures nocturnes plus élevées présentaient des pertes hydriques totales évaporatives et une tendance à un mélanisme dorsal plus faible. De plus, les femelles provenant des populations exposées à des températures journalières maximales plus élevées présentaient des préférences thermiques plus faibles. Ces ajustements physiologiques et comportementaux pourraient constituer des stratégies de thermo-hydrorégulation efficaces pour tamponner les contraintes thermiques, hydriques et énergétiques imposées par un environnement plus chaud.

La couverture forestière contribuait de manière importante la variation géographique des traits phénotypiques et reproductifs des femelles le long du gradient environnemental (**Article 1**). Au contraire, la disponibilité de l'eau dans l'habitat n'était pas le paramètre environnemental le plus soutenu pour expliquer la variation des traits phénotypiques et reproductifs. Les femelles issues des populations avec une couverture forestière importante présentaient une longueur relative des télomères plus élevée, un investissement reproductif plus important et présentaient en meilleure

condition corporelle au moment de la capture et après la parturition. D'une part, la couverture forestière peut fortement tamponner les effets des conditions macroclimatiques stressantes (e.g., forte chaleur, sécheresse) sur les ectothermes en générant des microclimats thermiques et hydriques hétérogènes et favorables à la thermo-hydrorégulation (Scheffers *et al.*, 2014; Woods *et al.*, 2015; Pincebourde *et al.*, 2016; Sears *et al.*, 2016; Stark *et al.*, 2023). D'autre part, la structure de la végétation peut influencer l'abondance des proies (e.g., araignées: Uetz, 1979; insectes: Lassau *et al.*, 2005) et expliquer la covariation apparente entre la couverture forestière, la longueur relative des télomères (e.g., McLennan *et al.*, 2022), la condition corporelle et l'investissement reproductif des femelles (**Article 4**; Wang *et al.*, 2017). Alors que les activités anthropiques (e.g., exploitation forestière) et les changements climatiques peuvent directement impacter la structure de la végétation (Dale *et al.*, 2001; Sun *et al.*, 2022), notre étude appelle à une meilleure prise en compte de l'hétérogénéité de l'habitat dans les politiques de conservation des ectothermes et de restauration des espaces naturels (Kearney *et al.*, 2009; Neel & McBrayer, 2018; Nowakowski *et al.*, 2018; Stark *et al.*, 2023).

Notre étude ne permet pas de déterminer si ces ajustements physiologiques et comportementaux reflètent des changements plastiques ou une différenciation génétique entre les populations en réponse à l'adaptation locale aux conditions environnementales (Bradshaw & Holzapfel, 2006). Néanmoins, l'expérience de jardin commun (**Expérience 6**) nous permettra de mieux comprendre dans quelle mesure la variation géographique des traits liés à la thermo-hydrorégulation est d'origine plastique ou génétique.

Conclusion

Cette thèse avait pour objectif d'étudier les effets du climat et de la phénologie sur les traits physiologiques, comportementaux, reproductifs et les traits d'histoire de vie d'un ectotherme vivipare. La diversité des études menées et des approches utilisées au cours de cette thèse a permis de mieux décrire les variations spatiales, temporelles et interindividuelles des dates de parturition ainsi que leurs conséquences sur les femelles reproductrices et la progéniture. En milieu naturel, les dates de parturition étaient fortement plastiques et principalement déterminées par la taille corporelle, les températures maximales journalières au cours de la période d'activité post-hivernale ainsi que par la couverture forestière. Nous avons également estimé pour la première fois l'héritabilité des dates de parturition chez un squamate en milieu naturel. La faible héritabilité des dates de parturition suggère que les conséquences des changements phénologiques induits par les changements climatiques dépendront des limites et de la balance coûts-bénéfices de la plasticité thermique des dates de reproduction. Enfin, nos études expérimentales ont permis de mettre en évidence que l'accélération thermique de la gestation par le réchauffement diurne et nocturne augmente les coûts reproductifs immédiats pour les femelles, mais a des effets positifs sur les traits d'histoire de vie des juvéniles via une date de naissance plus précoce. Nos résultats appellent à une meilleure prise en compte du réchauffement nocturne, de la structure de l'habitat et des conséquences des modifications phénologiques afin de mieux comprendre et prédire les effets des changements climatiques sur les ectothermes terrestres.

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ANNEXE



Mâle adulte *Zootoca vivipara* en position de thermorégulation. © Arnaud Badiane

Article 5

Microhabitat humidity rather than food availability drives thermo-hydroregulation responses to drought in a lizard

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The regulation of energy, water and thermal balance involves integrated processes that should drive ecological responses of ectotherms to climate change. Functional tradeoffs between thermoregulation and hydroregulation are exacerbated during hot or dry spells, but how microhabitat hydric properties and trophic resource availability influence these tradeoffs remains unknown. Here, we investigated the effects of microhabitat humidity and food availability on thermo-hydroregulation strategies in the ground-dwelling common lizard *Zootoca vivipara* during a simulated hot and dry spell event. We exposed lizards to a five-day long acute water restriction in hot conditions in the laboratory and manipulated hydric quality of the retreat site (wet or dry shelter) as well as food availability (ad libitum food or food deprivation). Water restriction and food deprivation caused physiological responses such as muscle catabolism and mobilization of caudal energy reserves. Lizards also developed behavioural strategies to conserve water or energy via decreased thermoregulation effort, higher shelter use and increased eye closure behaviours through time. These physiological and behavioural changes were importantly buffered by the presence of a wet shelter but not by food availability. A wet retreat site reduced the behavioural conflicts between thermoregulation and hydroregulation, allowed lizards to maintain a better condition and reduced physiological dehydration. Instead, food intake did not play a major role in the regulation of hydration state and increased behavioural conflicts between thermoregulation and hydroregulation. A better consideration of thermo-hydroregulation behaviours and microhabitat hydric quality is required to address ectotherm responses to future climate change.

Keywords: behaviour, food, microhabitat, shelter, thermo-hydroregulation, tradeoff, water



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Introduction

Behavioural thermoregulation can mitigate the impact of climate warming in ectotherms (Kearney 2013, Gunderson and Leal 2015). Recent empirical studies and mechanistic models indicate that the behavioural capacity of ectotherms to buffer consequences of climate warming will be constrained by water availability in the environment, which may further exacerbate the deleterious effects of heat stress (Kearney et al. 2018, Sannolo and Carretero 2019, Rozen-Rechels et al. 2020a, b). A proximate conflict exists between regulation of water balance and thermoregulatory behaviours, since basking and maintenance of high body temperatures typically increase water loss rates and eventually lead to dehydration (Anderson and Andrade 2017, Dmi'El 2001). Conversely, dehydration risks can lead to water conservation strategies such as reduced activity, thermal depression, diurnal or nocturnal selection of cool and wet microhabitats or minimisation of time spent with the eyes open, which can compromise energy acquisition, body condition and survival (Davis and DeNardo 2009, Sannolo and Carretero 2019, Rozen-Rechels et al. 2020a, b, Le Galliard et al. 2021). Despite the relevance of this functional tradeoff for behavioural patterns of activity or microhabitat selection, we have limited knowledge of environmental factors that influence conflicts between thermoregulation and hydroregulation (Dezetter et al. 2023).

The availability and overall quality of microhabitats should importantly influence behavioural tradeoffs between thermoregulation and hydroregulation. In terrestrial ectotherms, wet and cold microhabitats provide thermal shelters to escape extreme surface temperatures (Beck and Jennings 2003, Moore et al. 2018). They also reduce evaporative water loss, dehydration stress and physiological alterations caused by dehydration such as muscle wasting (Dezetter et al. 2023). Yet, only few studies have quantified the effects of microhabitat quality on thermo–hydroregulation strategies during hot and dry weather event (Dezetter et al. 2023). Food resources should also influence thermo–hydroregulation strategies because investment in these behaviours should be constrained by energy intake according to the cost–benefit model of thermoregulation (Angilletta Jr. 2009, Huey and Slatkin 1976). Food intake could influence hydroregulation behaviours if it allows to recoup some of the energetic costs of hydroregulation and because food can provide dietary water, a scenario which we called the ‘food for water hypothesis’ (Chabaud et al. 2023). This hypothesis has been little tested so far in terrestrial ectotherms and some studies indicate that they are more dependent on free water rather than dietary water to regulate their water balance (Wright et al. 2013, Lillywhite 2017, Perez et al. 2021, Chabaud et al. 2023).

Here, we designed an experiment to quantify the effects of food availability and microhabitat humidity on thermo–hydroregulation strategies, as well as body condition and whole-organism energetics, during a hot and dry weather event simulated in the laboratory in the common lizard *Zootoca vivipara*. This lacertid is found in cool and moist environments and is highly sensitive to water restriction (Herczeg et al.

2003, Rozen-Rechels et al. 2020a, b). We simulated a summer drought with water restriction and manipulated food availability (ad libitum food versus no food) as well as the humidity of a surface shelter (access to a wet shelter or to a dry shelter). By manipulating the hydric quality of a surface shelter which are generally used by lizards during inactivity phases, we focused on the buffering role of surface shelters rather than on the microhabitat selection strategies that have already been studied in lizards (Pintor et al. 2016, Rozen-Rechels et al. 2020a, b). In the same time, we quantified the behavioural adjustments of the lizards as well as their body condition, plasma osmolality and energy-related plasma metabolites. We examined the following four hypotheses and predictions. First, water and food restriction should challenge homeostasis and compromise the energy and water balance of lizards. We predict a decrease in body condition in response to water restriction and food deprivation, an increase in plasma osmolality in response to water restriction and a reduction in circulating glucose and triglycerides caused by food deprivation. Second, compensatory physiological mechanisms should occur under conditions of water and food restriction. We predict muscle catabolism and mobilisation of caudal lipid reserves to release amino acids, lipids, and bound water and recoup some of the missing inputs of food and water (Brusch et al. 2018, 2020, 2023). Third, behavioural responses should mitigate water and energy constraints. We predict a decrease in selected body temperatures and an increase in shelter use in response to water and food restrictions. Frequency of water conservation behaviours such as eye closure behaviours should also increase in response to dehydration. If wet shelter reduces water losses, lizards provided with wet shelter should use it more and dehydration should be negatively correlated with the frequency of shelter use (Dezetter et al. 2023). Fourth, deleterious effects of water restriction and the behavioural tradeoff between thermoregulation and hydroregulation should be weaker when shelters are optimal (i.e. wet microclimatic conditions) and when food is available if food provides a net dietary water intake.

Material and methods

Study species and sampling

Between 21 April and 24 May 2021, we captured 60 adult male European common lizards *Zootoca vivipara* inside semi-natural populations maintained in outdoor enclosures at CEREEP-Ecotron IleDeFrance. Lizards were captured in three sequential capture sessions to generate three sequential batches of 20 lizards. Prior to experiments, we acclimated lizards for a minimum of five days in standard laboratory conditions (Rozen-Rechels et al. 2020a, b) in order to standardise habituation to laboratory conditions and food satiety.

Experimental conditions and study design

The experiment was performed in 20 neutral arenas lit automatically between 8:30 a.m. and 6:00 p.m. by a

UVB-enhanced neon tube and halogen heating bulbs in order to generate a thermal gradient (operative temperatures from hot to cold spot: $35.8^{\circ}\text{C} \pm 7.5$ SD to $22.1^{\circ}\text{C} \pm 2.5$ SD). Each arena was filled with 3 cm of peat and water-filled petri dishes to provide lizards with free-standing water. In the cold side of the arena, we installed a 'shelter' that was thermally sub-optimal for basking but had optimal hydric conditions or not depending on treatment conditions in our study (Supporting information). We manipulated both food availability (ad libitum feeding with 200 ± 20 mg of crickets per day for the control treatment or no feeding) and humidity of the shelter (access to a wet shelter for the control treatment or access to a dry shelter) in a balanced full-factorial experimental design. Each batch of 20 lizards was divided into four experimental groups formed by the factorial combination of the two treatments. The study was repeated three times independently with our three batches of lizards. During the course of the experiment (Supporting information), lizards spent seven successive days alone in the same arena including one day of acclimation (called 'day -1') when lizards were maintained under control conditions with water, ad libitum food, wet shelter, and three water sprays per day. During 'day 0', we observed lizards under the same control conditions as during the acclimation day. At the end of this first day, we removed water cups from all arenas, removed crickets for the food-deprived arenas, and replaced the wet shelter with a dry shelter for dry shelter treatment group. From day 1 to day 5, a limited amount of water was provided to the lizards at 8:30 a.m. by spraying arenas with water for five seconds. This manipulation was done to generate a chronic, sub-lethal water restriction similar to exposure to several days of warm and dry weather in natural conditions (Dupoué et al. 2020). After the last behavioural observation on day 5, all individuals were provided with water and food ad libitum.

Pre- and post-experimental measurements

At the beginning and at the end of the experiment (day -1 and day 5), lizards were bled using a standard protocol (Meylan et al. 2003) to measure plasma osmolality, circulating triglyceride and glucose levels in plasma in order to quantify metabolic changes during the experiment. Plasma osmolality (an indicator of hydration status in species lacking a salt gland which increases in dehydrated individuals) was measured using a vapour pressure osmometer and circulating triglyceride and glucose levels were measured in plasma by colorimetric assays (Triglyceride Colorimetric Assay kit and Glucose Colorimetric Assay kit, ref. 10010303 and 10009582, Cayman Chemical, USA). At the beginning (day -2) and at the end of the experiment (day 5), lizards were weighed using a precision scale and scanned using a flatbed scanner to measure tail width at the 9th sub-caudal scale row using ImageJ software (ver. 1.52v), as a proxy for tail reserves. Hind limb thickness was measured to the nearest 0.01 mm on both legs using a spessimeter (ID-C1012BS, Mitutoyo, Japan).

Behavioural measurements

We recorded body temperature, basking behaviours (increased exposure to radiation from heat bulbs or not) and the position of lizard (inside or outside the shelter) for 6 days (day 0 to day 5) with an instantaneous sampling every 30 min from 9 a.m. to 5 p.m. (i.e. 17 readings during the day). Surface body temperature was recorded using an infrared thermometer (Raytek, Raynger MX2). We then calculated body temperature T_b using a calibration curve (Supporting information). When the lizard was visible, we noted whether its eyes were open or closed. When the lizard was not visible, the roof of the shelter was slowly lifted to note the presence or not of the lizard in the shelter.

Statistical analyses

Analyses were performed with R software ver. 4.2.0 (www.r-project.org). We used mixed models to control for the fully randomised design of our experiment where we attributed different individuals from different treatments to the same arena three times (three experimental batches). We also controlled for inter-individual variability by including a random effect of individual identity. For each analysis, we built a full model, checked its assumptions and performed a goodness-of-fit test. Non-significant effects were then eliminated using a stepwise model selection procedure starting from the full model. First, we calculated intra-individual changes in body mass, in average limb thickness, in tail width, in plasma osmolality, in triglyceride and in glucose concentration by subtracting the final values measured after the experiment from the initial values measured before the experiment. To explain these morphological and physiological changes, we fitted linear mixed models (Pinheiro et al. 2012) with experimental batch, the initial centred value of the morphological or physiological trait and interactive effects of the two experimental treatments as fixed effects. For the analysis of the change in plasma osmolality, we added the individual-centred daytime shelter use rate during the experiment (calculated as the number of observations where the lizard was in the shelter divided by the total number of daytime observations during the experiment) in interaction with the shelter and food treatments as fixed effects to test the relationship between shelter use and dehydration. To study thermo-hydroregulation behaviours, we counted the number of times each day out of 17 observations where lizards exhibited basking behaviour, when they closed their eyes, and when they were inside the shelter. We analysed basking, eye closure behaviour and shelter use as success-failure events with generalised linear mixed models assuming a binomial distribution and a logit link using the *glmer* function from the 'lme4' package (Bates et al. 2014). T_b was analysed using linear mixed models. We analysed these four behavioural traits with the experimental batch and the factorial, linear or quadratic effects of time (number of days since start of the experiment) in interaction with the shelter and food treatments as fixed effects. All statistical results are reported in the Supporting information.

Table 1. Summary statistics of morphological and physiological changes in 60 males *Zootoca vivipara* from the four treatment groups (n = 15 per group). Morphological and physiological changes were calculated by subtracting the initial value measured at the beginning of the experiment from the final value measured at the end of the experiment. Shelter and food treatments had an additive effect on change in body mass ($F_{1,33} = 82.95$, $p < 0.0001$, $F_{1,33} = 69.41$, $p < 0.0001$ respectively), in limb thickness ($F_{1,37} = 18.24$, $p = 0.0001$, $F_{1,37} = 10.17$, $p = 0.003$), in tail width ($F_{1,36} = 9.96$, $p = 0.003$; $F_{1,36} = 6.39$, $p = 0.02$) and in the concentration of circulating triglycerides ($F_{1,33} = 4.61$, $p = 0.04$; $F_{1,33} = 152.5$, $p < 0.0001$). Circulating glucose concentrations were influenced by food treatment ($F_{1,33} = 14.64$, $p = 0.0005$) but not by shelter treatment ($F_{1,33} = 0.13$, $p = 0.71$). Data are provided as mean (\pm SE) for each treatment group and different letters indicate significant differences between groups ($p < 0.05$; Tukey's HSD post hoc test). Δ = intra-individual change.

Treatment groups	Wet shelter		Dry shelter	
	Food	Food deprivation	Food	Food deprivation
Variables				
Δ body mass (g)	-0.22 ± 0.05^a	-0.65 ± 0.05^b	-0.67 ± 0.05^b	-1.04 ± 0.05^c
Δ limb thickness (mm)	-0.07 ± 0.02^a	-0.14 ± 0.02^{ab}	-0.15 ± 0.02^{bc}	-0.21 ± 0.02^c
Δ tail width (mm)	-0.14 ± 0.11^a	-0.43 ± 0.11^{ab}	-0.47 ± 0.11^{ab}	-0.68 ± 0.11^b
Δ osmolality (mOsmol kg ⁻¹)	32.3 ± 9.23^a	28.5 ± 7.99^a	88.5 ± 7.71^b	84.5 ± 8.39^b
Δ [triglycerides] (mg dl ⁻¹)	256.4 ± 28.9^a	-57.2 ± 28.5^b	378.3 ± 29.7^c	-47.8 ± 29.6^b
Δ [glucose] (mg dl ⁻¹)	49.5 ± 11.0^{ab}	24.1 ± 11.0^b	71.8 ± 11.0^a	8.22 ± 11.8^b

Results

All lizards lost condition during the experiment, as manifested by a decrease of body mass, limb thickness and tail width (Table 1). Mass, limb thickness and tail width losses were additively influenced by shelter treatment and food treatment. Food restricted lizards and lizards provided with dry shelter lose more body mass, limb thickness and tail thickness than others. We also found an overall increase in plasma osmolality for all experimental groups indicating strong physiological dehydration ($+57.09$ mOsmol kg⁻¹ \pm 5.6 SE). Dehydration was influenced by the interaction between shelter use rate and shelter treatment but food treatment did not affect dehydration. On average, dehydration was greater in lizards provided with a dry shelter compared to a wet shelter. Surprisingly, dehydration was positively correlated with daily shelter use in lizards provided with a wet shelter, whereas it was not correlated in lizards provided with a dry shelter (Fig. 1B). In addition, fed lizards showed a significant increase in plasma glucose concentration relative to food-deprived lizards, and a greater increase in circulating plasma triglyceride concentration was observed in fed than food-deprived lizards and also to some extent in lizards from the dry shelter group than from the wet shelter group (Table 1).

During water restriction, daytime shelter use increased and was influenced by the interaction between time, shelter treatment and food treatment (Fig. 1A). In food-deprived animals, daytime shelter use increased similarly in dry and wet shelter treatment groups, whereas in fed lizards, daytime shelter use increased more strongly in lizards provided with a dry shelter. Average daily T_b and basking behaviours of lizards decreased through time as the number of days of water restriction increase but these behavioural changes were only influenced by the shelter treatment (Fig. 2A–D). The diminution of T_b and basking behaviours was more pronounced in lizards provided with a dry shelter. Finally, we found strong effects of shelter treatment in interaction with time on the ocular behaviour of lizards. Eye closure rate increased

remarkably more in lizards provided with a dry shelter compared to lizards with a wet shelter (Fig. 2E).

Discussion

During the experiment, all lizards showed significant increase in plasma osmolality which indicates physiological dehydration (Peterson 2002, Rozen-Rechels et al. 2020a, b) and the food-deprived group had lower circulating triglyceride concentrations and blood glucose levels suggesting fasting patterns consistent with previous studies on lipid or glucose metabolism in reptiles (Moon et al. 1999, McCue 2007, Price 2017). Concurrently, water and food restrictions led to reductions in body mass, hind limb width and tail width. In snakes and birds, muscle wasting from the tail and limbs is caused by protein catabolism and is associated with a significant release of protein-bound water to improve the water status during water restriction (Gerson and Guglielmo 2011, Bruschi et al. 2018). In lizards, the tail is also a reserve organ consisting mostly of muscle and lipids stored as triglycerides (Avery 1974, Price 2017). Thus, our data suggest that fasting and dehydration caused mobilisation of caudal lipid reserves and muscle wasting to support water, energy, and amino acid requirements when water and dietary intakes are insufficient (Chabaud et al. 2023).

At the same time, lizards developed behavioural strategies during the water restriction period including a lower basking effort, a lower body temperature and a higher eye closure rate, and those responses were more strongly expressed in the dry shelter treatment. Our study is the first experimental demonstration of an adjustment of eye closure behaviour in response to hydric stress. In dry-skinned ectotherms with an eyelid, eye closure behaviour should play an important role in organismal hydroregulation because the eye surface is poorly resistant to water loss and may represent a significant proportion of the body surface (Waldschmidt and Porter 1987, Pirtle et al. 2019). In addition, eye opening is important for predators' detection and visual interactions with conspecifics so hydric

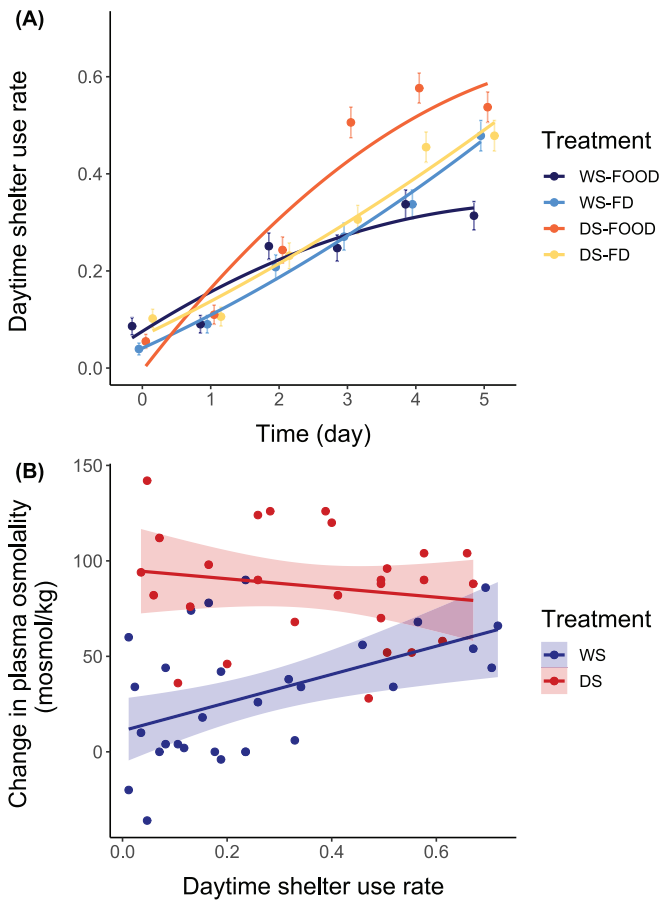


Figure 1. (A) Interactive effects of shelter and food treatment on daytime shelter use as a function of time (number of days since the start of the experiment). (B) Plasma osmolality change during the experiment as a function of daytime shelter use and shelter treatment. Colours in (A) represent experimental groups formed by the factorial combination of the two treatments (WS-FOOD (dark blue): wet shelter and ad libitum feeding, WS-FD (light blue): wet shelter and food deprivation, DS-FOOD (orange): dry shelter and ad libitum feeding, DS-FD (yellow): dry shelter and food deprivation). Points represent average daily shelter use (\pm SE) and solid lines represent the average shelter use adjusted with a quadratic time effect. We found a significant effect of the interaction between time, shelter treatment and food treatment on shelter use ($\chi^2_1 = 8.68$, $p = 0.003$). Colours in (B) represent lizards with access to wet shelter (WS (dark blue)) or dry shelter (DS (red)). Points represent individual shelter use score during the experiment and a positive change in osmolality indicates physiological dehydration. The change in plasma osmolality was influenced by the interaction between shelter use rate and shelter treatment ($F_{1,30} = 4.44$, $p = 0.04$) independently of food treatment ($F_{1,30} = 2.27$, $p = 0.14$). Dehydration was positively correlated with daytime shelter use in lizards with access to wet shelter ($F_{1,10} = 7.13$, $p = 0.02$) but it was not correlated in lizards with access to dry shelter ($F_{1,8} = 3.68$, $p = 0.09$). Daytime shelter use rates were calculated as the number of observations where the lizard was in the shelter divided by the total number of daytime observations of the day in (A) or of the experiment in (B). Water restriction begins on day 1.

stress may decrease vigilance and increase risks of predation. Altogether, these behavioural responses indicate a tradeoff between heat and water balance regulation mediated by the hydric costs of thermoregulation (Rozen-Rechels et al. 2020a, b). Hydric quality of the shelter rather than food availability was the main modulator of these thermo–hydroregulation strategies and an important buffer against the deleterious effects of water restriction. Presence of a wet shelter at day and night limited very strongly dehydration, muscle and lipid reserves mobilisation, thermal depression and the increase of eye closure rate, which can play an important role in organismal hydroregulation (Waldschmidt and Porter 1987, Pirtle et al. 2019). These findings highlight the importance of shelter and wet microhabitat quality in the behavioural responses of ectotherms to future changes in climate conditions (Beck and Jennings 2003, Moore et al. 2018).

Contrary to earlier studies (Pintor et al. 2016, Dezetter et al. 2023), lizards with access to a wet shelter did not use it more often than the ones with a dry shelter and we found a positive relationship between individual dehydration state and the daytime wet shelter use rate, whereas we predicted the opposite relationship since wet shelter should reduce evaporative water loss rates. These results suggest condition-dependent wet shelter use, for example if lizards decided to use the wet shelter below a certain dehydration level, and highlight the potential thermoregulatory costs of hydroregulation behaviours. Behavioural selection of a wet microclimate inside the shelter allowed lizards to maintain a better hydration state more efficiently but also involved the selection of a thermally suboptimal microhabitat. Thus, wet shelter use had a strong opportunity and energetic cost because it was detrimental to thermoregulatory activities essential for energy intake such as prey capture and assimilation rates (Van Damme et al. 1991), which potentially explains why this behaviour was less frequent in weakly dehydrated individual lizards (which privileged thermoregulation activities) than in strongly dehydrated individuals (which privileged hydroregulation activities). On the other hand, individual dehydration state was not correlated with the daytime dry shelter use rate because a dry shelter does not effectively reduce water losses and dehydration contrary to a wet shelter.

Food availability did not influence mean daily thermoregulation effort contrary to the predictions of the cost–benefit model of thermoregulation and results of some earlier studies (Huey and Slatkin 1976, Brown and Griffin 2005). Thus, common lizards have limited behavioural acclimation responses to energy imbalance, maybe because fasting was too short or because physiological responses to fasting were prioritized over behavioural responses. Finally, in accordance to a recent study (Chabaud et al. 2023), none of our findings support the ‘food for water hypothesis’ because ad libitum food conditions did not reduce dehydration nor the morphological and behavioural impacts of water restriction. On the contrary, shelter use in the presence of dry shelter and ad libitum food was more frequent, which suggests that food consumption and processing require a good hydration status and thus food availability increases reliance on free standing

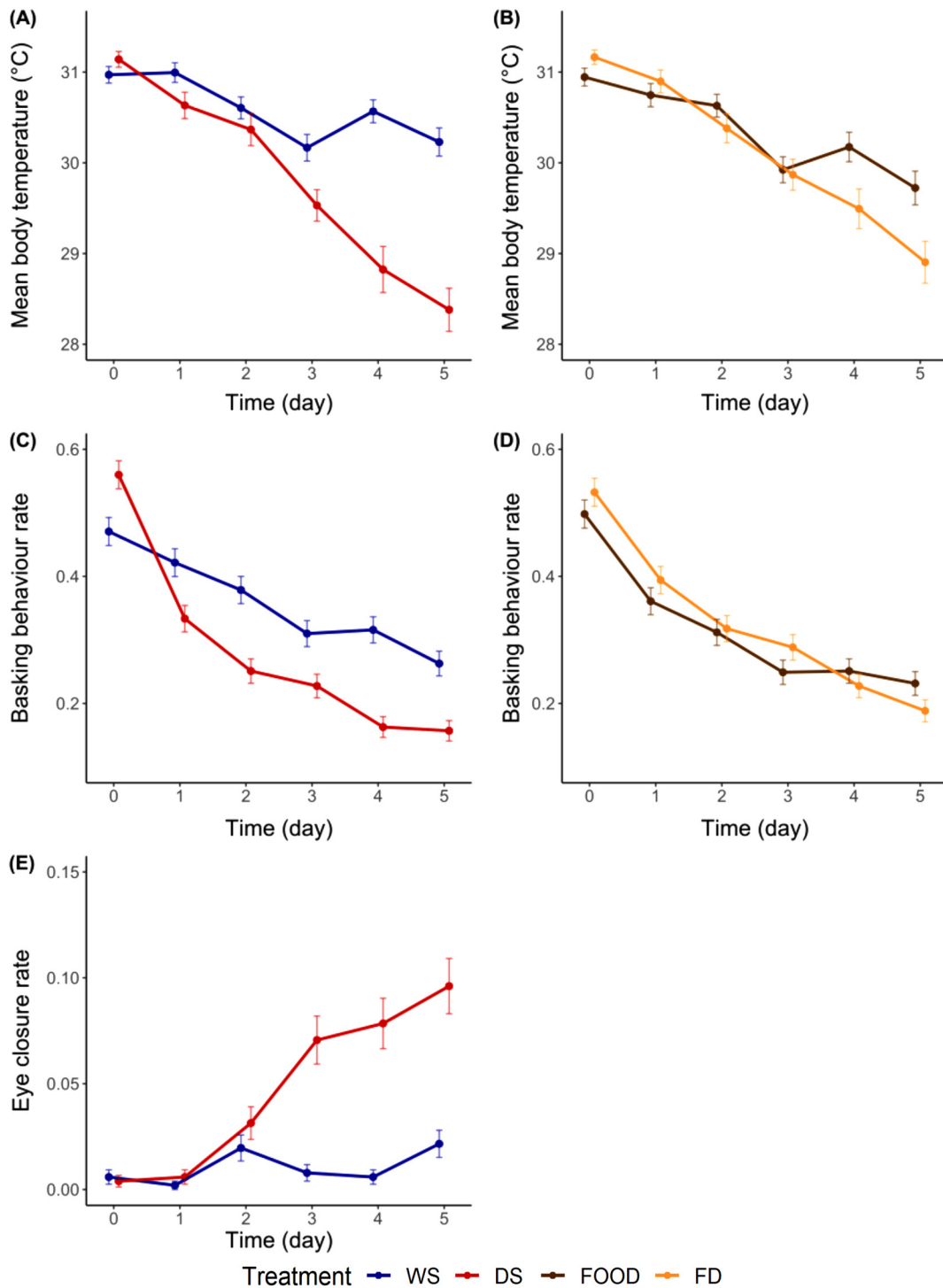


Figure 2. Effects of experimental treatments on thermo-hydroregulation behaviours of male *Zootoca vivipara*. Mean body temperature (A–B), mean basking rate (C–D), and eye closure rate (E) of lizards as a function of day and experimental treatment (WS: wet shelter, DS: dry shelter, FOOD: food ad libitum, FD: food deprivation). Points and error bars represent temperature, basking rate, and average daily eye closure rate of lizards (\pm SE). Basking and eye closure rates was calculated as the number of observations where the lizard exhibited basking behaviour or had its eyes closed divided by the total number of observations of the day. Water restriction begins on day 1. Shelter treatment in interaction with time significantly influenced mean body temperature ($F_{1,2514} = 11.04$, $p < 0.0001$), mean basking rate ($\chi^2_5 = 45.35$, $p < 0.001$), and eye closure rate ($\chi^2_5 = 17.01$, $p = 0.005$) in contrast to food treatment ($p > 0.05$ for all).

water, as suggested for several snake species and a carnivorous lizard (Wright et al. 2013, Lillywhite 2017, Murphy and DeNardo 2019). Therefore, our experiment indicates that food acquisition can exacerbate the conflict between thermoregulation and hydroregulation, most likely because behavioural optimisation of food capture, processing and digestion implies behavioural selection of elevated body temperatures or increased basking effort, which are water costly thermoregulation behaviours. An alternative explanation is that feeding itself increases water requirements or that prey capture and digestion requires a good hydration state as seen in some carnivorous snakes (Lillywhite 2017). Thus, food-deprived lizards use dry and wet shelters similarly, whereas in the presence of food, lizards with a dry shelter must spend more time inside the shelter to regulate their hydration state than lizards with a wet shelter.

Conclusions

Our study challenges previous studies that have only focused on the effects of temperature or water availability on thermoregulatory behaviours of ectotherms. Food intake did not play a major role in regulating the hydration status of this insectivorous species but food intake influenced water balance regulation by increasing a behavioural tradeoff between thermoregulatory and hydroregulatory activities. Our findings demonstrate the urgent need to take into account the dual effect of warming and drought events, behavioural interactions between thermoregulation and hydroregulation and the buffering role of microclimatic conditions to understand the ecological and evolutionary responses of ectotherms to climate change (Moore et al. 2018).

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Permits (H4)– Experiments were performed under the approval of Charles Darwin Animal Experimentation Ethics Committee (APAFIS#30217-2021030322398713) in an animal breeding facility accredited with permit 17/DDPP/SPA/E/57.

Author contributions **Théo Bodineau**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Validation (equal); Writing – original draft (lead); Writing – review and editing (lead). **Chloé Chabaud**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Beatriz Decenci re**: Investigation (supporting). **Simon Agostini**: Investigation (supporting). **Olivier Lourdais**: Conceptualization (supporting); Methodology

(supporting); Writing – review and editing (supporting). **Sandrine Meylan**: Conceptualization (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jean-Fran ois Le Galliard**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Supervision (lead); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Zenodo Repository: <https://doi.org/10.5281/zenodo.7711397> (Bodineau et al. 2024).

Supporting information

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

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Supplementary Information

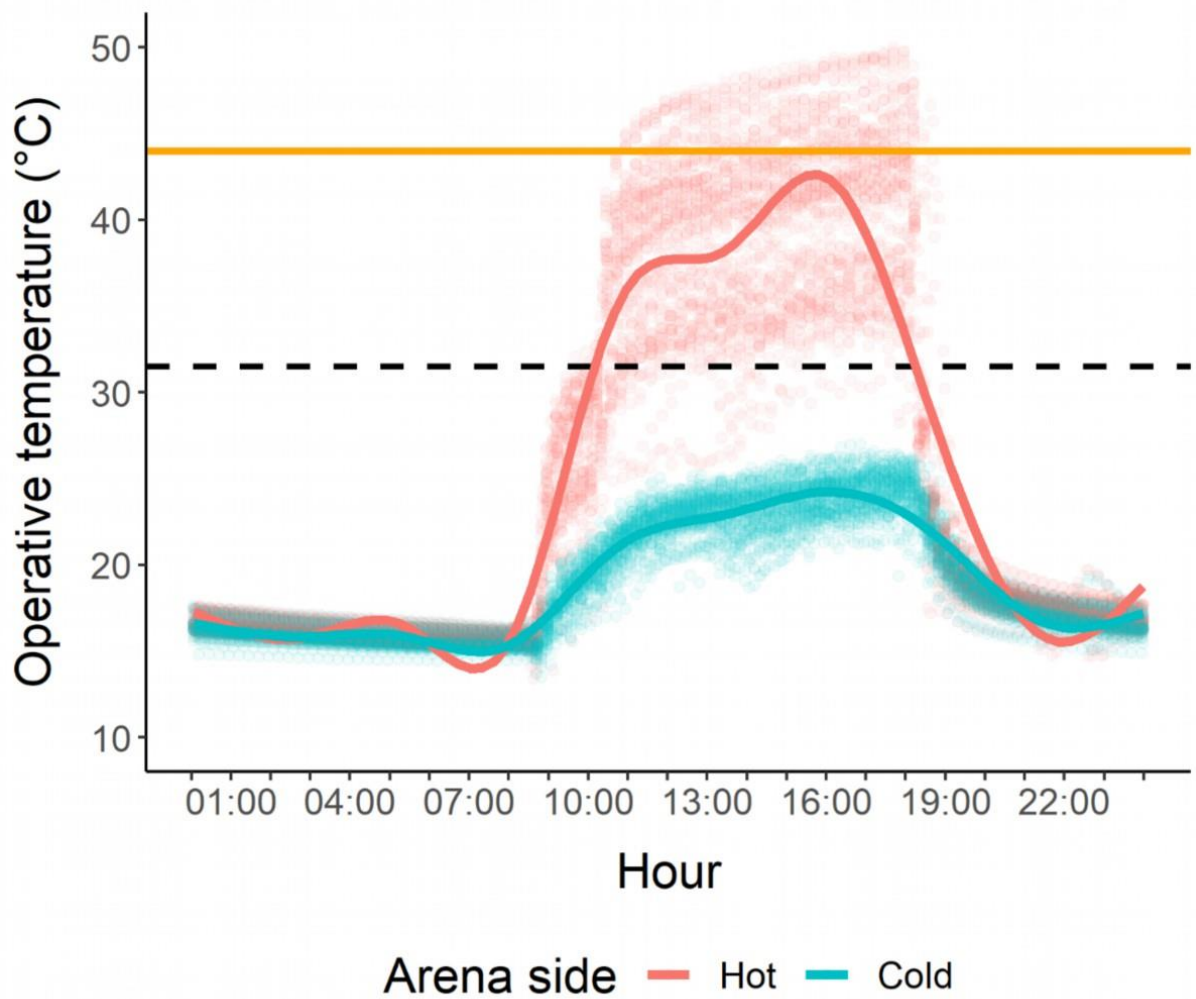


Figure S1: Daily variation of operative temperature on the hot and cold side of the thermal gradient. Jittered points correspond to raw operative temperature values. Smoothing with a generalised additive model was applied to visualise the nonlinear patterns (solid blue and red line). Thermal preferences (black dashed line) and upper critical thermal limit (orange solid line) of *Zootoca vivipara* (Gvoždík & Castilla, 2001) are represented.

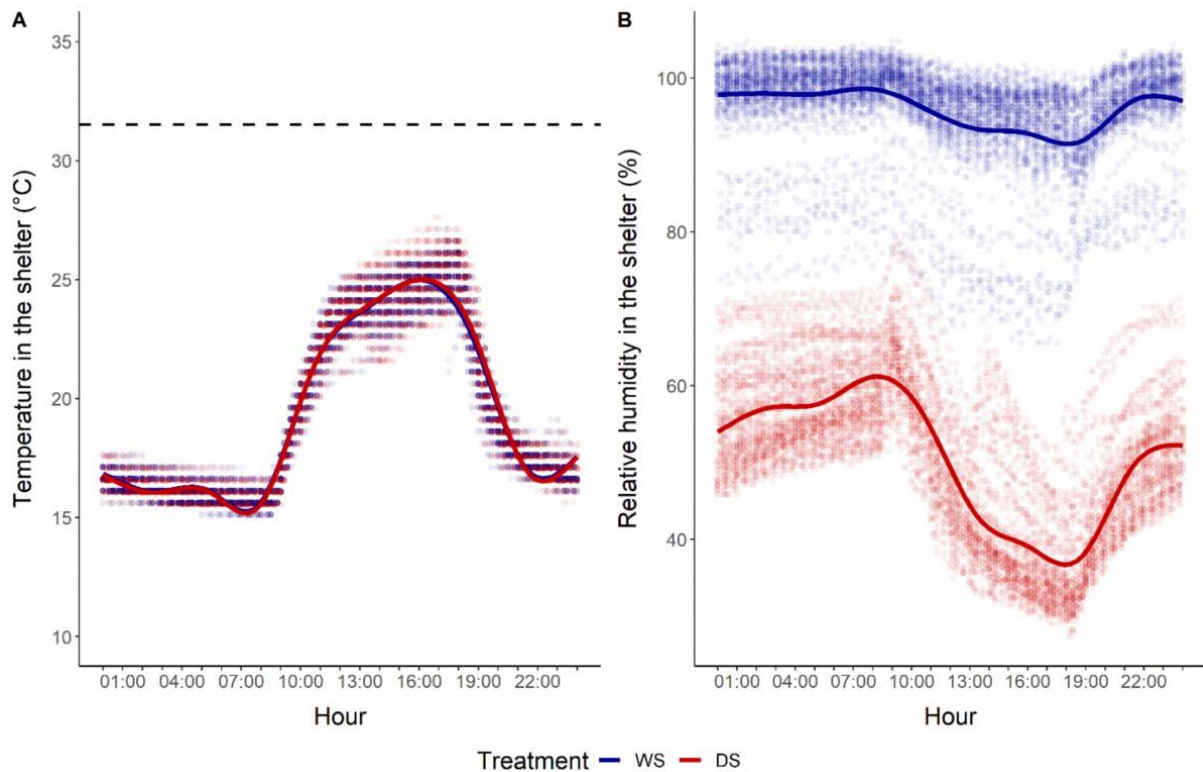


Figure S2: Daily variation of temperature (A) and relative humidity (B) in shelters as a function of shelter treatment (WS: wet shelter, DS: dry shelter). Jittered points correspond to raw values, red and blue lines are predictions from a generalised additive model. Thermal preference of *Zootoca vivipara* (Gvoždík & Castilla, 2001) is represented by a black dashed line. Mean temperature in the shelter did not differ significantly between dry and wet treatments ($F_{1,16123} = 2.28$, $p = 0.95$).

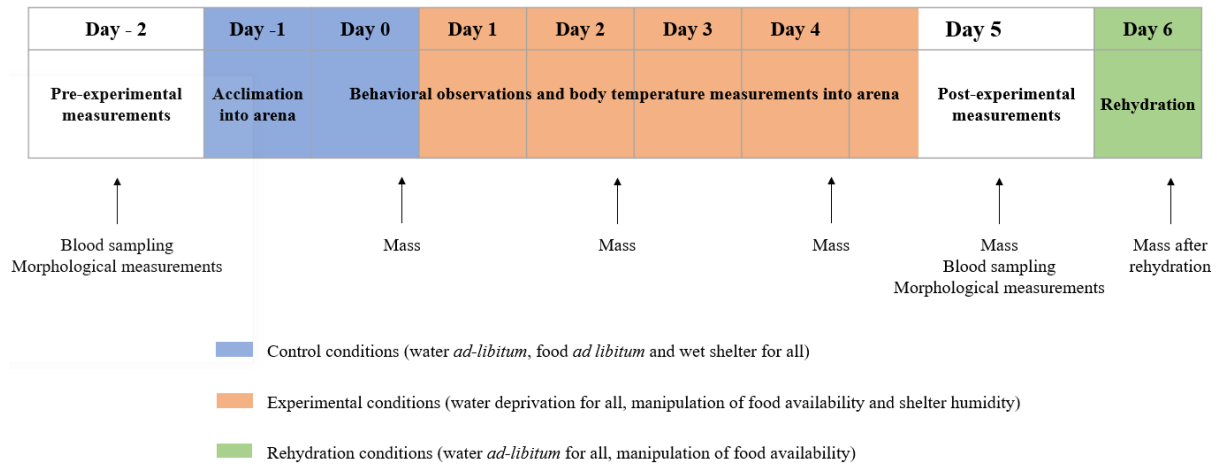


Figure S3: Chronology of the experiment for each experimental batch.

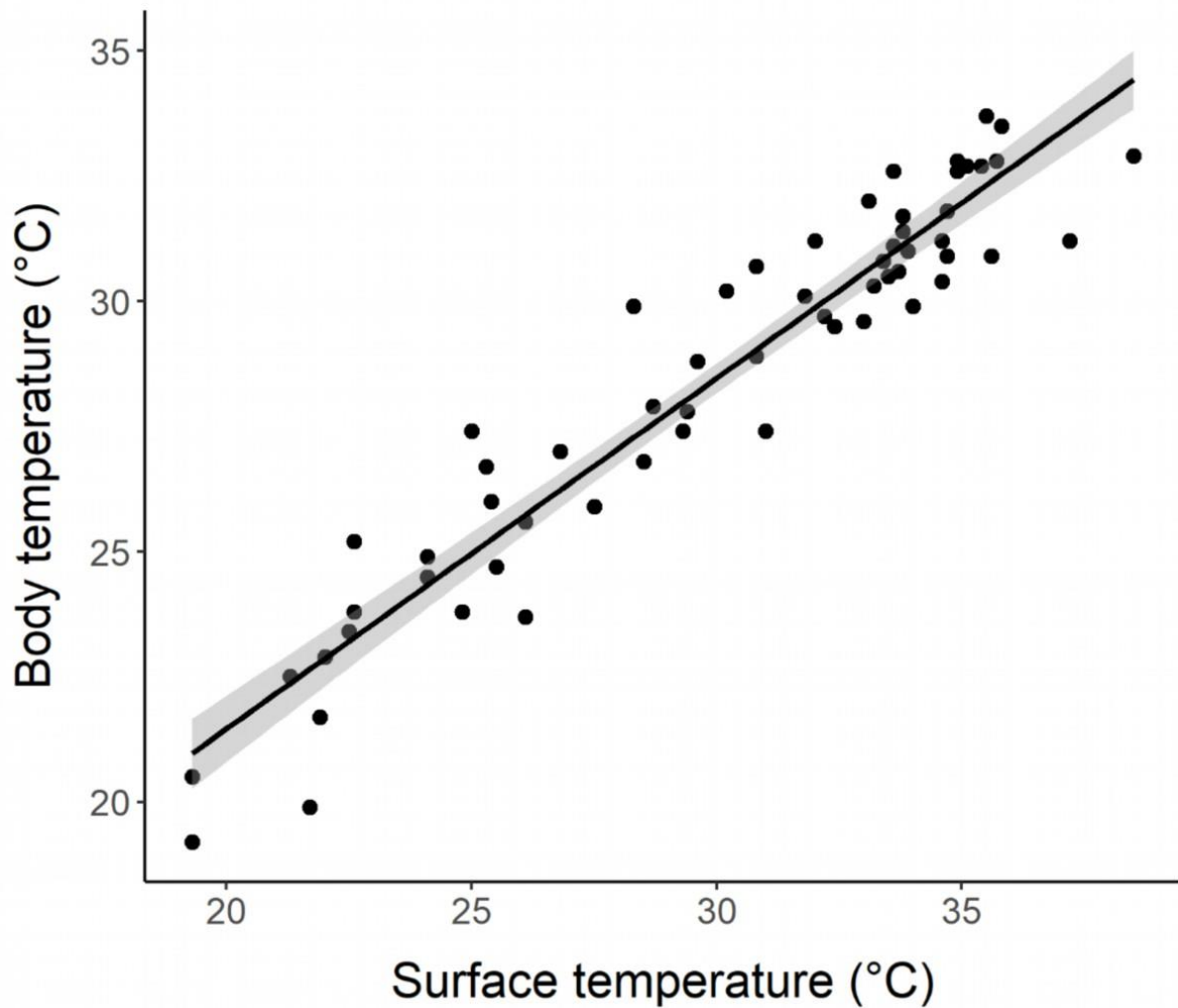


Figure S4: Relationship between internal body temperature measured with a K-type thermocouple inserted in the cloaca and surface body temperature measured with an infrared thermometer. Surface body temperatures and cloacal temperatures were measured consecutively for each individual using an infrared thermometer (Raytek, Raynger MX2) and a K-type thermocouple (HI 935005N, Hanna) after the last behavioural record of day 0. The linear regression (with 95% confidence interval) is plotted against raw data. Cloacal temperatures were strongly correlated with surface temperatures ($N=60$, $T_b = 7.46 (\pm 0.90) + 0.70 (\pm 0.03) \times T_{IR}$, $R^2 = 0.91$).

Table S1: Output of models used to test the effects of treatments (shelter and food, see main text) and covariates on morphological, physiological and behavioural changes during a simulated drought in *Zootoca vivipara*. Linear mixed models were used to explain changes in body mass, limb thickness, tail width, osmolality, circulating triglycerides concentration and circulating glucose concentration, as well as body temperatures. Generalised linear mixed models assuming a binomial distribution and a logit link were used to analyse daytime shelter use, basking behaviour and eye closure behaviour.

Variables	Fixed effects	F or χ^2	P
Δ body mass (g)	Initial mass	F _{1,33} =17.8	<0.001
	Experimental batch	F _{2,33} =3.75	0.03
	Food	F _{1,33} =69.4	<0.0001
	Shelter	F _{1,33} =83.0	<0.0001
	Shelter x food	F _{1,32} =0.31	0.58
Δ limb thickness (mm)	Initial limb thickness	F _{1,37} =8.56	0.006
	Experimental batch	F _{2,35} =0.56	0.58
	Food	F _{1,37} =10.17	0.003
	Shelter	F _{1,37} =18.24	0.0001
	Shelter x food	F _{1,34} =0.09	0.76
Δ tail width (mm)	Initial tail width	F _{1,36} =12.16	0.001
	Experimental batch	F _{2,36} =4.37	0.04
	Food	F _{1,36} =6.39	0.02
	Shelter	F _{1,36} =9.96	0.003
	Shelter x food	F _{1,34} =0.21	0.64
Δ osmolality (mOsmol.kg ⁻¹)	Initial osmolality	F _{1,30} =2.40	0.13
	Experimental batch	F _{2,30} =4.86	0.01
	Shelter use rate	F _{1,30} =2.77	0.11
	Food	F _{1,30} =2.27	0.14

Variables	Fixed effects	F or χ^2	P
	Shelter	$F_{1,30}=68.8$	<0.0001
	Shelter x food	$F_{1,28}=0.73$	0.4
	Food x shelter use rate	$F_{1,29}=0.48$	0.49
	Shelter x shelter use rate	$F_{1,30}=4.44$	0.04
	Shelter x food x shelter use rate	$F_{1,27}=0.18$	0.67
Δ [triglycerides] (mg.dL ⁻¹)	Initial triglycerides concentration	$F_{1,33}=7.15$	0.01
	Experimental batch	$F_{2,33}=2.28$	0.12
	Food	$F_{1,33}=152.5$	<0.0001
	Shelter	$F_{1,33}=4.61$	0.04
	Shelter x food	$F_{1,32}=3.70$	0.06
Δ [glucose] (mg.dL ⁻¹)	Initial glucose concentration	$F_{1,33}=7.36$	0.01
	Experimental batch	$F_{2,33}=1.09$	0.35
	Food	$F_{1,33}=14.6$	<0.001
	Shelter	$F_{1,33}=0.13$	0.71
	Shelter x food	$F_{1,32}=2.94$	0.09
Daytime shelter use	Time	$\chi^2_1=29.96$	<0.0001
	Time ²	$\chi^2_1=10.55$	<0.001
	Experimental batch	$\chi^2_2=3.93$	0.14
	Food	$\chi^2_1=1.18$	0.28
	Shelter	$\chi^2_1=1.20$	0.27
	Shelter x food	$\chi^2_1=3.95$	0.05
	Time x food	$\chi^2_1=0.40$	0.53

Variables	Fixed effects	F or χ^2	P
	Time ² x food	$\chi^2_1=0.02$	0.88
	Time x shelter	$\chi^2_1=8.91$	0.003
	Time ² x shelter	$\chi^2_1=3.41$	0.06
	Time x food x shelter	$\chi^2_1=8.68$	0.003
	Time ² x food x shelter	$\chi^2_1=2.98$	0.08
Body temperature (°C)	Time	$F_{5,2514}=8.98$	<0.0001
	Experimental batch	$F_{2,36}=2.08$	0.14
	Food	$F_{1,36}=0.01$	0.91
	Shelter	$F_{1,36}=0.09$	0.76
	Shelter x food	$F_{1,35}=0.27$	0.61
	Time x food	$F_{5,2509}=1.45$	0.20
	Time x shelter	$F_{5,2514}=11.04$	<0.0001
	Time x food x shelter	$F_{5,2504}=1.03$	0.40
Basking behaviour	Time	$\chi^2_5=74.12$	<0.0001
	Experimental batch	$\chi^2_2=6.04$	0.05
	Food	$\chi^2_1=0.09$	0.77
	Shelter	$\chi^2_1=3.33$	0.068
	Shelter x food	$\chi^2_1=0.65$	0.42
	Time x food	$\chi^2_5=7.46$	0.19
	Time x shelter	$\chi^2_5=45.4$	<0.001
	Time x food x shelter	$\chi^2_5=4.2$	0.52
Eye closure behaviour	Time	$\chi^2_5=13.1$	0.02
	Experimental batch	$\chi^2_2=8.13$	0.02
	Food	$\chi^2_1=1.93$	0.16

Variables	Fixed effects	F or χ^2	<i>P</i>
	Shelter	$\chi^2_1=0.21$	0.65
	Shelter x food	$\chi^2_1=0.29$	0.59
	Time x food	$\chi^2_5=3.29$	0.66
	Time x shelter	$\chi^2_5=17.0$	0.005
	Time x food x shelter	$\chi^2_5=4.9$	0.43

Δ = intra-individual change

Time = number of days since the start of the experiment

Significant tests are bolded (i.e., $P \leq 0.05$).

Abstract

Reproducing in changing climates: determinants and consequences of breeding phenology changes in a viviparous reptile

Modifications in daytime and nighttime thermal conditions induced by climate change can affect organisms by disrupting physiological processes, functional traits, reproductive strategies, and life history traits. Phenological changes are one of the main responses to climate change in many organisms and have significant implications for individual reproductive success. In ectotherms, changes in breeding dates are particularly pronounced due to the thermodynamic effects on physiological processes and the reproductive cycle. This thesis explores the effects of climate and breeding phenology on physiological, behavioural, reproductive and life history traits of females and their offspring in a terrestrial ectotherm, the common lizard (*Zootoca vivipara*). We used an integrative approach combining cross-sectional and longitudinal studies to explore environmental, individual determinants and selection on parturition dates in natural settings, as well as experimental studies to quantify benefits and costs of the thermal plasticity of gestation in the laboratory. Daily maximum temperatures during the post-winter activity period, forest cover, and body size were important determinants of parturition dates. Our results highlight constant directional selection favouring earlier parturition dates, but a limited adaptive potential of this phenological trait to climate change through microevolutionary processes. Finally, thermal acceleration of gestation induced by daytime and/or nighttime warming disrupts maternal homeostasis, but earlier birth dates have positive effects on offspring survival and growth. Overall, our results suggest that studying the consequences of phenological changes in squamates should focus on the limits and cost-benefit balance of thermal plasticity in breeding dates. We also emphasise the importance of considering nighttime warming, physiological and behavioural adjustments to cope with it, as well as habitat structure to understand and predict the responses of terrestrial ectotherms to climate change.

Keywords: climate change, phenology, reproduction, phenotypic plasticity, adaptation, ectotherm.

Résumé

Se reproduire dans des climats changeants : déterminants et conséquences des modifications de la phénologie de la reproduction chez un reptile vivipare

Les modifications des conditions thermiques diurnes et nocturnes induites par les changements climatiques peuvent affecter les organismes par une perturbation des processus physiologiques, des traits fonctionnels, des stratégies de reproduction et des traits d'histoire de vie. Les changements phénologiques constituent l'une des principales réponses aux changements climatiques chez de nombreux organismes et ont des conséquences majeures sur le succès reproducteur des individus. Chez les ectothermes, les changements des dates de reproduction sont particulièrement marqués compte tenu des effets thermodynamiques sur les processus physiologiques et le cycle reproductif. Cette thèse vise à explorer les effets du climat et de la phénologie de la reproduction sur les traits physiologiques, comportementaux, reproductifs et les traits d'histoire de vie des femelles et de leur progéniture chez un ectotherme terrestre, le lézard vivipare (*Zootoca vivipara*). Nous avons utilisé une approche intégrative combinant des études transversales et longitudinales afin d'explorer les déterminants environnementaux, individuels et la sélection sur les dates de parturition en milieu naturel, ainsi que des études expérimentales pour quantifier les bénéfices et les coûts de la plasticité thermique de la gestation en laboratoire. Les températures maximales journalières durant la période d'activité post-hivernale, la couverture forestière et la taille corporelle étaient des déterminants importants des dates de parturition. Nos résultats mettent en évidence une sélection directionnelle constante favorisant une date de parturition précoce, mais une faible capacité de réponse évolutive de ce trait à la sélection. Enfin, l'accélération thermique de la gestation induite par le réchauffement diurne et/ou nocturne altère l'homéostasie maternelle, mais une date de naissance plus précoce a des effets positifs sur la survie et la croissance de la progéniture. Dans l'ensemble, nos résultats suggèrent que l'étude des conséquences des changements phénologiques chez les squamates doit se concentrer sur les limites et la balance coût-bénéfice de la plasticité thermique des dates de reproduction. Nous soulignons également l'importance de considérer le réchauffement nocturne, les ajustements physiologiques et comportementaux pour y faire face, ainsi que la structure de l'habitat pour comprendre et prédire les réponses des ectothermes terrestres face aux changements climatiques.

Mots clés : changement climatique, phénologie, reproduction, plasticité phénotypique, adaptation, ectotherme.