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Causes et conséquences évolutives de la phénologie de l'hibernation

Approches évolutives des changements de phénologie dans le contexte des changements globaux

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Publications and communications of thesis results

Published publications:

Constant, T., Giroud, S., Viblanc, V. A., Tissier, M. L., Bergeron, P., Dobson, F. S., & Habold, C. (2020). Integrating mortality risk and the adaptiveness of hibernation. *Frontiers in physiology*, 706.

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Constant, T., Dobson, F. S., Habold, C., & Giroud, S. (In prep). Trade-offs in dormancy phenology in endotherms and ectotherms.

Constant, T., Chignec, H., Zahn, Habold, C., & Giroud, S. (In prep). Experimental study confronting aging theories in a hibernating mammal.

Constant, T. & Chignec, H., Zahn, S., Habold, C., & Giroud, S. (In prep). Hibernation and early life condition in the context of Pace of life Syndrome.

Constant, T., Chignec, H., Zahn, S., Giroud, S., & Habold, C. (In prep). Telomeres, a complex biomarker of aging in a species with telomere lengthening.

Scientific communications:

Constant, T., Dobson, F.S., Giroud, S., Habold, C. (2021) Trade-offs in dormancy phenology in endotherms and ectotherms. International hibernation symposium 2021, presentation oral (en ligne), 1-5 august 2021

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Chignec, H., Constant, T., Zahn, S., Giroud, S., Habold, C. (2021) Link between hibernation, growth and reproduction in the common hamster (Cricetus cricetus). International hibernation symposium 2021, Poster (en ligne), 1-5 august 2021

Chignec, H., Constant, T., Zahn, S., Giroud, S., Habold, C. (2021) Link between hibernation, growth and reproduction in the common hamster (Cricetus cricetus). 5th edition of the symposium of animal ecophysiology (CEPA), Poster, 2-4 November 2021, Montpellier, France

Scientific vulgarization:

Interview on the publication entitled “Integrating mortality risk and the adaptiveness of hibernation” organized by the master in scientific communication of Strasbourg:
https://www.youtube.com/watch?v=nKKDL3l6HqI

Resumé

Dans le contexte des changements globaux, les activités humaines modifient l'environnement et sont ainsi responsables d'une perte de biodiversité pouvant mener à une 6ème extinction de masse (Tilman et al. 2017). Un changement de phénologie, *i.e.,* le début et la fin d'une activité saisonnière, est une des réponses des espèces végétales et animales aux changements environnementaux comme le réchauffement climatique (Cohen et al. 2018). La plupart des études se sont jusqu'à présent focalisées sur la phénologie de la reproduction. Cependant, pour mesurer et prédire l'ensemble des effets induits par les changements globaux, il est plus que nécessaire d'étudier l'ensemble des activités saisonnières dont les stratégies adaptatives -tels que l'hibernation ou la migration- permettant aux espèces de survivre lorsque les conditions environnementales se dégradent. C'est dans ce contexte que s'inscrit **cette thèse qui vise à mieux comprendre les causes et conséquences évolutives de la phénologie de l'hibernation**. Plus précisément, nous allons chercher à comprendre quelles sont les pressions évolutives qui expliquent la variation de la phénologie de l'hibernation (cause évolutive) et les conséquences sur les traits d'histoire de vie des espèces hibernantes.

Un décalage de phénologie permet à certaines espèces de s'adapter à ces changements, ou représente au contraire un piège évolutif. Ainsi, identifier un changement de phénologie n'est pas un élément suffisant pour tirer des conclusions quant aux conséquences sur la dynamique des populations végétales et animales (Visser and Both 2005). Pour cela, il est nécessaire de comprendre comment (approche mécanistique) et pourquoi (approche évolutive) les organismes alignent la phénologie de leur activité avec une certaine période de l'année (le pic de nourriture par exemple). Cependant, à ce jour, les études sur la phénologie privilégient l'approche mécanistique par rapport à l'approche évolutive. Par

conséquent, **la première partie de ma thèse met en lumière, sur la base d'une revue de la littérature, de nouvelles approches d'écologie évolutive visant à estimer si le changement de phénologie permet de répondre de façon adéquate au changement de l'environnement (Constant, T., Dobson, F. S., Habold, C., & Giroud, S. En préparation. Towards evolutionary ecology approaches to phenological shifts)**. Plus précisément, ces approches visent à montrer (1) l'intérêt d'étudier la cause et les conséquences évolutives de toutes les activités du cycle annuel (approche de survie annuelle), (2) la diversité des causes évolutives (approche communautaire) et (3) l'importance des compromis entre les composantes de la fitness pour comprendre l'évolution de la phénologie et leurs conséquences (approche des compromis, Fig. 1d). Ces approches présentant les informations manquantes concernant les causes et conséquences ultimes de la phénologie seront une base sur laquelle les objectifs de cette thèse seront développés.

Dans la seconde partie de ma thèse, j'ai utilisé une approche de phylogénie comparative pour étudier les conséquences évolutives de la phénologie de l'hibernation sur l'histoire de vie des hibernants (Constant, T., Giroud, S., Viblanc, V. A., Tissier, M. L., Bergeron, P., Dobson, F. S., & Habold, C. (2020). Integrating mortality risk and the adaptiveness of hibernation. Frontiers in physiology, 706.). Les hibernants présentent une longévité plus importante en comparaison avec des espèces non-hibernantes de même taille (Turbill et al. 2011). D'après la théorie des traits d'histoire de vie, la réduction des risques de mortalité intrinsèques ou extrinsèques pendant l'hibernation devrait permettre à ces espèces d'atteindre une longévité plus importante. Si cette hypothèse se vérifie, alors les risques devraient diminuer d'autant plus que la durée d'hibernation augmente. Ainsi, à partir d'une méta-analyse sur 82 espèces de mammifères hibernants, j'ai testé si l'augmentation de la durée de l'hibernation augmentait la longévité entre les espèces hibernantes. Cette relation a effectivement été mise en évidence après avoir tenu compte statistiquement des effets de la masse corporelle des espèces et du style de vie sur la longévité.

Le chapitre suivant se concentre sur les causes évolutives de l'hibernation chez les espèces hétérothermes et plus largement de la dormance saisonnière (Constant, T., Dobson, F.S., Habold, C., & Giroud, S. Trade-offs in dormancy phenology in endotherms and ectotherms. Prêt à la soumission). D'un point de vue physiologique, l'hibernation est constituée d'une succession d'épisodes d'hypométabolisme et d'hypothermie (torpeurs) qui permettent de réduire drastiquement la dépense énergétique. L'hibernation est depuis longtemps supposée être employée pour survivre à une période de pénurie énergétique saisonnière. Néanmoins, des observations récentes semblent montrer qu'elle pourrait se dérouler alors que l'environnement permettrait le maintien d'une balance énergétique positive de l'individu. La réduction des risques de mortalité extrinsèque comme la prédation a été proposée comme une cause évolutive susceptible d'expliquer ces observations en contradiction avec la vision traditionnelle (une réponse à la limitation énergétique) de l'hibernation (Ruf et al. 2012). À partir d'une méta-analyse comprenant plus d'une vingtaine de mammifères hibernants, j'ai testé l'hypothèse selon laquelle la phénologie de l'hibernation serait expliquée par un compromis entre les bénéfices d'hiberner pour la survie (réduction des risques de mortalité extrinsèque) et les bénéfices pour la reproduction d'être actif, indépendamment de la limitation énergétique de l'environnement. J'ai prédit que la différence entre les sexes observée dans la phénologie de l'hibernation pourrait être expliquée par des différences d'investissement dans la reproduction. En accord avec cette hypothèse, j'ai trouvé que le sexe qui investit le plus de temps dans la reproduction reste plus longtemps actif et passe moins de temps en hibernation, indépendamment des limitations énergétiques. De plus, j'ai montré que cette hypothèse permettait d'expliquer la phénologie de l’hibernation à d’autres échelles (intra-spécifique notamment) et la phénologie de la dormance des ectothermes.

L’approche de phylogénie comparative a néanmoins l’inconvénient de se baser sur des corrélations et donc de limiter l’interprétation des causes et effets. Ainsi, de manière complémentaire, **j’ai développé une approche expérimentale en laboratoire permettant de tester plus finement les conséquences évolutives de l’hibernation chez un mammifère hibernant, le hamster commun (*Cricetus cricetus*).**

À l’échelle interspécifique, j’ai pu montrer qu’une augmentation de la durée de l’hibernation était associée à une longévité plus importante. Néanmoins, les facteurs mécanistiques responsables de cette augmentation restent encore inconnus. Plusieurs hypothèses ont été formulées afin d’expliquer la longévité des hibernants. Il est supposé que la réduction du métabolisme diminue les dommages au niveau cellulaire et ralentit le vieillissement (théorie des radicaux libres ; Wu and Storey 2016). Dans ce cas, plus la réduction du métabolisme est importante, plus le vieillissement serait ralenti. Une hypothèse alternative propose que les épisodes de torpeur à basse température corporelle (torpeur profonde) induiraient au contraire des dommages cellulaires mais que la saison d’hibernation, du fait de son inhibition à la reproduction et la croissance, serait favorable à un investissement dans la maintenance du soma de l’individu (Humphries et al. 2003). Dans ce cas, il est supposé que plus la période d’hibernation est longue avec des torpeurs peu profondes, plus un investissement dans la maintenance somatique de l’individu devrait être observé. Enfin, une troisième hypothèse suppose que la réduction des risques de mortalité extrinsèque pendant l’hibernation conduisant à une survie annuelle importante devrait favoriser un investissement important dans la maintenance quelle que soit la période de l’année. **Dans cette étude, j’ai**

mis en place un plan expérimental qui permet de confronter pour la première fois ces trois hypothèses (Constant, T., Chignec, H., Habold, C., & Giroud, S. En préparation. Experimental study confronting aging theories in a hibernating mammal). J'ai enregistré les profils d'hibernation et mesuré la variation de la longueur des télomères avant et après la période d'hibernation de 4 groupes de 12 à 13 femelles hamsters. Ces groupes ont été placés dans des conditions de photopériode et de température ambiante qui favorisent une longue ou une courte hibernation avec pas ou beaucoup d'épisodes de torpeur profonde. En accord avec l'hypothèse de la réduction du métabolisme, les résultats montrent que l'augmentation du temps total passé en torpeur est le facteur le plus important pour expliquer l'élongation des télomères pendant la période d'hibernation, ce qui suggère que le faible taux métabolique pendant l'hibernation ralentit le vieillissement, en particulier avec une température corporelle élevée en torpeur. Par ailleurs, en accord avec l'hypothèse de la maintenance pendant l'hibernation, il semblerait que l'effet positif du temps passé en torpeur sur la longueur des télomères puisse être expliqué par un ralentissement de la croissance pendant cette période. Cela suggère une redirection de l'énergie allouée à la croissance et probablement à la reproduction vers la maintenance somatique. Néanmoins, l'élongation des télomères n'est pas spécifique à la période d'hibernation. L'investissement dans la maintenance semble limité et soumis à un compromis d'allocation dans le temps de tel sorte qu'une élongation des télomères pendant l'hibernation conduit à une érosion pendant la saison active (et inversement pour une érosion pendant l'hibernation). En accord avec la théorie des traits d'histoire de vie, ces résultats pourraient soutenir l'hypothèse d'un investissement important dans la maintenance au cours de l'année favorisé par une réduction des risques de mortalité extrinsèque. Ces résultats montrent une possible influence des trois hypothèses pour expliquer la plus grande longévité des hibernants.

J'ai ensuite cherché à mieux comprendre **les conséquences du compromis entre survie et reproduction de la phénologie de l'hibernation mises en évidence à l'échelle interspécifique.** Le compromis entre reproduction et survie est à la base de la théorie du 'pace of life syndrome' (PoLS) (Réale et al. 2010). Le 'pace of life syndrome' propose que les individus, espèces ou populations puissent être répartis le long d'un continuum lent-rapide selon leur investissement d'énergie et de temps entre la reproduction et la survie. À l'extrême « lent », nous retrouvons des caractères physiologiques, immunitaires et comportementaux associés à un investissement plus important dans la survie. **Dans cette étude, nous souhaitons donc tester si la phénologie de l'hibernation, soumise au même compromis entre survie et reproduction, peut être intégrée le long de ce continuum lent-rapide (Chignec, H. & Constant, T., Habold, C., & Giroud, S. En préparation. Hibernation and early life condition in the context of Pace of life Syndrome)**. Je prédis donc qu'une longue hibernation serait associée à une croissance lente, un faible investissement dans la reproduction, une érosion des télomères limitée et un comportement averse au risque. Le hamster commun est un modèle idéal afin de tester cette hypothèse car il présente de larges différences interindividuelles dans la phénologie de son hibernation ainsi que dans de nombreux traits d'histoire de vie. Nous avons donc suivi ces différents caractères de la naissance jusqu'à l'âge d'un an et demi parmi un groupe de 34 hamsters. Au contraire, les résultats obtenus ne soutiennent pas cette prédiction mais plutôt une covariation de l'hibernation avec un POLS plus rapide. Une hibernation longue et profonde est associée à une croissance rapide, une érosion plus importante des télomères, un comportement plus exploratoire (en interaction avec le sex-ratio biaisé, voir ci-dessous), une progéniture plus nombreuse (bien que non significative, mais incluse dans le meilleur modèle) avec une faible masse corporelle à la naissance. A l'échelle individuelle, une hibernation longue et profonde serait le résultat d'un manque de masse grasse avant l'hibernation conduisant à une diminution de la probabilité de survie future. Une faible probabilité de survie dans le futur est justement supposée favoriser le développement d'un POLS plus rapide. Nous proposons que l'hibernation ne puisse pas être intégrée dans le POLS chez le hamster commun car son expression ne s'explique pas par un compromis entre reproduction et survie. Néanmoins, elle peut être un indicateur du POLS à l'échelle individuelle en reflétant les chances de survie future.

Afin d'apprécier l'influence d'un facteur sur la longévité, il a pendant longtemps été nécessaire de réaliser un suivi jusqu'à la mort de l'organisme, ce qui représente une contrainte importante pour les espèces longévives tels que les hibernants. Pour résoudre ce problème, des marqueurs biologiques de la longévité ont été développés comme la taille des télomères (Wilbourn et al. 2018) ou l'érosion des télomères (Whittemore et al. 2019). Une plus petite taille de télomère ou un taux d'érosion important au cours de la vie serait associé à une longévité plus faible. Néanmoins, une élongation de la longueur des télomères a été mesurée au cours de leur vie chez deux espèces hibernantes (Hoelzl et al. 2016, Tissier et al. 2021), remettant en question l'utilisation des télomères comme marqueur du vieillissement. J'ai donc réalisé **une étude de validation de l'érosion des télomères comme marqueur de longévité chez le hamster commun, un hibernant peu longévif (Constant, T., Chignec, H. Giroud, S., & Habold, C. (En préparation). Telomeres, a complex biomarker of aging in a species with telomere lengthening)**. Un suivi longitudinal de la variation de la longueur relative des télomères (RTL) a été réalisé de la naissance à la mort chez 24 hamsters communs. Parallèlement, les profils d'hibernation et l'investissement dans la reproduction ont été mesurés chaque année afin d'analyser leurs effets sur la longueur des télomères. Nous avons constaté une érosion des télomères des hamsters pendant l'hibernation qui s'accélère au cours de la vie des individus. Après avoir contrôlé pour l'effet de l'âge, il apparaît que la longueur des télomères et leur variation sont peu répétables au cours de la vie d'un individu et ne permettent pas de prédire la durée de vie restante. Il semblerait donc qu'en plus de l'effet saisonnier et de l'âge, il existe une variation importante et non expliquée de la RTL au cours du temps qui empêche l'établissement de l'âge biologique d'un individu. Cependant, lorsque les télomères atteignent une longueur critique, les chances de mourir l'année suivante augmentent considérablement. Les télomères chez le hamster réunissent donc certaines caractéristiques utiles pour un biomarqueur du vieillissement comme leurs variations avec l'âge chronologique, une sensibilité aux évènements stressants (variations saisonnières des télomères) et une capacité à prédire la vie restante à très court terme (en moyenne 6 mois avant la mort). Néanmoins, ils ne permettent pas de caractériser l'âge biologique entre des individus de même âge ce qui limite leur utilisation à des questions spécifiques. Les résultats de cette thèse, obtenus à partir de l'analyse des télomères, devront être pris avec précaution et comparés à d'autres études employant d'autres méthodes d'analyse du vieillissement comme la méthylation de l'ADN (Jylhävä et al., 2017).

A travers différentes méthodes, cette thèse aura permis d'apporter une contribution à la fois fondamentale et appliquée à la compréhension de la phénologie des organismes. Sur la base des connaissances actuelles des aspects évolutifs de la phénologie, j'ai tout d'abord proposé plusieurs approches à implémenter pour mieux comprendre les changements de phénologie actuels. Ces approches ont ensuite été appliquées pour mieux comprendre la phénologie de l'hibernation. D'après les informations compilées, je suggère qu'il existe plusieurs causes évolutives de la phénologie de l'hibernation. La pénurie énergétique est probablement un facteur qui explique une partie de la durée de l'hibernation chez de nombreuses espèces hibernantes. Tandis que le moment précis de l'immergence et l'émergence de l'hibernation semblent être expliqué par un compromis entre les bénéfices pour la survie de limiter les risques de mortalité extrinsèque et la reproduction. Comme le proposent Ruf et al. (2012), l'hibernation peut être considérée comme une stratégie employée pour augmenter la survie lorsque les conditions environnementales ne menacent pas directement la vie, mais qui sont sous-optimale pour la reproduction. Les études sur les conséquences évolutives de la phénologie de l’hibernation montrent l’importance de ne pas extrapoler des résultats à l’échelle individuelle alors que les résultats sont obtenus à d’autres échelles (populations, espèces). En effet, j’ai montré dans cette thèse que l’augmentation de la durée de l’hibernation entre espèces était associée à une longévité plus importante. Mais contrairement à ces résultats, chez le hamster commun, l’augmentation de la durée de l’hibernation entre individus semble plutôt être associée à des traits d’histoire de vie rapide. Par ailleurs, la longévité plus importante des hibernants, comparés aux espèces non hibernantes de même taille, pourrait être expliquée par plusieurs hypothèses non exclusives dont certaines reposent sur les conditions physiologiques particulières pendant l’hibernation ou la réduction de la mortalité extrinsèque. Néanmoins, ces résultats ont été obtenus en utilisant les télomères comme biomarqueurs du vieillissement, alors que nous avons pu montrer la complexité de l’utilisation de ce biomarqueur chez une espèce capable d’allonger ses télomères comme le hamster commun. J'espère que cette thèse ouvrira la voie à une intégration plus importante de la phénologie dans les théories évolutives afin de mieux comprendre les changements de phénologie actuels.

Abreviations

e.g.: for example

i.e.: that is

POLS: Pace Of Life Syndrome

***q*PCR**: quantitative polymerase chain reaction

ROS: reactive oxygen species

RTL: relative telomere length

T_b (torp): (Torpor) body temperature

***Viz*.:** which is

Thesis contents

Overall introduction

Note: part of this introduction is the subject of a publication entitled “Towards evolutionary ecology approaches to phenological shifts” presented in supplementary materials.

I. Ultimate causes and consequences of phenology in the context of global change

A. Phenological shift and consequences

Biodiversity is facing increasing anthropic pressures (*i.e.*, global change) such as habitat destruction, pollution and climate change, which threaten the persistence of many animal and plant species (Tilman et al., 2017). Among the observed responses is a shift in their annual timing of life history events (*i.e.*, phenology) such as dormancy, migration or breeding (Cohen et al., 2018). These are common and important adjustments for many species, especially those living in seasonal environments , where the impacts of changing climates are greatest (Pörtner et al., 2022). Seasonal species are supposed to have a relatively similar phenology each year due to fluctuating but somewhat predictable changes in their environment. Phenological shift, as such, is not a phenomenon specific to global change. It is also an adaptation that allows species to adapt to “natural” interannual changes in living conditions. What is unusual is the magnitude and in some case the one-way direction of these changes (Pörtner et al., 2022). Although a variety of anthropic pressures may be responsible for phenological shifts (Lian et al., 2021; Senzaki et al., 2020; Zeng et al., 2013; Zohner, 2019), a major focus over the past decade has been climate and environmental changes (Donnelly and Yu, 2017). Taking as example the influence of climate change, an advance in spring phenology and a delay in fall phenology can be broadly observed with a change of a few days per decade. The mean responses across groups of species for spring phenology rang from advances of 2.3 to 6.1 days per decade and for autumn phenology rang from delay of 1.9 and 4.8 days (Ge et al., 2015; Parmesan and Yohe, 2003; Root et al., 2003; Vitasse et al., 2021).

These responses are not universal and much variation occurs in their magnitude and direction within and among taxonomic groups (Ge et al., 2015; Parmesan and Yohe, 2003; Vitasse et al., 2021; Walther et al., 2002). Amphibians appear to be the most responsive taxon with an advance on the onset of reproduction between 6.1 and 7.6 days per decade (Parmesan, 2007; While and Uller, 2014), while some species show a delayed response in the spring or no adjustment at all (Chen et al., 2017; Forrest, 2016; Klaus and Lougheed, 2013; Lane et al., 2012). Recently, some elements have been identified to explain differences in responsiveness across species such as trophic level , *i.e.*, greater responsiveness by lower level; Thackeray et al., 2016) or altitude , *i.e.*, greater responsiveness by northern populations (While and Uller, 2014). Although, phenological shift has been widely documented across taxa and geographic areas, it nevertheless appears to be complex and requires further investigations to understand the observed differences across species and their consequences.

A shift in phenology may allow adaptation to environmental changes or, on the contrary, may create a mismatch between activities and favorable conditions or between trophic level. Therefore, consequences of global change cannot be estimated simply on the basis of a shift or the absence of a shift (Visser and Both, 2005). Indeed, phenological shift have both positive and negative consequences on individual fitness, *i.e.*, the average contribution to the gene pool of the next generation, which may potentially influence population dynamics (Iler et al., 2021; Visser and Gienapp, 2019). Specifically, consequences at the population level are observed when a change in phenology affects the reproduction of short-lived species or the survival of long-lived species (Iler et al., 2021). In addition, a mismatch between adjacent trophic levels may threaten the balance of entire ecosystems (Solga et al., 2014). For instance, a threefold increase in the spring activity of some insects compared to plants may alter pollination (Parmesan, 2007). Thus, there is an absolute necessity to develop methods to interpret currently observed phenological shifts and predict their future evolution (Hodgson et al., 2011; Kharouba and Wolkovich, 2020; Pau et al., 2011). To achieve this objective, it is necessary to understand both the **physiological** and the **evolutionary aspects of phenology**.

B. Physiological and evolutionary aspects of phenology

Phenology is an adaptation of organisms to conditions that vary in a quasi-predictable manner (*e.g.*, seasonal changes). Throughout the year, individuals have only a limited period of time when conditions are most favorable, *i.e.*, the "optimal period", for performance of activities important for their survival and reproduction. For example, energy-demanding activities such as reproduction require high resource availability (Visser and Both, 2005), and thus are generally performed when annual vegetation or prey are at their greatest abundance. Individuals whose phenology of reproductive activity matches the highest resource periods are expected to benefit from superior fitness. Thus, natural selection should favor an allocation of time between different seasonal activities that maximizes fitness.

In this way, different physiological and molecular mechanisms, known as timekeeping mechanisms, may be selected to track, anticipate, and prepare for these optimal periods (Paul et al., 2008). Many seasonal species rely on highly reproducible environmental factors known as environmental cues or "zeitgeber" (*e.g.*, temperature, photoperiod) from year to year to keep track of time. For instance, species that rarely live longer than one year and/or with opportunistic reproduction need a flexible timekeeper (*e.g.*, interval timer) that relies on the seasonal variation of one or more environmental cues (Paul et al., 2008). However, this mechanism is sensitive to unusual variations in environmental conditions, which are assumed to increase with climate change and may therefore lead to a mismatch (Patterson et al., 2020). On the contrary, in risk averse species (*e.g.*, long-lived species) and/or those without reliable access to environmental cues such as hibernators in their burrows, phenology is produced by endogenous circannual clocks (Paul et al., 2008). These clocks, all synchronized by a master clock within the hypothalamic suprachiasmatic nuclei, are self-sustained under constant conditions but can be fine-tuned by environmental cues along the year (Paul et al., 2008). Regardless of the timekeeper mechanism, environmental cues play therefore an important role in annual rhythmicity. Environmental cues are accurate when strongly correlated with the optimal period from year to year. The modification of these cues *via* global changes may explain, at least partially, the observed phenological shift (McNamara et al., 2011).

Timekeeper mechanisms induce a direct physiological response of phenology, *i.e.*, proximate or mechanistic causes. These mechanisms and more particularly the environmental cues, should not be confused with the biotic and/or abiotic factors that characterize the favorable conditions of the optimal period (*i.e.*, ultimate or evolutionary causes), although some environmental cues may be present in both categories (ultimate and proximate cause). The study of ultimate and proximate causes of phenology is necessary to understand changes in phenological shift and presents a distinct methodology and concepts.

There is a scientific debate about the use of the terms “ultimate” and “proximate”, especially because some proximate factors could also play a role in the evolution of traits and thus also be considered as “ultimate”, making the dichotomy between the terms permeable (Laland et al., 2011). Nevertheless, it remains useful to distinguish “why” (evolutionary approach) and “how” (mechanistic approach) organisms match an activity such as reproduction with a specific time of the year. These two types of approach are based on different timeframes and scale, *e.g.*, individuals or population, to study the same trait (Haig, 2013). Mechanistic studies try to understand how, at a given time (synchronic), one or more individuals (representative of a particular class) synchronize their activity within a specific period. Thus, mechanistic studies are conducive to short-term correlative studies and laboratory experiments. On the other hand, evolutionary studies try to understand why, within a population, selection has favored over time (diachronic) a specific period for a given activity. Long-term monitoring in the wild is therefore generally necessary.

The complementary study of ultimate and proximate factors promotes a better understanding of current responses, and improve prediction of phenological evolution in the face of global change. However, the study of ultimate causes of phenology is relatively low in comparison to proximate mechanisms (table 1). Differences in methodology and in particular the long-term monitoring required for evolutionary studies may explain their restricted number. Thus, there is an important and crucial need to develop evolutionary approach of phenology.

Table 1. Number of publications on the ultimate and proximate causes of phenology according to the activities studied. The results are from a specific search conducted in Web of science on 12/14/2021. Searches include the following terms: (a) TS=(((phenolog*) OR (phenophase*)) AND ("evolutionar*" OR "ultimate$" OR "distal$" OR "fundamental$") NEAR ("cause*" or "factor$" or "mechanism$" or "influence$")) (b) TS=(("phenolog*" OR "phenophase*") AND ((("functional*" OR "proximate$" OR "mechanistic$") NEAR ("cause*" or "factor$" or "mechanism$" or "cue$" or "influence$")) OR "cue$")). The other searches included in addition to the terms used for (a) and (b) the terms: (c) “AND (reproduction OR breeding OR flowering OR masting OR fruiting))”, (d) “AND (growth))”, (e) “AND ("dormancy*" or "hibernation$" or "diapause$" or "quiescence$" or "overwintering"))”, (f) “AND (migration*))”.

	Ultimate (percentage of total)	**Proximate (percentage of total)**
Total [(a,b)]	305	1066
Breeding [(c)]	180 (59%)	602 (56%)
Growth [(d)]	73 (24%)	303 (28%)
Migration [(e)]	36 (12%)	165 (15%)
Dormancy [(f)]	15 (5%)	143 (13%)

C. Ultimate causes and consequences

Ultimate causes (or selective agents) are factors in the social or ecological environment that interact with phenotypic traits by affecting fitness and thus the distribution of the trait in the population (Wade and Kalisz, 1990). An ultimate cause can be identified by measuring the correlation between its variation in time or space and the variation of the distribution of the phenotypic trait in the population. However, natural selection or phenotypic plasticity (see definition below) may not track the ultimate cause perfectly and decrease the detection of the correlation. This does not mean that the selective agent has a weak influence (Merilä and Hendry, 2014). It is then possible to use complementary approaches to find this relationship, such as by the “space for time substitution” method (Pickett, 1989). This method posits that if the variation of the ultimate cause in time (*e.g.*, global warming) is supposed to influence the distribution of phenotypes, it is also possible that the same influence is found in space (*e.g.*, temperature gradient with altitude or latitude). Nevertheless, without demonstrating a causal link, the relationship between the phenotypic and environmental change often remains presumed, especially with the concomitant change of many other environmental factors, as it is the case with global warming (Merilä and Hendry, 2014).

For a direct test of a causal link, it is necessary to modify the ultimate cause in nature, and then measure the effect on the trait distribution (Wade and Kalisz, 1990). Because of the difficulty of setting up this type of study, most of the research of this type is carried out in controlled laboratory conditions or in micro/mesocosms (Merilä and Hendry, 2014; Van Doorslaer et al., 2007). At the interspecific scale, the phylogenetic comparative method can be used to identify an ultimate cause by comparing its variation with the distribution of the phenotypic trait among species, which also allows testing for past selection, which is termed macroevolution (Paradis, 2014). Nevertheless, precautions must be taken when studying macroevolution because traits may have evolved in the past, but no longer be under current natural selection. Thus, evolutionary studies are more conducive to longer-term studies in natural environments with causal links that are more difficult to establish compared to mechanistic studies.

A complementary approach is to evaluate the ultimate consequences, *i.e.*, how organisms evolve in response to the ultimate cause. First, ultimate causes affect the fitness of an organism. Fitness is a complex metric supposed to reflect the average contribution of an individual to the gene pool of the next generation, for which a large number of measures have been proposed ranging from more “theoretical” to more “practical” ones. In the wild or laboratory, population monitoring may provide practical fitness estimates such as annual adult survival and reproductive success (see Dobson et al., 2020; Viblanc et al., 2022). Then, current selection (also termed “microevolution”) and response to selection can be observed within and between generations of a population by a change in the distribution (*e.g.*, mean value) of a phenotypic trait (here phenology) and allele frequencies of the associated genes (Wade and Kalisz, 1990). A part of the trait variation within and between generations may be explained by phenotypic plasticity. Phenotypic plasticity is a trait itseld, and thus subject to selection, to produce different phenotypes in response to contrasted environmental conditions (Lane et al., 2019; Nussey et al., 2007). In addition, another part of phenotypic variation between generation is attributed to genetic variation (heritability) and studied by quantitative genetic methods (Lane, 2012). Several methods allow evaluation of whether the phenotypic change is related to a genetic or plastic change, such as "animal model analyses" or "common-garden studies” (see review by Merilä and Hendry, 2014). To summarize, there are 3 sources of phenotypic variation: **microevolution** of traits, **plasticity** of traits, and **microevolution of plasticity**.

Finally, phenotypic variation can be considered adaptive if fitness in the population is maintained following environmental change, otherwise the change is considered non-adaptive. A distinction can be made between whether it is the direction or pace of phenotypic change that is adaptive, with complete adaptation requiring both direction and pace (Boutin and Lane, 2014). Some methods are used to determine whether a phenotypic change is adaptive such as « reciprocal transplants » or « phenotypic selection estimates » (review in Merilä and Hendry, 2014). Measuring the current level of phenotypic plasticity, genetic variability and heritability allows estimation of the adaptability of a species or population to environmental change. Adaptability is the “ability to become adapted to live and reproduce under a particular range of environmental conditions” (Angeler et al., 2019). Furthermore, in the same way as for ultimate causes, the consequences of past selection can be studied at the interspecific scale by comparative phylogenetic methods. With proper precautions, the consequences of a past selection may also provide insight on future selections.

Hence, measuring phenological shift or absence of shift does not indicate whether it is adaptive or how much organisms should shift in order to become adaptive. Answers to these questions can be provided by methods based on the ultimate causes and consequences of phenology.

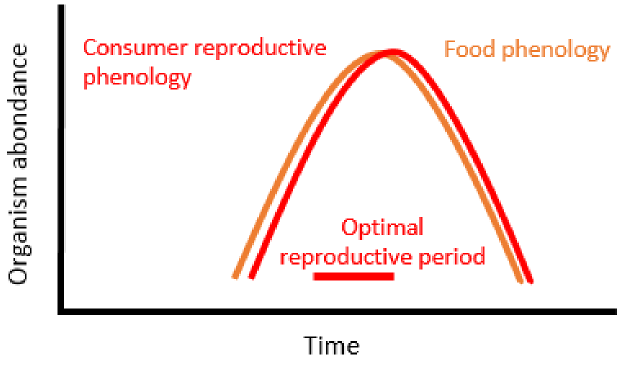
D. A method for studying phenological shifts

The first step is to identify the ultimate causes and thus the optimal period of activity under study. Then, to measure to what extent the phenological shift alters or not the match with the optimal conditions, it is necessary to measure the gap, in time units (*e.g.*, day or month), between the optimal period of the activity and its phenology (Fig. 1) (Visser and Both, 2005). There may not be a mismatch if the timekeeper mechanisms still track the optimal period, with or without adaptation due to environmental changes (*via* microevolution or phenotypic plasticity). However, current adaptive responses appear insufficient for keeping up with the speed of global change (Radchuk et al., 2019). On the contrary, in this changing environment, previously reliable timekeepers may no longer be adaptive. In this case, organisms may be "trapped" by their evolutionary responses to cues and suffer survival or reproductive costs. This phenomenon is called evolutionary trap (Schlaepfer et al., 2002).

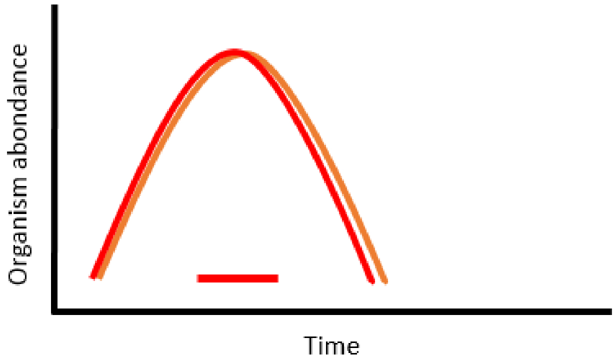
Then, ultimate consequences allow an understanding of current trait changes and predict future phenological shifts, given the specific population dynamics. For this purpose, the second step is to measure the effect of the gap between the optimal period of activity and the current phenology on fitness (ultimate consequence), with negative consequence supposed to increase with the gap's length. This step may be performed from a monitoring of the population in the wild or in laboratory experiments to isolate specific effects, with the necessary precautions for the interpretation. Furthermore, predictions of population dynamics can also be improved by studying such trait phenomena as phenotypic plasticity or microevolution (see section "ultimate causes and consequences"). Phenotypic plasticity is assumed to be an important mechanism for short-term response and may be limited in responding to long-term directional change (Bernstein et al., 2008). "Natural" year-to-year shifts that occurred in the past were the basis of the evolution of plasticity in phenological events. It is on this plasticity that current shifts are initially based, and it is when anthropogenic shifts exceed the scope of adaptive plastic responses that species will fail to adjust. Thus, phenotypic plasticity is assumed to be an important mechanism for short-term adaptation and may be limited in responding to long-term directional change (Bernstein et al., 2008). Microevolutionary change is therefore assumed to be necessary for population survival in the long term (Phillimore et al., 2010).

Although the first step based on ultimate causes of phenology is a prerequisite, few evolutionary approaches have been proposed to improve it (Visser and Both, 2005) unlike the second step on ultimate consequences (Charmantier and Gienapp, 2014; Dobson et al., 2020; Nussey et al., 2007; Viblanc et al., 2022; Zettlemoyer and Peterson, 2021). In addition, the study of phenological shifts would greatly benefit from the improvement of fundamental knowledge about the ultimate causes and consequences of phenology. In the following, we will present under-studied approaches that can be used to improve our knowledge of the evolutionary causes and consequences of phenology. More specifically, these approaches aim to show (1) the interest of studying the phenological shift of other activities than reproduction (*viz*., annual survival approach) (2) the diversity of ultimate causes (*viz*., community approach) and (3) the importance of trade-offs between fitness components to understand the evolution of phenology and their consequences (*viz*., trade-offs approach). These approaches presenting the missing information in the field of ultimate causes and consequences of phenology were a basis on which the objectives of this thesis have been developed.

a) Historical relationship



b) Environmental changes with matching



c) Environmental changes with no matching

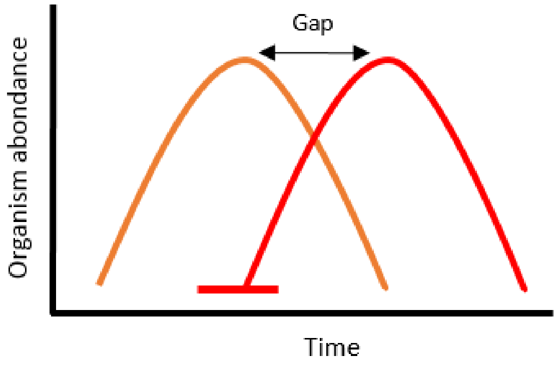


Figure 1. Schematic representation of environmental changes effect on phenology with matching or non-matching between phenology and the optimal period. In this example, the optimal period for the phenology of reproduction corresponds to the peak of food availability. The advance of food availability, compared to a) the historical relationship, leads to b) an advance of the phenology of reproduction or c) a gap between the optimal period and the

phenology of reproduction (c). The length of black double arrow indicates the extent to which a species should shift to adapt to its changing environment. This figure was inspired by Iler et al. (2021).

II. Missing knowledge of ultimate causes and consequences of phenology

A. Annual survival approach

The annual survival approach is based on the simple premise that during the year several seasonal activities exist, and their phenology may influence survival and reproduction. Focusing on the impact of environmental changes on the phenology of only one of these activities may produce inaccurate predictions about future population dynamics. As studies have so far focused on reproduction (Table 1), we propose an approach to investigate the link between phenology and survival that could be applied to virtually all species. We introduce this approach using hibernation and migration, as it is particularly relevant for these species with strong seasonal patterns of survival

The focus of the research on reproduction phenology (*i.e.*, reproductive success approach) may be explained by its major influence on the life histories of species. Plant breeding phenology (flowering, fruiting, and masting) influences the duration of primary production and thus the phenology of higher trophic levels (Morellato et al., 2016). This focus may also be explained by the fact that plant and animal reproduction phenology has economical relevance for humans (Chmielewski, 2003). Such knowledge enables estimating of future yields (Diao et al., 2021) or increasing productivity (Chemineau et al., 1992). In many animals, the timing of reproduction can have a considerable influence on reproductive success and thus on population dynamics. For some species, reproductive success depends on whether the key events of reproduction (hatching, lactation, weaning) matches the peak of food availability (Both, 2010), or if births occur early enough in the year so that newborns have time to grow, develop, and accumulate sufficient energy reserves before the onset of adverse environmental conditions and subsequent recurrent event such as hibernation (Franceschini-Zink, 2008; Murie and Harris, 1982; and see Bieber et al., 2012). Nevertheless, these researches focus only on one part of the year (the reproduction period) while the survival strategies employed during the rest of the year when conditions deteriorate are understudied. To be more specific, some studies have already focused on the phenological shift of these survival strategies to deteriorating conditions (*e.g.*, dormancy and spring migration), but especially for their key role on reproductive success (Charmantier and Gienapp, 2014; Gallinat et al., 2015; Gordo, 2007; Lane et al., 2012). However, a parameter rarely estimated, but potentially sensitive to phenological shift, is the relatively high survival rate during such activities compared to the reproduction period.

Spending a lot of time in reproduction is supposed to increase mortality risks because of oxidative stress related to high energy expenditure (Alonso-Alvarez et al., 2004) and predation risk from increased locomotor activity to find partners as well as visual, olfactory, and vocal signals (Magnhagen, 1991). Among traits that favor survival during adverse conditions, some animals remain on the breeding sites and drastically modify their behavior, morphology and physiology. Other adaptations are characterized by prolonged inactivity of several months, associated with hypometabolism and hypothermia such as hibernation, dormancy and diapause. This type of life history is found across the animal kingdom, and even occurs in *Echinoderms* (Bao et al., 2010; Klanian, 2013), despite earlier evidence to the contrary (Guppy et al., 1994; Hand, 1991). There are important differences between some groups of species, with respect to physiological aspects of “dormancy” (later used as an overarching term as in Wilsterman et al., 2021). For example, ectotherms (invertebrates, fishes, reptiles and amphibians) have little or no physiological control over the induction of hypometabolism and hypothermia compared to endotherms. So, ectotherm dormancy is assumed to be more temperature-dependent (Staples, 2016 but see Constant et al, 2022 in prep). Heterothermic endotherms (mammals and birds) are species capable of maintaining a high and relatively constant body temperature but unlike homeothermic endotherms, heterotherms are able to actively and drastically modify their metabolism and body temperature during phases called torpor (for more details see section “Energetic constraint”). However, strong similarities have allowed the recent creation of a universal framework that classifies these strategies along just 3 axes (induction, recalcitrance and magnitude) irrespective of their phylogeny (Fig. 2; Wilsterman et al., 2021).

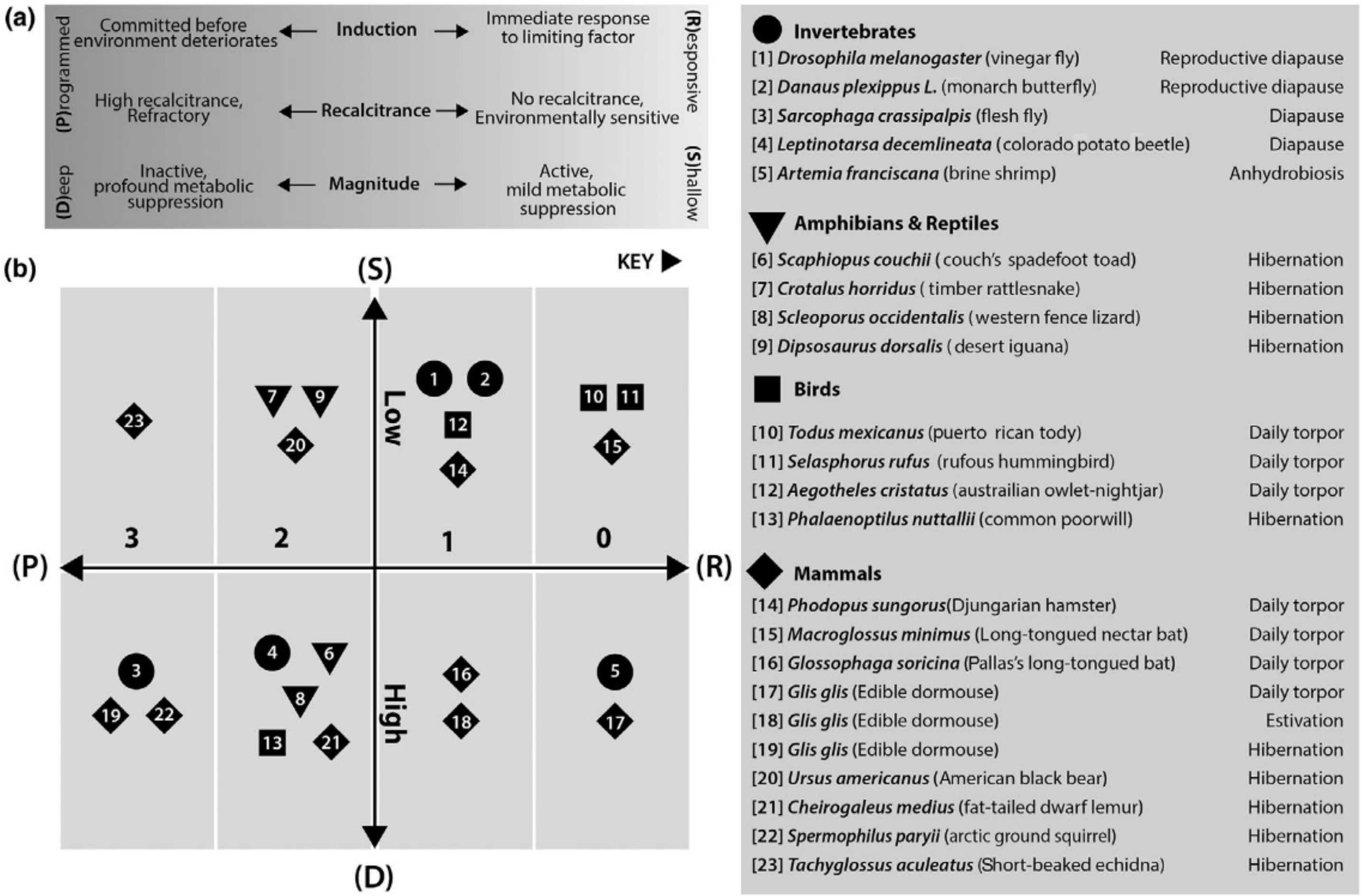


Figure 2. The major axes distinguishing animal dormancies. (a) The three axes of dormancy, which differentiate deep, programmed dormancies from shallow, responsive dormancies (see text for further description of axes). (b) Using the framework to classify dormancies of invertebrates, amphibians and reptiles, birds and mammals. We compiled information from the literature on the degree of programming and metabolic suppression (as a measure of magnitude) of representative dormancies for some well-studied dormancy models (Table S4). Some species or individuals may display multiple types of dormancies in different life stages or in response to different environmental challenges, and these dormancies can be compared within the framework as well. Glis glis [17, 18, 19] is included here as a well-described example. We collapsed induction and recalcitrance into one axis describing the degree of

programming (P = programmed, R = responsive), with grades of 0 (responsive induction, low recalcitrance); 1 (programmed induction, low recalcitrance); 2 (programmed induction and moderate recalcitrance), or 3 (programmed induction, high recalcitrance). We characterized dormancy magnitude (D = Deep, S = shallow) as a dichotomous variable (high/low) based on the degree of metabolic suppression (per cent of basal or standard metabolic rate in a dormant animal compared to a similarly staged non-dormant animal), where high corresponds to >90% for endotherms and >70% for poikilotherms. Note that feeding rate was used in Drosophila melanogastor as no metabolic rate data were available. Species key is on the right. Figure and legend were extracted from (Wilsterman et al., 2021).

Dormancy is associated with a high survival rate when compared to the active season (Bauwens, 1981; Litzgus et al., 1999; Ruby and Dunham, 1984; Sperry et al., 2010; Tanner and Jorgensen, 1963; Turbill et al., 2011; Wilson and Cooke, 2004) and increased longevity at both intra- and interspecific levels, compared to similar size non-dormant species (Lyman et al. 1981, Wiklund et al. 2003, Wilson and Cooke 2004, Collatz 2006, Turbill et al. 2011, Magombedze et al. 2018). The causes responsible for the increased longevity and survival associated with hibernation is discussed in the following section "Community approach”.

In contrast, other animal species escape from deteriorating living conditions by changing their physical location. This type of seasonal migration, called "refuge" migration, consists of an annual two-way movement between at least one place, often favorable for reproduction, and another place that improves the survival of adults or newborns for the rest of the year (Shaw, 2016). This pattern is common throughout the tree of life in taxa with a high capacity for mobility (Alerstam et al., 2003). According to several studies, migratory individuals or species show either higher (Moenkkoenen, 1992; Møller, 2007; Winger and Pegan, 2021; Zúñiga et al., 2017) or lower (Buchan et al., 2020; Soriano-Redondo et al., 2020) annual survival or longevity compared to residents. Similarly, additional studies, mainly on birds, show a lower, similar or higher survival during the non-reproductive period than during the breeding season (lower: Leyrer et al., 2013; Robinson et al., 2020; similar: Robinson et al., 2020; Rockwell et al., 2017; Sillett and Holmes, 2002; higher: Blackburn and Cresswell, 2016; Buechley et al., 2021; Dokter et al., 2018; Lok et al., 2015; Swift et al., 2020). Mortality during migratory movement appears to vary among species ranging from low (Conklin et al., 2017; Leyrer et al., 2013; Senner et al., 2019) to high mortality risk (Rockwell et al., 2017; Rushing et al., 2017). Such variation could be explained by different strategies and contexts of seasonal migration among species (Winger and Pegan, 2021), but also perhaps by a greater sensitivity of migratory species to current anthropogenic changes (Both et al., 2010; Buchan et al., 2020). Across taxa, it is assumed that migration is adaptively favored if the costs incurred during the migration movement (*e.g.*, high predation risk, negative energy balance) are less important than the benefits of changing habitat (Alerstam et al., 2003; Fryxell and Sinclair, 1988). The causes responsible for the increased longevity and survival associated with migration is discussed in the following section "Community approach”.

Phenological shifts may modify the time allocated between seasonal activities with different survival values, such as reproduction compared to dormancy or migration. These changes alter survival over time and thus the annual survival with potential consequences on population dynamics. The “space for time substitution” method may help to investigate the relevance of this annual survival approach using the example of climate change (Blois et al., 2013). This method is based on the use of contemporary spatial phenomena to understand and model temporal processes that are not observable (future or past). For example, some ectotherms and endotherms show decreasing time allocated to dormancy and decreased survival, with decreasing altitude and latitude, and thus warmer climate (Adolph and Porter, 1993; Bronson, 1979; Murie and Harris, 1982; Nevo and Amir, 1964; Pianka, 1970; Turbill and Prior, 2016). Thus, differences in annual activity patterns at the spatial scale is associated with annual survival variation, which presumes an application of this annual survival approach to climate change in time (Turbill and Prior, 2016). Based on this approach, phenological shift, even if it leads to a perfect match with the environmentally influenced change in optimal period, may induce changes in annual survival. In addition, this effect may influence the entire life history of organisms if phenological shifts affect the allocation of time between different activities associated with competing fitness components (see trade-off approach).

On the contrary, an imperfect match with the optimal period may also lead to a discrepancy between preparation (*e.g.*, quantity and quality of energy reserves to store) and energy requirements during these periods, which may decrease the usually high survival rate during dormancy (Chinellato et al., 2014; Cordes et al., 2020; Reading, 2007; but see Ozgul et al., 2010) and non-breeding periods of migrators (Belpaire et al., 2009; Klaassen et al., 2012). In addition, changes in environmental conditions are also likely to promote other mortality risks associated with disease or parasite transmission (migration: Crossin et al., 2008; hibernation: Maher et al., 2012). The adaptability of species (microevolution and phenotypic plasticity) should therefore be a determinant factor for maintaining a high survival rate during these activities.

These illustrations of some migrating and dormant species are perhaps one of the most striking in terms of survival differences between seasonal activities, but an annual survival approach as stated above could be extended to other species that show significant variation in mortality between their seasonal activities. The annual survival approach highlights the need for knowledge about the ultimate causes and consequences, not only on reproduction, but also on other seasonal activities to predict future impact on annual survival. Ideally, the annual survival approach should be coupled with the study of other life history traits because a change in a single life history trait may influence trade-offs between energy allocation and thus overall life history (Healy et al., 2019).

B. Community approach

The community approach is based on the principle that the optimal period of an activity may be explained by several ultimate causes. By focusing on a single pairwise interaction (phenology-environmental factor), the determination and impact of the optimal periodmay be misidentified. In this section, we focused primarily on biotic factors that can influence the optimal period of an activity to develop the concept of phenology as a means of defense against extrinsic mortality risks (*e.g.*, competition, predation) or on the contrary as a competitive advantage. Nevertheless, the inclusion of abiotic factors should constitute an even broader approach (ecosystem approach).

Among seasonal activities, the optimal period for reproduction is the most studied. It is assumed that the main ultimate cause is the peak of food availability and its influence on reproduction (Bronson, 2009; Visser and Both, 2005). The temporal match-mismatch hypothesis suggests that the consumer species (*i.e.,* predators, herbivores) match their period of peak energy demand with that of peak resource (*i.e.*, prey, plants) availability (Visser and Gienapp, 2019). This hypothesis has been widely demonstrated from the relationship between the peak of food availability and egg laying or hatchling in birds (Both, 2010; Tomás, 2015), but is also verified in other taxa such as primates (Meyers and Wright, 1993), bats (Cumming and Bernard, 1997), rodents (Kenagy et al., 1989), and fish larvae (Durant et al., 2007). Recently, it has been generalized to interactions between plants and pollinators (Hegland et al., 2009), and parasites and their hosts (Paull and Johnson, 2014). Because of its major influence, the timing of the resource peak may be used as a yardstick to determine whether breeding phenology has been sufficiently adapted to climate change (Visser and Both, 2005). Additional metrics have been suggested, including the height and width of the resource peak (Visser and Gienapp, 2019). Indeed, the impact of a lag in the reproduction period, in relation to the food peak, on reproductive success could be reduced in years of high food abundance.

However, this pairwise concept between food peak and reproduction phenology may not be sufficient to determine the optimal period of reproduction, questioning its efficacy as a yardstick (Nakazawa and Doi, 2012). It has recently been suggested that the study of a species phenology should be integrated into the functioning of its ecosystem, and should thus take into account interspecific interactions (Lindén, 2018; Nakazawa and Doi, 2012). Indeed, antagonistic (*e.g.*, predation, competition) and beneficial (*e.g.*, mutualism, cooperation, and symbiosis) interactions should favor respectively, a mismatch and a match between species (Lindén, 2018). For example, high nesting predation during the breeding season can lead to delays (Hušek et al., 2012; Reneerkens et al., 2016) or advances (Götmark, 2002) in laying dates in relation to food peaks. In this case, the optimal period for reproduction is the result of a trade-off between high food availability and predation risk (Fig. 3a). There are examples in other taxa of the influence of interspecific relationships (other than a consumer towards his resource) on reproductive phenology. In plants for example, flowering phenology might be determined by competition for pollinators (de Jong and Ahlén, 1991). An exterme example is the winter firefly (*Ellychnia corrusca*) where reproduction takes place in the spring to escape its specialist predators that are active in the summer (Deyrup et al., 2017).

The influence of these other interspecific relationships does not seem to be limited to the reproductive period, but would concern the whole annual cycle including survival strategies (*e.g.*, dormancy and migration) supposed to be employed only during adverse season. Dormancy is still widely seen as an adaptation only used for energetic reasons in unfavorable conditions (temperature extremes, lack of food, water stress). And indeed, in various taxa, increased energy constraints along latitudinal and altitudinal gradients (associated with a decrease in primary productivity and temperature, etc.) is accompanied by an increase in dormancy duration (Pianka, 1970; Turbill and Prior, 2016; Wilsterman et al., 2021). Energy constraints are assumed to influence at least part of the optimal dormancy period. Other abiotic factors have been proposed to favor dormancy, such as water stress especially in summer (*i.e.*, estivation) and in non-Holarctic regions (Abe, 1995; Nowack et al., 2020). Nevertheless, other evidence suggests that dormancy is not initiated solely in response to deficiencies in energy, water, or poor food quality.

Several observations in both heterothermic endotherms and ectotherms seem to suggest that dormancy may occurs while energetic conditions may enable activity. Decreased metabolism in dormancy reduces the need to forage, and allows remaining hidden in safe shelters or by displaying camouflage (Denlinger, 2009). Thus, dormancy is supposed to reduce the risks of extrinsic mortality (*e.g.*, predation, competition) in at least some species (Ruf et al., 2012). For example, the edible dormouse (*Glis glis*) and the Eastern chipmunk (*Tamias striatus*) are rodents that express hibernation while there is sufficient food and water for activity, but supposedly to escape predators (Hoelzl et al., 2015; Humphries et al., 2002;

Munro et al., 2008). A similar example is observed in insects where the female common brimstone butterfly (*Gonepteryx rhamni*) delays exit from dormancy compared to males (3 weeks), despite favorable energetic conditions, presumably to avoid extrinsic mortality prior to breeding (Fig. 3b) (Wiklund et al., 1996). In some species, early entry or exit from dormancy may limit competition with other species. For instance, in the Eastern Montpellier snake (*Malpolon insignitus*), early emergence would provide a competitive advantage at basking sites over another species using the same dormancy burrow (Dyugmedzhiev et al., 2019). Although, no causal link demonstrate that these factors are ultimate causes of seasonal dormancy, some experiments have been able to demonstrate the influence of predation (Turbill and Stojanovski, 2018; Turbill et al., 2019) and competition (Levy et al., 2011) on the induction of daily torpor (torpor lasting less than 24 hours) in several species (see section "Energetic constraint" for more details).

The causes of migration vary across species and ecosystems. Refuge migration is evolutionarily favored in response to seasonal changes in food availability, weather, or predation risk (Shaw, 2016). In both terrestrial and marine mammals, predation risk for adults or newborns (migratory movement to specific calving areas) is believed to be an important factor promoting migration to a safer location (Avgar et al., 2014; Fryxell and Sinclair, 1988; Shaw, 2016). Several experiments with partial migration of fish populations elegantly demonstrate that the influence of risk or perceived risk of predation are important factors determining individual migration (Brodersen et al., 2008; Hulthén et al., 2015; Skov et al., 2011). In both mammals and fishes, migration can even be towards a less favorable place from an energetic point of view, but with a less intense risk of predation (Fig. 3c) (Brodersen et al., 2008; Hebblewhite and Merrill, 2011). Finally, other types of antagonistic interaction could be important causes of migration, such as parasite avoidance (Poulin and de Angeli Dutra, 2021).

There are still too few studies regarding the importance of interspecific interactions as ultimate causes of phenology, compared to food availability. Present evidence suggests that such factors may have a significant influence, and may be spread across taxa and activities. Thus the way organisms organize their activities (*e.g.*, daily, annual) can be seen as a mean of defense against predators and/or a way to limit competition, allowing the coexistence of species within an ecosystem, or on the contrary to confer a competitive advantage (see coexistence theory; Blackford et al., 2020). A prominent example on a daily time scale is the hypothesis that in the past, mammals were nocturnal to avoid predation and competition with dinosaurs during daytime (Gerkema et al., 2013). An interesting perspective is the recent addition of a temporal dimension to the “landscape of fear” theory. This theory proposes that the perception of predation risk by a prey species influences its organization in space and time (Kohl et al., 2018). This adaptive role of phenology has long been underestimated and could have consequences for the life histories of species.

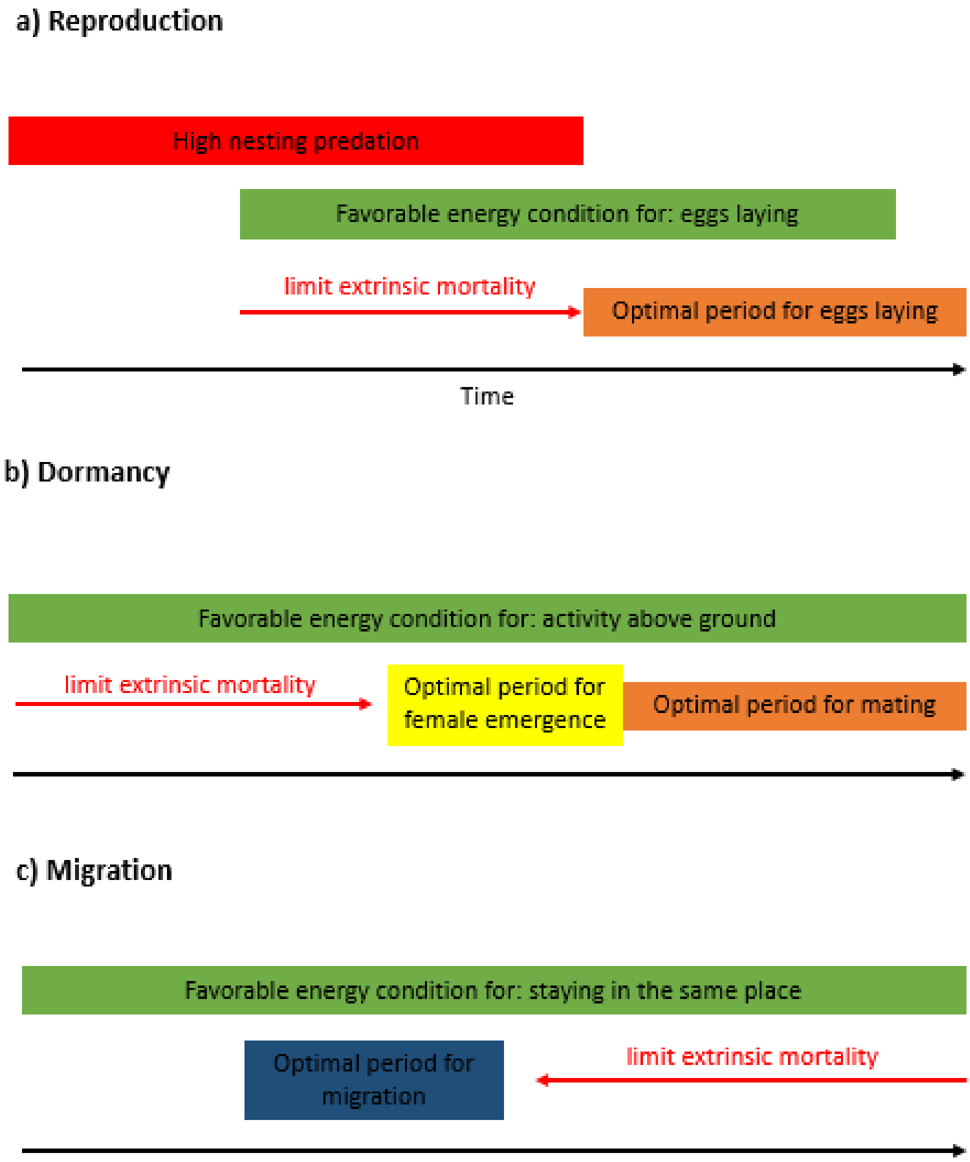


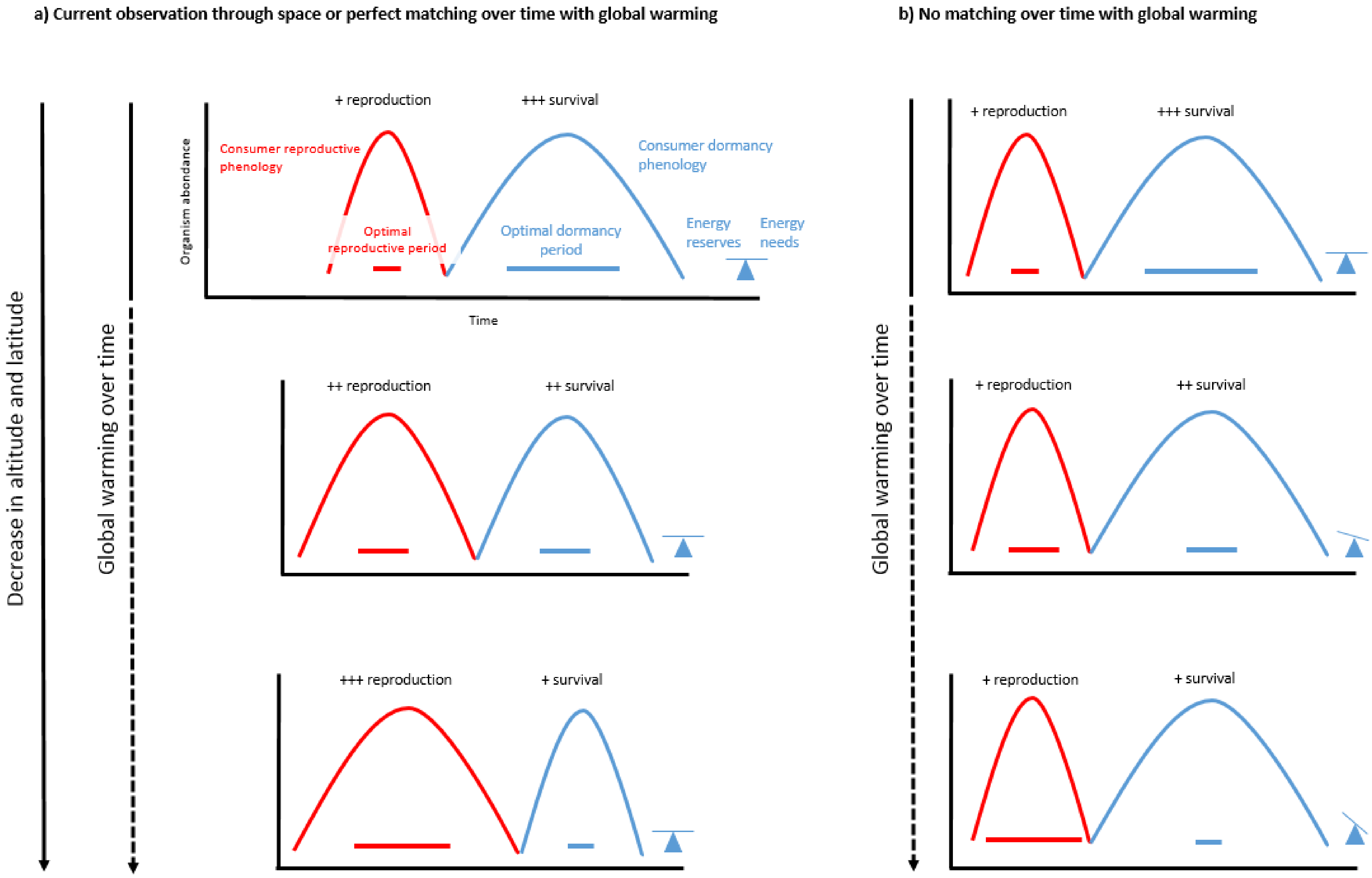
Figure 3. Schematic representation of interspecific relationship (*e.g.*, predation) influence on optimal period of phenology for several seasonal activities. In these examples, food availability (supposed to be the major cause of optimal period in the reproductive success approach), does not explain the optimal period of these activities alone. The red arrow represents the survival benefits of a phenological shift compared to what might be expected from an energetic point of view. These examples represent a) a high early clutch predation favor a later reproductive timing compared to food peak (Reneerkens et al., 2016), b) females of dormant

species emerge late compared to males whereas the energetic conditions are favorable, perhaps to limit the risks of dying before mating (Wiklund et al., 1996), c) partial migratory fish population where part of the individuals seem to migrate to limit predation risks while energetic conditions are less favorable on the migration site (Brodersen et al., 2008; Hebblewhite and Merrill, 2011).

C. Trade-off approach

The trade-off approach is complementary to the ideas developed in the reproductive success, annual survival and community approaches. It is based on the principle that, like energy, time is a finite resource that must be shared between different activities. Time allocation can create trade-offs between activities that influence different components of fitness (*e.g.*, growth, reproduction, survival). In evolutionary ecology, trade-offs may explain the maintenance of different life history patterns at different scales of life (*e.g.*, inter-specific, inter-individual). The trade-off approach is intended to better understand phenology evolution and its integration in evolutionary theories.

The time allocation trade-off should provide an understanding of the evolution of seasonal activities which influence competing fitness components. For example, hibernation phenology may have evolved based on a trade-off between the survival benefits of being in hibernation and the reproductive benefits of being active (Willis, 2017). In several species, individuals that do not reproduce hibernates for up to several weeks earlier than other members of the same population (Choromanski-Norris et al., 1986; Michener, 1978; Millesi et al., 1998, 2008; Neuhaus, 2000; Nicol and Morrow, 2012). Phenological shifts in activities subject to a time allocation trade-off may have consequences for overall life history traits. In the “annual survival approach” discussed above, we suggested that annual survival of dormant species decreases with decreasing time allocated to dormancy and increasing ambient temperature in space. However, increasing temperature in space may also be associated with increased time allocated to reproduction and faster life history traits (Adolph and Porter, 1993; Bronson, 1979; Murie and Harris, 1982; Nevo and Amir, 1964; Pianka, 1970; Turbill and Prior, 2016). According to the method of space for time substitution, the effects of increasing temperature in space should be expected with global warming in time in the case of a perfect matching (between activity phenology and their optimal period; Fig. 4a). However, in the case of imperfect matching, reproductive success may not increase and annual survival may even decrease due to an imbalance between energy reserve and expenditure during dormancy (Fig. 4b).



a) Current observation through space or perfect matching over time with global warming

b) No matching over time with global warming

Figure 4. Schematization of the space for time substitution method applied to phenological shift with global warming. a) Represents the change in time allowed between reproduction and dormancy as well as life history changes observed with decreasing altitude and latitude. Thus, the optimal period for reproduction is expected to increase and the optimal period for hibernation is expected to decrease with decreasing latitude and altitude. Based on this method, the same pattern is assumed with global warming over time in the case of a perfect match between the phenology and their optimal period. Survival decreases as dormancy duration decreases due to the increased risk of mortality associated with aboveground activity. In this case, we assume a maintenance of the balance between energy reserves and expenditure during dormancy with phenological shift over time, having no additional impact on survival. b) Represents the case of no phenological shift and a mismatch between phenology and optimal period following global warming. In this case, we assume an imbalance between energy reserve and expenditure during dormancy, decreasing survival. For example, increasing ambient temperature during dormancy with climate change is thought to increase energy expenditure. The dotted part of the arrows represents the prediction in the future. Note: the scheme is intended to illustrate life history changes in time and space and the magnitude of these changes (especially between (a) and (b)) is not to scale.

Variation in phenology may therefore be associated with variation in life history traits. We can therefore speculate about the theories that explain variation in life history traits may be applied to explain variation in phenology at different scales (*e.g.*, inter-specific, inter-individual). Life history theory proposes that life histories first vary with the body size of species such that large animal species usually have later sexual maturity, lower annual reproductive rate, and longer longevity compared to small species (Dobson, 2007). However, at a given body size, species, populations or individuals can be distributed along a slow-fast continuum. At the slow end, there are species that invest more energy in survival with smaller litter size, slower growth and later sexual maturity than at the fast end (Stearns, 1989). The pace of life syndrome is an extension of this theory that proposes to add physiological, hormonal and behavioral parameters with a similar trade-off along this axis (Réale et al., 2010). For example, individuals with slow life history would tend to have a risk-averse behaviors, low sensitivity to oxidative stress and high immune response. The distribution of time allocated to activities with a strong trade-off between survival and reproduction may therefore be distributed along these axes.

A few studies have attempted to develop this concept across different taxa. In plants, for instance, species with a fast life history strategy have a more opportunistic phenology in spring (*e.g.*, development with increasing temperature) allowing them to have a longer growing season, but at the same time are more likely to be impacted by frost (Tang et al., 2016). In boreal birds, long-distance migration would result in higher annual survival than short-distance migration. However, the time spent on the breeding grounds is shorter and these birds have lower clutch sizes and annual fecundity (Winger and Pegan, 2021). The authors therefore propose that migration distance, which is linked to species phenology (MacMynowski and Root, 2007), should be included as an axis of pace of life in these bird species. The pace of life syndrome is also interesting for explaining the maintenance of inter-individual differences within the same population (Réale et al., 2010). Phenology of certain activities could therefore be associated with some behavioral, physiological or hormonal parameters. In Eurasian blackbird (*Turdus merula*), there seems to be a link between the exploratory character of individuals (fast-slow) and their breeding phenology that depends on perceived predation levels (Abbey-Lee and Dingemanse, 2019). Another example is that in a migratory fish population with migratory and resident individuals, bold individuals are more likely to migrate than shy ones (Chapman et al., 2011).

A last intriguing example is the case of the edible dormouse (*Glis glis*), a hibernating mammal. With increasing age, edible dormouse spent more time breeding and less time hibernating. Old individuals are less likely to encounter good conditions (masting year) to reproduce in the future (Bieber et al., 2018). It was suggested that they take more risk to reproduce (especially in terms of predation) and thus spend a longer period while breeding. The authors proposed that in this species, hibernation should be seen as « an age-affected life history trait that is flexibly used to maximize fitness ».

If the phenology of an activity involves trade-offs between survival and reproduction, then the optimal period within a population may be viewed as a continuum with each end being associated with an energy and time allocation strategy. Attention should be drawn to identify this type of trade-off that might maintain inter-individual differences in phenology. Furthermore, inter-individual differences are a prerequisite for natural selection, and as phenology has a strong genetic component (Forrest and Miller-Rushing, 2010), these studies could provide a better understanding of the adaptability under global change.

D. Application to phenological shifts

Ideally, studies aimed at better understanding and predicting the phenological shifts exhibited by a species should be conducted from a holistic approach that takes into account the full range of activities and the variety of trophic interactions of species, paying attention to inter-individual differences. But this type of study is complex to design and execute.

Therefore, researchers should investigate the different approaches presented here when: (1) the phenological shift does not reflect the general trend observed that is advanced spring phenology and delayed autumn phenology (see section “Community approach”) (2) the ultimate cause of phenology does not correspond to a common pairwise interaction with food availability (see section “Community approach”) (3) population dynamics are not consistent with the change in reproductive success with phenological shift suggesting an impact of phenological shift on other fitness component (see section “Annual survival approach”) (4) there is a large interindividual difference in the phenology of an activity (see section “Trade-off approach”). Furthermore, the integration of the phenology of certain activities into the pace of life syndrome and the landscape of fear seems to be an interesting prospect. It could provide a better understanding of the causes underlying the maintenance of interindividual differences in phenology and therefore of the adaptive potential of species in the face of anthropic pressure. These approaches show the need to study the diversity of ultimate causes in a variety of seasonal activities, to understand phenological shift (Fig. 5) but also the adaptive role of phenology in general. Following this principle, the studies constituting this thesis focused on the determination of evolutionary causes and consequences of dormancy phenology and more specifically the seasonal expression of hibernation in mammals.

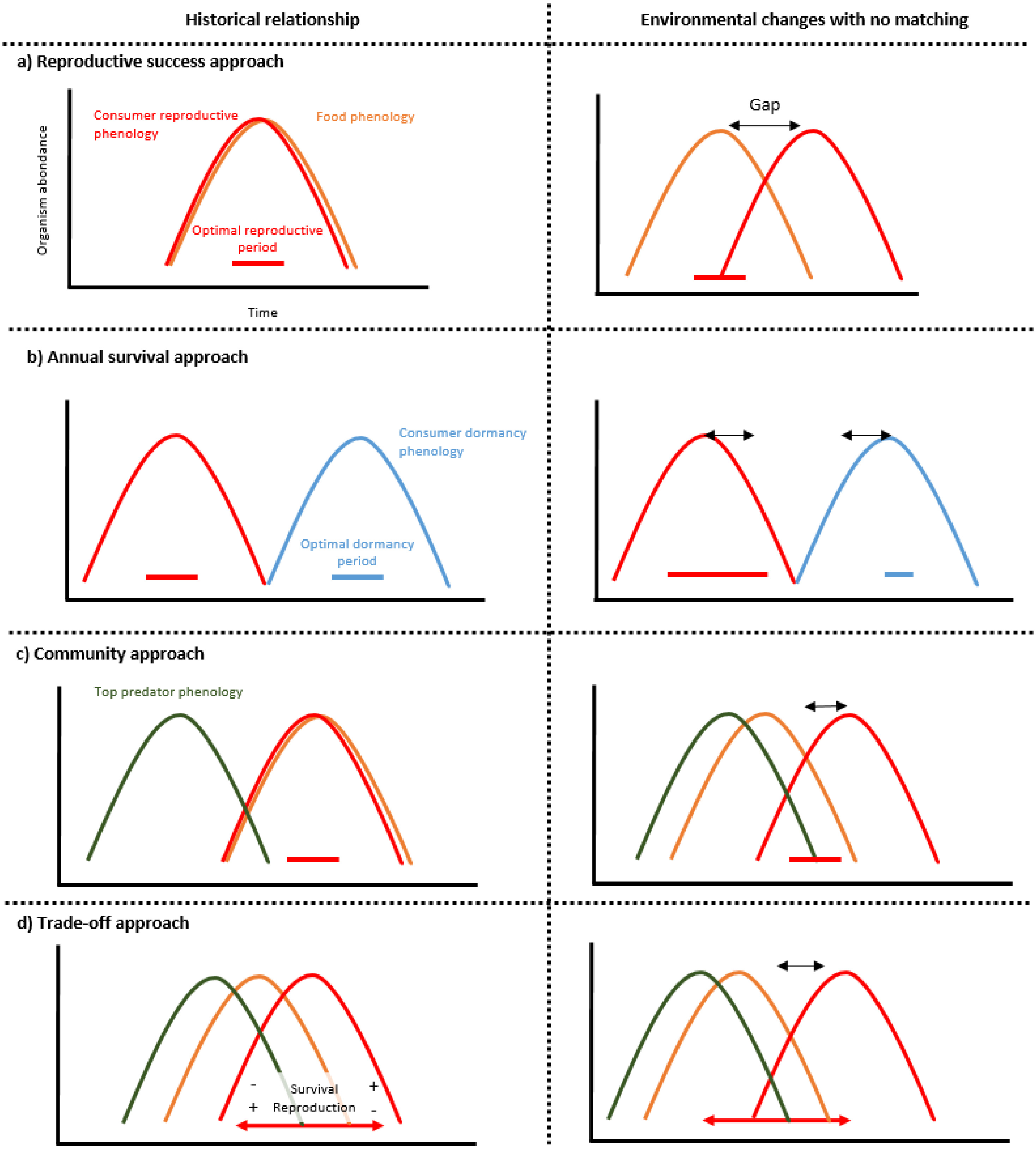

Historical relationship
Environmental changes with no matching
a) Reproductive success approach
Organism abondance
Consumer reproductive phenology
Food phenology
Optimal reproductive period
Time
Gap
b) Annual survival approach
Consumer dormancy phenology
Optimal dormancy period
c) Community approach
Top predator phenology
d) Trade-off approach
- Survival +
+ Reproduction -

Figure 5. Schematic representation of the optimal period of activity and its gap with phenology following environmental change according to the different approaches presented. The length of black double arrow indicates the extent to which a species should shift to adapt to its changing environment. a) The reproductive success approach is based on the measurement of the gap between the peak of food abundance and reproductive phenology. b) The annual survival approach takes into account the gap of different seasonal activities to measure the effect on annual survival. c) The community approach takes into account the different interspecific interactions that may influence optimal period. Note that the gap between the reproductive phenology and its optimal period is less important in this case compared to reproductive success approach due to predation pressure (see Reneerkens et al. 2016). d) In the case where phenology would represent a trade-off between survival and reproduction benefits, this approach shows that optimal period can be considered as a continuum depending on the life history strategies of individuals. Note the increase of the optimal period compared to other approaches because the trade-off approach takes into account the optimal conditions according to the different life history strategies. This figure was inspired by Iler et al. (2021).

III. Hibernation as a case study

A. Phenological shit in dormancy

Dormancy phenology like other seasonal activities is affected by global change. Dormancy in vegetation (Yang et al., 2015), zooplankton (Jones and Gilbert, 2016), insects (Forrest, 2016), amphibians (Ficetola and Maiorano, 2016; Green, 2017), or mammals (review in Wells et al., 2022) generally shows an advance in emergence date and a delay in initiation with global warming. These phenological shifts already influence individual fitness with consequences for population dynamics. For the yellow-bellied marmot (*Marmota flaviventris),* earlier emergence allows for earlier weaning of young and more time to build up reserves before hibernation begins. As a consequence, adults live longer and the population size increases rapidly (Ozgul et al., 2010 but see Tafani et al., 2013).

But dormancy phenology responses vary in direction and magnitude with different effects on fitness. Remaining on the example of hibernation, late snowmelt and the increased prevalence of late spring snowstorms delay emergence date with negative impact on population growth rate of Columbian ground squirrels (*Urocitellus columbianus*) (Lane et al., 2012). The same conditions induce a sex-dependent response in the Arctic ground squirrel (*Urocitellus parryii*) where the delay was observed only in females (Williams et al., 2017). In insects, some species do not respond to environmental change, or show a delay in the start and/or an advance in the cessation of their activity (Forrest, 2016; Karlsson, 2014; Pozsgai and Littlewood, 2014). As a consequence, a narrowing window of activity may be responsible for a decrease in the abundance of some populations of ground beetles (Karlsson, 2014). The influence of phenological shift in dormancy on population dynamics confirms the key role of dormancy on the life history of these species (Constant et al., 2020; Cushman et al., 1994; Schmidt et al., 2005; Veiga and Salvador, 2001; Wapstra et al., 2001).

Changes in dormancy phenology may have consequences at other ecological scales. In keystone species such as pollinating insects, parasitoid insects or zooplankton, variations in dormancy phenology could alter the ecosystem services they provide (*e.g.*, pollination; biological carbon sequestration or biological pest control) and thus modify entire ecosystems (Edwards and Richardson, 2004; Hegland et al., 2009; Ji et al., 2010; Kudo and Ida, 2013; Tougeron et al., 2020; Vadadi Fülöp and Hufnagel, 2014). In a more anthropomorphic point of view, changes in dormancy phenology may have consequences on the transmission of diseases (Huestis and Lehmann, 2014; Streicker et al., 2012) or human-wildlife conflicts (Johnson et al., 2018; Salman, 2018; Skendžić et al., 2021). For example, summer dormancy of the mosquito *Anopheles* spp., a vector of malaria, influences the population dynamics during the year and therefore the transmission of the disease (Huestis and Lehmann, 2014). An example of human-animal conflict is the case of the pine processionary moth (*Thaumetopoea pityocampa*). This species is the main pine forest defoliator and has urticating hairs, causing allergic reactions in humans and domestic animals (Cardil et al., 2017; Vega et al., 2011). This species presents cyclic population dynamics resulting in synchronous periodic outbreaks that are mainly explained by the ability to enter a prolonged dormancy of several years (Li et al., 2015). Understanding the evolution of its dormancy phenology with global change is necessary to better understand the expansion of this species (Robinet et al., 2014). These examples show the diversity of organisms, including humans that may be impacted by the future evolution of dormancy phenology.

B. A yardstick for phenological shift in dormancy

To understand current consequences and predict future evolution of dormancy phenology, it is useful to rely on the method presented above (section "A method for studying phenological shifts"). In the previous section ("Phenological shit in dormancy"), many studies have found evidence for a shift in dormancy phenology with climatic variables with sometimes consequences on fitness and population dynamic. However, to our knowledge no studies have tested so far whether climatic variables are proximate (*e.g.*, environmental cues) or ultimate causes of phenological shift and determined the gap between the optimal period of dormancy and current phenology. In addition, making predictions about future population trends based on proximate causes may be inaccurate if it does not take into account the selection pressures exerted by ultimate causes and potential phenotypic responses (*i.e.*, plastic or evolutionary). Thus, predictions should also take into account the adaptive capacity of the dormant species studied (section "Ultimate causes and consequences").

Current changes in hibernation phenology in response to climate change appear to be related to a plastic rather than an evolutionary response (review in Boutin and Lane, 2014; Lane et al., 2019) as observed for other biological traits (Boutin and Lane, 2014). However, phenotypic change by microevolution is assumed to be necessary for population survival in the long term (Phillimore et al., 2010). As a prerequisite for microevolution, the level of heritability of dormancy phenology is also an important factor to study in assessing the future adaptive capacity (Hoffmann et al., 2016 but see Hansen et al., 2011). Some species of plants (Jain, 1982; Li and Foley, 1997; Thompson et al., 2008), insects (Bégin and Roff, 2002; Dingle et al., 1977; Morris and Fulton, 1970; Tougeron, 2019), and mammals (Edic et al., 2020; Grabek et al., 2019; Lane et al., 2011) show high level of heritability (>50%) in dormancy phenology with variation within each taxon. This might suggest an ability of these organisms to adapt, but there are many other factors to consider, such as genetic and phenotypic diversity or the intensity of directional selection (Feiner et al., 2021; Lande and Shannon, 1996).

The basis of this yardstick is nevertheless dependent on our knowledge of the ultimate causes of dormancy phenology. Dormancy has long been considered as a strategy to cope with seasonal energy constraint, but recent studies may provide new insights. In addition, prediction on the evolution of population dynamics requires a better understanding of the influence of dormancy on fitness. In particular, several hypotheses have been proposed to explain the higher survival of dormant species but none of them prevail so far. In addition, how variation in dormancy phenology influences overall life history traits remains to be determined. For the remainder of this manuscript, we will focus on the ultimate causes and consequences of mammalian hibernation. Although mammalian hibernation is distinguished from other types of seasonal dormancy by differences in thermoregulation, we will focus on their similarities in order to answer fundamental questions about dormancy phenology.

C. Ultimate causes of hibernation phenology

1. Energetic constraint

Hibernation has long been studied from an energetic point of view, which has probably oriented the study of evolutionary causes on these aspects in the first place (Lyman et al., 1982). Hibernation is a highly effective physiological process used by endotherms to strongly reduce their energy expenditure. It consists of successive episodes of torpor, achieved by an active and drastic decrease in metabolic rate, leading to substantial lowering of body temperature, sometimes close to ambient temperature (Fig. 6; Geiser, 2004; Heldmaier et al., 2004). Torpor bouts during hibernation last from a few days to several weeks (with a mean of 5 days across hibernators), which distinguishes them from the daily torpor that lasts no more than 24 hours and is performed by daily heterotherms. Minimum body temperature is also higher during daily torpor than during hibernation (mean across species: 16.9°C for daily torpor *versus* 3.9°C for hibernation). As a result, the metabolic rate during daily torpor is reduced up to 35% of the basal metabolic rate (BMR) in daily heterotherms whereas the metabolic depression during seasonal torpor reaches ~4% of BMR in mammalian hibernators (Ruf and Geiser, 2015). Therefore, it appear that hibernation is the most efficient way to conserve energy in endotherms (van Breukelen and Martin, 2015).

During hibernation, each torpor bout is followed by energetically costly rewarming, also called arousal, where body temperature returns to euthermic values (Fig. 6). Arousal periods back to euthermia represent only 10-15% of total hibernation duration, but account for 75-85% of the total energy expenditure during this period (Heldmaier et al., 2004; Humphries et al., 2003a; Ruf and Geiser, 2015). However, they are crucial for the survival of hibernators, even if their exact finality remains unknown (Ruf et al., 2022). Some authors have suggested the elimination of metabolic (Clausen and Storesund, 1971) and toxic wastes (Buzadžić et al., 1990), re-activation of immune function (Prendergast et al., 2002), regulation of intracellular pH (Malan et al., 1988), sleeping (Daan et al., 1991) or feeding for some species (Humphries et al., 2003). However, some species such as the tailless tenrec (*Tenrec ecaudatus*), the fat-tailed dwarf lemur (*Cheirogaleus medius*), or the brown bear (*Ursus arctos*) hibernate at high body temperature (>30°C) without periodic arousals (Harlow et al., 2004; Dausmann 2005; Lovegrove et al., 2014). This indicates the existence of a threshold of body temperature below which a limited process, such as the clearance of accumulated metabolic waste, cannot occur and requires animals to return to euthermic values (Lovegrove et al., 2014). Overall, hibernation can reduce the organisms energy demands by ca. 85% of energy expended at euthermia during winter, even when accounting for the extra-energy cost of periodic arousals (John, 2005).

To supply the energy demand during this period, hibernators use two energy storage strategies. On one hand, fat-storing species that represent the majority of hibernating species accumulate fat for several weeks or months and fast throughout hibernation (*e.g.*, ground-squirrels). On the other hand, food-storing species constitute external reserves before hibernation and eat between torpor bouts (*e.g.*, pocket mice and chipmunks; Humphries et al., 2003a). However, these categories are not binary and some species may range along a continuum between these two strategies such as the garden dormouse (Humphries et al., 2003a). More recent studies also show that the common hamster could use internal fat stores (and food hoards) as energy supplies during hibernation (Siutz et al., 2012). Hibernation patterns (*e.g.*, duration, number, depths of torpor) are affected by the need for food-storing rodents to consume energy reserves during hibernation. As a result, euthermic bouts of food-storing rodents are four times longer and torpor bouts are half as long as those of fat-storing rodents (Fig. 6).

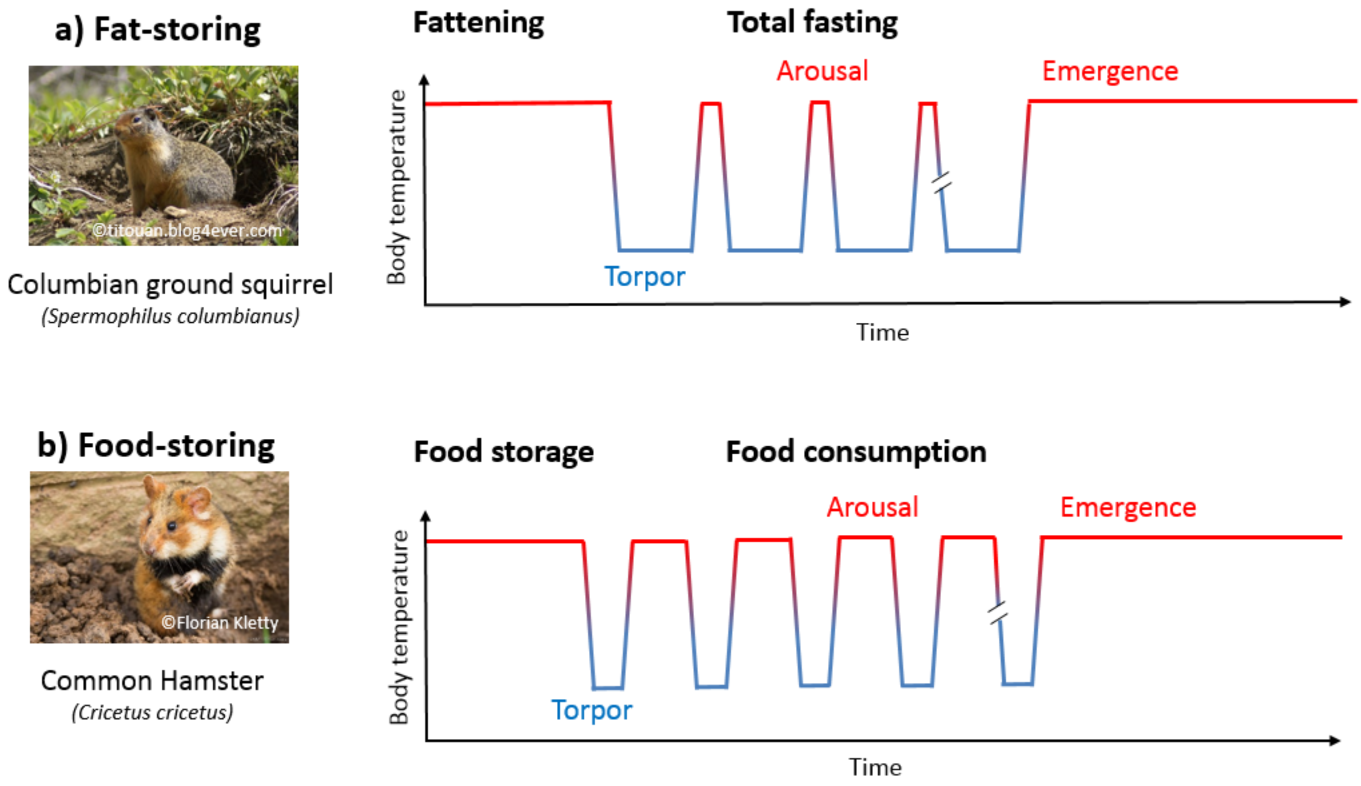


Figure 6. Graphic representing body temperature variation during hibernation (hibernation pattern) according to hibernation strategy a) fat-storing b) food-storing. The blue color represents the lower body temperatures during torpor and the red color represents the higher body temperatures during euthermia.

Most hibernators reproduce for a few months, then prepare for hibernation by accumulating energy reserves, and enter into hibernation (*i.e.*, immergence) from fall to spring (review in Geiser, 2020), when living conditions deteriorate (Fig. 7). Depending on the species, adult males or females immerge first with sometimes a gap of several weeks between them (Siutz et al., 2016; Sheriff et al., 2011; Kawamichi, 1989). Most of the time hibernators hide in a burrow or in an isolated shelter to hibernate. After several months, the males generally emerge before females, sometimes several weeks in advance (Kart Gür and Gür, 2015; Snyder et al., 1961; Holekamp and Nunes, 1989). As seasonal species, activity patterns of hibernators are repeated year after year with a marked similarity. Hibernation has long been associated with the cold environments of the northern hemisphere and view as a means of survival period of energy shortages when the energy availability of the environment is lower than the energy demand (Lyman et al., 1982). In this case, energy shortage would be the evolutionary cause of hibernation phenology and the survival of individuals the evolutionary consequence.

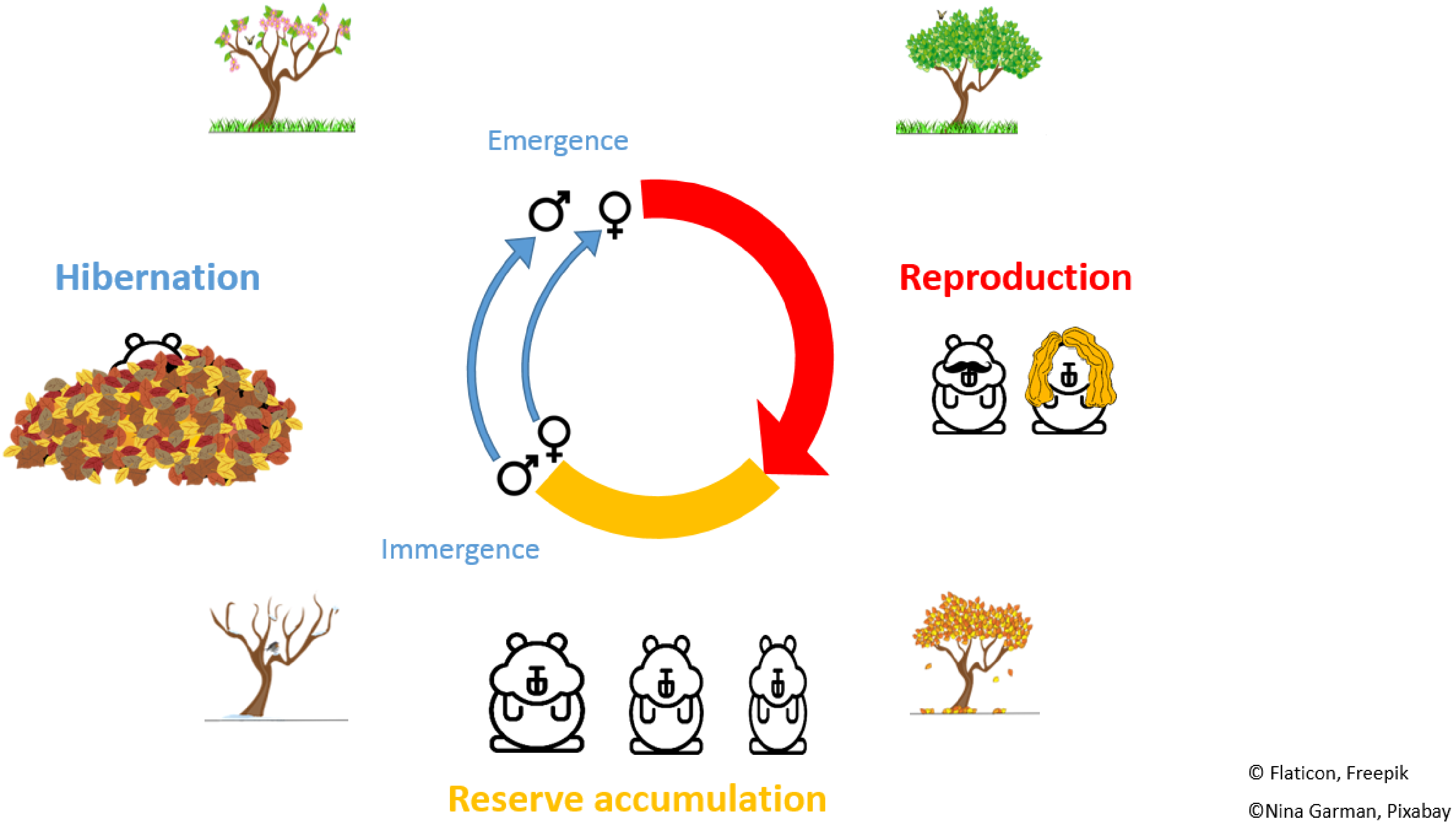


Figure 7. Schema representing the most common annual life cycle of adult hibernators (except bats). The sex difference in hibernation phenology is represented from the male and female symbolisms. The difference between the sexes in immergence depends on the species, with either males or females immerging first.

Surprisingly, very few studies have investigated and especially distinguish between proximate and ultimate causes of hibernation. The attribution of the adaptive role of hibernation as a response to environmental energy shortages has been reinforced primarily by studies that actually tested the proximate effect (mechanistic effect) of energy constraints on the expression of hibernation or torpor. Vuarin and Henry (2014) identified fifty-one laboratory studies that found a proximate cause of food shortage on torpor and hibernation expression. Food restriction in laboratory conditions caused torpor and increases its occurrence in many heterothermic mammals. Increased energy challenges during food restriction by decreasing ambient temperature accentuated the use of torpor (Geiser and Kenagy, 1988; Séguy and Perret, 2005; Wojciechowski et al., 2007). In nature, correlative and experimental studies also revealed links between food availability and hibernation expression. Small-scale variations in food availability between eastern chipmunks before immergence into hibernation, explained variations in torpor depths (Landry-Cuerrier et al., 2008). Access to food supplementation before hibernation caused a decrease in the amount of the time spent in torpor for two food-storing hibernators: male common hamsters (*Cricetus cricetus*) and Eastern chipmunks (Humphries et al., 2003a; Siutz et al., 2018). Although proximate factors may also be ultimate factors, these studies do not provide evidence that energy constraint is an ultimate cause of hibernation.

To investigate the ultimate causes of hibernation it is necessary to identify the conditions that explain why species are hibernating (in other words, why evolution has favored this specific annual rhythm) at that particular time of the year. It is therefore necessary to focus on the factors that explain the phenology and duration of hibernation. To test the energy shortage hypothesis, it is necessary to determine whether species emerge and immerge from hibernation based on their energy balance. To do this, it is required to assess both the food availability in the environment as well as the energy expenditure at the time of immergence and emergence. To our knowledge, Humphries et al. (2002) is the only study that measured the relationship between energy balance and hibernation phenology in the wild. They show that chipmunks immerge at a time when food availability would meet their energy requirements. Other evidence suggest that energy constraints are one of the ultimate causes of hibernation. A decrease in the period of food availability and colder temperatures with higher altitude increased the duration of hibernation among populations of golden-mantled ground squirrels (*Callospermophilus lateralis*), Colombian ground squirrels (*Urocitellus columbianus*), and woodchucks (*Marmota monax*) (Bronson, 1979; Dobson et al., 1992; Zervanos et al., 2010). It is therefore likely that at least part of the hibernation period is explained by energy constraints. However, the adaptive role of hibernation as a response to energy shortage, although widely accepted, is likely to receive only limited support.

2. Recent perspectives

Studies in the last decades have shown that hibernation is taxonomically and geographically widespread, which may suggest a greater diversity of ultimate causes. Hibernation is present on all continents (except Antarctica) and even in the tropics with rather mild climates throughout the year (Nowack et al., 2020). Hibernation is present in all three subclasses of mammals, *i.e.*, monotremes, placentals and marsupials (Geiser, 2020). To date, Nuttall's nightjar (*Phalaenoptilus nuttallii*) is the only bird species considered to be hibernating (Woods et al., 2019). This research revealed that hibernation may take place in other situations than during cold winter. Some species perform multiday torpor bouts in summer (*i.e.*, aestivation) with physiological mechanisms similar to hibernation, but with reduced energy saving because of higher ambient temperature, energy savings are lower than in winter (Geiser, 2010; Wilz and Heldmaier, 2000). Food and water shortage due to high ambient temperature are expected to be the ultimate cause of aestivation (Geiser, 2010). Moreover, in non-Holarctic region, there are non-seasonal hibernating species (*e.g.*, some elephant shrew and marsupials species) that can enter hibernation at any time of the year (Geiser and Körtner, 2010; Lovegrove et al., 2001). Hibernation in Holarctic and non-Holarctic species is based on similar physiological mechanisms, but some ultimate causes are assumed to differ (Nowack et al., 2020). Decreasing food quality (*e.g.*, vitamins, micronutrients, essential amino acids) and/or water shortage have been proposed as ultimate cause of hibernation in non-Holarctic species (Nowack et al., 2020). For the moment, only the proximate cause of water shortage has been demonstrated by inducing early hibernation in Syrian hamsters (*Mesocricetus auratus*) (Ibuka and Fukumura, 1997). Nevertheless, other evidence around the world suggests that hibernation is not initiated solely in response to deficiencies in energy, water, or poor food quality.

Hibernation while environmental conditions are still favorable for above ground activity has been reported several times (Grigg and Beard, 2000; Hoelzl et al., 2015; Munro et al., 2008). In fact, hibernation may also reduce the risk of extrinsic mortality such as predation and competition (Ruf et al., 2012; Turbill et al., 2011) and/or intrinsic mortality such as aging (Wu and Storey, 2016). This hypothesis was mainly developed from the study of the edible dormouse. This species expresses a prolonged hibernation of 8 to 11.7 months with no apparent energetic constraints (Hoelzl et al., 2015). Indeed, the plant growing season exceeds the dormouse active season by two months (in the case of an 8-month hibernation; Bieber et al., 2014) and prolonged hibernation is also observed in animals fed *ad libitum* (Bieber and Ruf, 2009). This prolonged hibernation is supposed to reduce predation risk. Moreover, it is suggested that older dormice invest more in reproduction despite predation risk, which would explain the decrease in hibernation duration with age in this species (see section “Trade-off approach” for more details). But for the moment, it is questionable whether dormouse’s hibernation is an exception related to its particular pace of life. Indeed, dormice live up to 12 years, which is exceptional for a species of 120g, and most females only breed once or twice in their lifetime when conditions are most favorable (Bieber and Ruf, 2009). However, to date there has been no review of the possible influence of extrinsic mortality risks on hibernation phenology across hibernators or studies demonstrating whether these factors could be ultimate cause of hibernation phenology.

The reduction of mortality risks during hibernation seems nevertheless more widespread than initially thought. During hibernation, the survival rate is superior to the activity period with a rate sometimes close to 100% survival. As a consequence, hibernators (especially species <1.5 kg) have a slower life history compared to non-hibernating species of the same size (Turbill et al., 2011). However, the physiological and molecular mechanisms underlying this higher longevity are still debated and several hypotheses remain to be tested. Determining evolutionary consequences and in particular which hibernation features promote higher longevity should have important insights in the context of phenological shift.

D. Ultimate consequences of hibernation

1. Reduction of cellular damage

The first hypothesis to explain higher longevity of hibernators (i.e., metabolic reduction hypothesis) assumes that reduced metabolism during torpor decreases the accumulation of intracellular oxidative damages (Lyman et al., 1981; Wilkinson and South, 2002; Wu and Storey, 2016). Oxidative damage or stress occurs when the production of reactive oxygen species (ROS) is not counterbalanced by the protective system such as antioxidants or DNA repair enzymes (Jones and Sies, 2007). Many experimental studies involving a reduction of metabolic rate through a decrease in body temperature or caloric restriction have shown a slowing of aging in ectotherms (Liu and Walford, 1966; Miquel et al., 1976; Tatar, 2007; Van Voorhies and Ward, 1999) and endotherms (Conti et al., 2006; Duffy et al., 1990; Lane et al., 1996; Weindruch et al., 1979). These results are in agreement with the “free radical theory of aging” which posits that aging is caused by accumulation of ROS-induced damages. A positive correlation was found between the lifespan of 288 Turkish hamsters (*Mesocricetus brandti*) and the amount of time spent in hibernation, suggesting that the process of aging is slowed during hibernation (Lyman et al., 1981). Recently, studies have attempted to understand the effect of hibernation on aging and thus longevity through its influence on relative telomere length (RTL). Telomeres are non-coding and highly repetitive regions of DNA at the end of eukaryotes’ chromosomes protecting the coding part of DNA (Greider, 1996). Telomeres shorten with chronological age, the time elapsed since birth (Haussmann et al., 2003; Horn et al., 2010), and oxidative stress (Chatelain et al., 2020). Thus telomere length or telomere shortening has been proposed as one of the hallmarks of cellular stress and aging in mammals (Whittemore et al., 2019).

In semi-captive edible dormouse, a negative effect of body mass loss during hibernation (index of the time spent in euthermia) on RTL supports the idea that torpor use slows down aging (Turbill et al., 2013). Another study on edible dormice in the wild, shows that RTL shortened in all animals after prolonged hibernation of 7.5 to 11.4 months. Although the frequency of periodic arousal seems to be the main factor explaining this erosion, the immediate net effect of hibernation is RTL shortening (Hoelzl et al., 2016a). The acceleration of aging with arousals should therefore be absent in bears that practice shallow torpor (> 30°C) and do not arise. Indeed, contrary to edible and garden dormice, bears shows a greater telomere erosion with a decrease in hibernation duration (Kirby et al., 2019). A recent experimental study performed on edible and garden dormice (*Eliomys quercinus*) demonstrated that more than the frequency of torpor, it is above all the depth of torpor that has an impact on telomere erosion. Although making more frequent and shallower torpor is more energetically costly, arousals requires a lower increase in metabolic rate (due to lower temperature differential with euthermic body temperature) and is therefore expected to produce less ROS production than deeper torpor (Nowack et al., 2019).

All this evidence seems to suggest that aging slows during torpor with the reduction of metabolism, but potentially resume upon arousal phases due to energy costs. Nevertheless, precautions must be taken because these tests have only been performed on ear tissues or buccal cells. Furthermore, a recent study on arctic ground squirrel (*Urocitellus parryii)* shows that telomere shortening is tissue specific and that metabolically active tissues might incur higher levels of molecular damage (Wilbur et al., 2019).

Other mechanisms at the cellular level suggest that aging slows during hibernation. The reduction of energy expenditure is achieved in part through the inhibition of the insulin signaling pathway, which regulates several metabolic functions directly linked to aging and longevity, such as cell growth and protein synthesis (Lizcano and Alessi, 2002). In addition, hibernators dispose of molecular mechanisms including up-regulation of protein chaperones, increased antioxidant defenses, and activation of pro-survival signaling such as the FOXO pathway enabling them to survive even when most of their vital function is reduced to an extreme degree (review in Wu and Storey, 2016).

These benefits of reduced metabolic rate on aging are expected to be greater for small hibernators since they benefit from a greater decrease in metabolic rate (as a % of basal metabolic rate) than large hibernators (Ruf and Geiser, 2015). This may explain why the beneficial effect of hibernation on longevity decreases with size (Turbill et al., 2011). However, alternative hypotheses are proposed to explain the higher longevity of hibernators.

2. Investment in maintenance

Although torpor brings energetic benefits, it also seems to be associated with significant physiological costs such as reduced immune competence (Maniero, 2000; Prendergast et al., 2002), partial memory loss (Millesi et al., 2001; Weltzin et al., 2006; but see McNamara and Riedesel, 1973; Clemens et al., 2009) and dehydration (Thomas and Geiser, 1997). In addition, arousal after deep torpor increases oxidative stress (Nowack et al., 2019) and may have deleterious consequences such as lipid peroxidation (Carey et al., 2000; Harlow and Frank, 2001) and shortening of chromosomal telomeres (Hoelzl et al., 2016; Turbill et al., 2013). Considering the costs and benefits of torpor, Humphries et al., (2003a) developed “the torpor optimization hypothesis”, which suggests that hibernators do not maximize the use of torpor but instead use the energy at their disposal to limit the depth and duration of torpor and therefore the associated costs (a cost/benefit approach). It would explain why individuals with the most internal or external energy reserves spend less time in torpor than others and have shallower torpor with more frequent arousal (Bieber et al., 2014; Boyles et al., 2007; Humphries et al., 2003b; Siutz et al., 2018; Zervanos et al., 2010).

The second hypothesis to explain hibernator's longevity is in line with the principle that torpor induces more physiological damages than benefits. It postulated that higher longevity, instead of being the result of a decrease in metabolic rate, may be due to an adaptive response to resource shortage that would induce a change in the allocation of energy away from growth and reproduction toward somatic maintenance (Humphries et al., 2003a). Indeed, for most hibernators torpor inhibits the development of the reproductive system (Barnes et al., 1986; Millesi et al., 2000). There are however some exceptions (McAllan and Geiser, 2014; Wilsterman et al., 2021. In addition, resumption of the reproductive system may start during the inter-torpor bouts at euthermia (Dai Pra et al., 2022; Millesi et al., 2000). Surprisingly, to our knowledge, no study has tested the effect of body growth slowing with deep torpor. Some elements suggest this effect such as reduced teeth growth in hibernating rodents (Klevezal and Anufriev, 2013) and the inhibition of somatic growth factors like insulin-like growth factor during torpor (Schmidt and Kelley, 2001). This hypothesis (*i.e.*, maintenance hypothesis) has been developed and validated under certain conditions in a mathematical life history model (Shanley and Kirkwood, 2000).

In addition, telomere elongation during hibernation in captivity have been measured in at least two hibernating species (garden dormouse and edible dormouse) and is suggested to occur during the inter-torpor bouts at euthermia (Nowack et al., 2019; Turbill et al., 2012, 2013). This phenomenon has already been measured in several different taxa including non-hibernating species and from different tissues (*e.g.*, leukocyte, buccal cells, tail tissue) and is unlikely to be related to measurement artifact (Criscuolo et al., 2020; Fairlie et al., 2016; Haussmann et al., 2003; Hoelzl et al., 2016a, 2016b; Olsson et al., 2018; Tissier et al., 2021). Long telomeres are more sensitive to oxidative stress because they have many guanine and cytosine that are prime targets of oxidative stress (Bauch et al., 2014). Therefore, telomere elongation may have a “ROS-trap” role to protect the coding parts of the DNA from oxidative damage in anticipation of a high stressful period (*e.g.*, reproduction, bad season). However, telomere elongation is done at the cost of energy (Hoelzl et al., 2016a; Nowack et al., 2019). Telomere elongation seems to be in line with the “maintenance hypothesis” and may explain the higher longevity of hibernators. Humphries et al, proposes this hypothesis as an alternative to the “metabolic reduction hypothesis”. Nevertheless, it seems possible to consider that these two hypotheses are non-exclusive with both a slowing down of aging with the decrease in metabolism and an important investment in maintenance during inter-torpor or arousal bouts.

However, telomere elongation is not restricted to hibernation period contrary to what the “maintenance hypothesis” might suggest. Telomere elongation has been measured in edible dormouse during the active season when sufficient food is available (Hoelzl et al., 2016a; Turbill et al., 2013). Elongation was also measured with increasing age in two hibernating species (edible dormouse and Eastern chipmunk) but without knowing at what time of year the investment in maintenance occurs (Hoelzl et al., 2016b; Tissier et al., 2021). If telomere elongation does not occur specifically during hibernation, this may suggest that physiological conditions during hibernation are not more favorable to investment in maintenance than at other times of the year.

The life history trait theory predicts that a low risk of dying in the future should favor investment in somatic maintenance (Healy et al., 2019; Martin, 2015). Thus, the reduction of extrinsic mortality risk during hibernation may favor a higher investment in somatic maintenance not only restricted to the hibernation period (*viz*. hypothesis of reduced extrinsic mortality; (Ruf et al., 2012). This third hypothesis, may explain why small hibernators in particular show a slower life history than non-hibernators of the same size, because smaller species are expected to suffer higher predation rate (Cohen et al., 1993; Sinclair et al., 2003).

Finally, it is important to note that there is little information on the benefits and costs of telomere elongation for fitness, specifically in hibernators. Telomere elongation calls into question the use of telomeres as a proxy for aging and requires studies to better understand this process.

IV. Aims of the thesis

This introduction reveals that the understanding of phenological shifts requires more evolutionary approaches based on ultimate causes and consequences of phenology. I have proposed several approaches to provide information in understudied areas. Until now most studies on phenological shift have focused on reproduction. The annual survival approach suggests that other seasonal activities should not be neglected because the change in the annual organization of time may affect annual survival. This thesis fits into this context by focusing on the ultimate causes and consequences of hibernation phenology. Hibernation will be considered as an example of seasonal dormancy with a chapter that will be devoted to highlight similarities with the dormancy phenology of ectotherms.

This thesis is organized in five chapters, each composed by a scientific article. Two main approaches separate the thesis into two main parts. In the first part, comprising two chapters (chapter 1 and 2), I used comparative phylogeny methods that allow us to test hypotheses on past selection on a large number of species (see section "Ultimate cause and consequence" for more details). Specifically, I was interested in understanding whether the evolutionary causes and consequences of hibernation were consistent across hibernators.

In the first chapter, I investigated, based on the trade-off approach, whether annual organization of hibernators has consequences for energy allocation that are large enough to affect their life history. For this purpose, I tested whether increased hibernation duration among hibernators was associated with increased longevity in 82 geographically and taxonomically diverse hibernating species. I then discussed the ultimate causes of hibernation phenology based on a review of the literature.

In the second chapter, I specifically focused on the ultimate causes of dormancy, extending this question to other types of seasonal dormancy. The study of seasonal dormancy has been phylogenetically separated limiting our general knowledge of dormancy. A common underestimated feature is the high survival rate during dormancy. Based on the trade-off approach, I investigated the existence of a trade-off between the survival benefits of being in dormancy and the reproductive benefits of being active that might explain dormancy phenology. I specifically tested whether this trade-off explains the sex difference in hibernation phenology in more than 20 hibernating species. I predicted that the sex that devote the most time and energy to reproduction spend less time in dormancy. Due to limited data, I was not able to conduct the same test in ectotherms. However, unlike hibernators, several studies had already investigated this question in ectotherms. I therefore compared this hypothesis between ectotherms and endotherms on the basis of the results obtained in this study and studies previously published in the literature.

However, the comparative phylogeny approach has the disadvantage of being mostly correlative and thus limiting the interpretation of cause and effect. In a complementary way, I developed in a second part of this thesis (Chapters 3, 4 and 5), an experimental approach in laboratory to test more finely the evolutionary consequences of hibernation in a mammal, the common hamster (*Cricetus cricetus*).

In the third chapter, I set up an experimental design to confront for the first time the metabolic reduction hypothesis and the investment in maintenance hypothesis to explain the higher longevity of hibernators. I recorded the hibernation pattern and measured the RTL variation before and after hibernation period of 4 groups of 12 female common hamsters. These groups were placed under conditions of photoperiod and ambient temperature conditions that favored either long or short hibernation with no or many episodes of deep torpor. According to metabolic reduction hypotheses, long hibernation with deep torpor should have promoted slower aging. On the contrary, according to the investment in maintenance hypothesis, long hibernation and shallow torpor should have promoted a lower aging rate.

In the fourth chapter, I attempted to understand the ultimate consequences of the trade-off between survival and reproduction of the hibernation phenology highlighted at the interspecific scale (chapter 2). This trade-off is similar to the trade-off spreading species along the slow-fast continuum, so I hypothesized that hibernation phenology may be integrated into the Pace Of Life Syndrome (POLS). I assumed that individuals with long hibernation would be associated with slow growth, low reproductive investment, limited telomere erosion and risk averse behavior. I therefore tested the covariation of hibernation phenology with these traits in a group of 34 hamsters followed from birth to 1.5 years of age.

In the last chapter, I conducted a study whose purpose was to validate the use of telomere length or shortening as a biomarker of aging in the common hamster, a short-lived hibernator. Longitudinal monitoring of telomere length variation was performed from birth to death in 24 common hamsters. First, I investigated whether hamsters, like other hibernating species, are able to elongate their telomeres. Then, I tested the relationship between relative telomere length (RTL) variation and chronological age. In addition, hibernation patterns and reproductive investment were measured annually to analyze their effects on RTL variation and longevity.

Finally, in the last part of my thesis, I discussed all these results in the context of phenological shifts and compared them with the seasonal dormancy of ectotherms.

Chapter 1


©Šarunas Burdulis

The Columbian ground squirrel
(*Urocitellus columbianus*)


©Arjan Haverkamp

The gray mouse lemur
(*Microcebus murinus*)


©Andrei Sakhno

The grey long-eared bat
(*Plecotus austriacus*)


©Wildlifecartoons

The short-beaked echidna
(*Tachyglossus aculeatus*)

“Hey guys! My favorite four hibernators! I have found some interesting results on hibernation, but some of you might not be too happy... Let me explain…”

Integrating mortality risk and the adaptiveness of hibernation

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1 Introduction

Energy is the fundamental requirement for life. Its acquisition, storage, and metabolic use shape the diversity of lifestyles in all living organisms (Brown et al., 2004). Because energy availability to organisms is limited under natural conditions, in terms of its acquisition in time and space, as well as its quantity and quality, organisms have to simultaneously maximize investments into all biological functions, and to compromise the allocation of metabolic energy among competing demands (Hirshfield and Tinkle, 1975; Lack, 1966; Reznick, 1985; Williams, 1966). For example, demographic characteristics may affect energy investments among biological traits such as growth, reproduction, and somatic maintenance. These trade-offs have led to the evolution of specific life history strategies (Stearns, 1992).

Attributes of life histories generally scale with body size such that large animal species usually take longer to develop and mature, have lower annual reproductive rates, and live longer compared to small species (Blueweiss et al., 1978; Speakman, 2005). However, life history variations that are specific to a particular body size are also observed along a fast-slow continuum (Bielby et al., 2007; Dobson and Oli, 2007; Jeschke and Kokko, 2009; Jones et al., 2008; Oli, 2004). For a given body size, most species trade off investments between reproduction and self-maintenance. For example, a species with fast life history strategy will exhibit faster growth, earlier reproduction, larger annual reproductive investment, and reduced maximum life span compared to a species with a slow life history strategy, which will typically promote self-maintenance and survival over reproduction (but see Bielby et al., 2007; Jeschke and Kokko, 2009).

The evolution of the fast-slow continuum in life history strategies appears to be contingent upon individual mortality risk (Healy et al., 2019; Martin, 2015; Promislow and Harvey, 1990). Individual mortality can be due to either intrinsic (wear-and-tear of the body) or extrinsic factors, such as predation, disease, or environmental hazards. Species with slow life histories typically exhibit adaptations that limit both sources of mortality (Lewis et al., 2013; MacRae et al., 2015; Munshi-South and Wilkinson, 2010; Wu and Storey, 2016; Blanco and Sherman, 2005; Healy, 2015; Healy et al., 2014; Holmes and Austad, 1994; Shattuck and Williams, 2010; Sibly and Brown, 2007; Turbill et al., 2011; Wilkinson and South, 2002). Besides these molecular (such as oxidative stress tolerance), physiological/anatomical (such as chemical protection, horns and antlers) or lifestyle (such as arboreality) adaptations that reduce mortality risk, the organization of activity time budgets should be particularly important in shaping the variety of life histories observed in the wild. Mortality rates may change depending on the time allocated to each activity, resulting in trade-offs for which both time and energy can be optimized. For instance, activities that contribute the most to reproductive success are often energy-intensive (Alonso-Alvarez et al., 2004) and associated with higher risks of extrinsic mortality (Magnhagen, 1991). However, the temporal dimension of energy allocation trade-offs in relation to the evolution of life history strategies has been little examined (see Healy et al., 2014).

Here, we first examined the extent to which patterns of relative activity and inactivity can explain variation in life history traits in mammals. We specifically focused on hibernating species because of their marked seasonal cycle of activity/inactivity, which is associated with very different risks of mortality. From an intrinsic perspective, hibernation is a period of metabolic depression where energy requirements are reduced to minimal levels compared to the active season (Ruf and Geiser, 2015). It has been suggested that energy restriction slows down the aging process (Walford and Spindler, 1997; Masoro, 2006) and is associated with an enhancement of somatic maintenance (Shanley and Kirkwood, 2000). From an extrinsic perspective, even if mortality during hibernation occurs, hibernating mammals are usually hidden in burrows or shelters, which may reduce risks of predation, infections or injuries for several continuous months. As a result, hibernating species generally exhibit lower rates of mortality than similar-sized non-hibernating species during part of the year, resulting in slower life history strategies (Turbill et al., 2011; Wilkinson and South, 2002). However, previous studies linking hibernation to longevity considered hibernation as a binary trait (if animals hibernate or not), rather than a continuous adaptive response (hibernation season duration) that allows animals to restrict their period of activity during parts of the year. Yet, early data from captivity highlight a positive correlation between longevity and hibernation duration in Turkish hamsters (*Mesocricetus brandti*) (Lyman et al., 1981). In addition, a strong negative effect of mean annual temperature on hibernation season duration and annual survival rate, which is highly correlated with longevity (Turbill et al, 2011), has been shown among populations of hibernating rodent species (Turbill and Prior, 2016) This raises the question of whether, across hibernating mammals the time spent being inactive (hibernation season duration) influences maximal longevity, a key feature characteristic of fast and slow life history strategies

In the present study, we tested for a positive association between the hibernation season duration and longevity across 82 mammalian species. For this examination, we tested for effect of body size on longevity while controlling statistically for phylogeny. If indeed hibernation season duration is part of a strategy allowing minimizing mortality, we predicted that longer hibernation season duration should be positively associated with species maximum longevity, especially in small mammals (< 1.5 kg) that exhibit greater longevity than non-hibernators of the same size (Turbill et al. 2011). In addition, if metabolic reduction during hibernation slows aging (Lyman et al., 1981; Turbill et al., 2013; Wu and Storey, 2016), we predicted that the effect of hibernation season duration on longevity should increase with the percentage of metabolic reduction during hibernation compared to euthermia.

2 Material and methods

2.1 Review criteria

We conducted the review using the search engine Google Scholar (https://scholar.google.com) and considered articles up to and including December 2019. We based our survey on the hibernating species listed in Ruf and Geiser (2015) and Turbill et al (2011), and further identified nine other species, mainly ground squirrels and bats, not mentioned in any of the lists. All the 152 hibernators that were examined in this process are summarized in Electronic Supplementary Materials (see Table S1). We excluded species for which hibernation was restricted to only a few populations or under specific conditions, namely two species, the black-tailed prairie dogs (*Cynomys ludovicianus*; Gummer, 2005; Lehmer et al., 2006) and the polar bears (*Ursus maritimus*; Amstrup and DeMaster, 2003). We did not include non-seasonal hibernating species capable of entering multi-day torpor at any time of the year. Indeed, for such cases, it is difficult to accurately measure the time spent in hibernation over a year, which may also vary considerably among individuals and between years. Thus, we excluded hibernating elephant shrew species (*Elephantulus* sp.) and hibernating marsupials with the exception of the mountain pygmy possum (*Burramys parvus*), reported to be a seasonal hibernator (Geiser and Körtner, 2010; Lovegrove et al., 2001).

2.2 Longevity and body mass data

Data on maximum longevity, hereafter referred as longevity, and average body mass for the list of hibernating species previously identified were mainly obtained from the AnAge data base (The Animal Aging and Longevity Database; https://genomics.senescence.info/species/search_list.php; Human Ageing and Genomic Resources; Magalhães and Costa, 2009), and complemented these data with information from the PanTHERIA data base (https://ecologicaldata.org/wiki/pantheria; Ecological Archives, Ecological Society of America; Jones et al., 2009) from two reviews on mammalian longevity (Heppell et al., 2000; Wilkinson and South, 2002) or from a specific search in Google Scholar combining the following terms: “longevity” OR “life history” AND scientific or common names of species. For this specific search in Google Scholar, we considered both old and new nomenclatures for ground squirrel species, and only selected long-term field studies since they provide a good estimate of maximum longevity. Moreover, we specifically investigated the source of the data (captive vs. wild) and only retained longevity data where the source was available, to control for captivity effects on longevity (see Electronic Supplementary Material, Table S2 for references).

We determined the arboreality lifestyle of the species in order to statistically control (see below section 2.5) for higher longevity (Healy et al., 2014; Kamilar et al., 2010; Shattuck and Williams, 2010). We conducted a review of peer-reviewed scientific journal Mammalian Species (https://academic.oup.com/mspecies) and used Google Scholar. The search criteria were based on combining the following terms: "arboreal" OR "semi-arboreal" OR "climb tree" AND scientific or common names of species. We completed our search by examining the mammalian lifestyle databases of the following articles (Healy et al., 2014; Hidasi-Neto et al., 2015). Our arboreality factor includes 16 arboreal and semi-arboreal species, which feed, nest, or escape from predators, at least frequently, by climbing into trees (see Electronic Supplementary Materials, Table S2).

2.3 Hibernation season duration data

2.3.1 Reviewing strategy

Relatively few studies have investigated hibernation duration with body temperature recorders on wild mammals. However, several studies have estimated hibernation season duration from capture-mark-recapture records or direct observations, thus assessing periods of inactivity. Although for some species, the duration of hibernation measured as the period between the first and last torpor bout is probably shorter than the period of inactivity (Siutz et al., 2016; Williams et al., 2014; Young, 1990) , these measures should still provide reasonable estimates of the duration of energy savings, thereby allowing species to be compared with each other.

We reviewed the literature to retrieve estimates of the hibernation season duration as the time (in days) spent between immergence and emergence from the hibernaculum or den (with little or no movement outside). The search criteria were based on combining the following terms: "hibernation" OR "hibernation duration" OR "denning" (exclusively for bears) OR "roosting" (exclusively for bats) AND scientific or common names of species. In order to minimize heterogeneity in the scales at which the data were measured (*e.g.*, individual, population), we considered maximum hibernation season duration obtained from same-sex adult groups, either male or female depending on the species (and recorded maximum hibernation season duration from overall population data when more precise data were unavailable).

2.3.2 Inclusion and exclusion criteria

We prioritized studies for which the methodology for estimating hibernation season duration of is described (capture-mark-recapture, direct observation and body temperature recording). These criteria included 64 species. We also included studies based on road kills as an index of activity/inactivity. This criterion has already been used to evaluate changes in hedgehog abundance (Bright et al., 2015; Morris and Morris, 1988; Wembridge et al., 2016) and was used for 2 species in our data set (Algerian hedgehog (*Atelerix algirus*) and Southern white-breasted hedgehog (*Erinaceus concolor*)). Finally, in cases where the above criteria were not available, we included studies for which a precise hibernation period was mentioned but the methodology could not be assessed. This criterion included 16 species (see Electronic Supplementary Material; Table S2, labeled species)

We excluded studies for which periods of extreme inactivity were measured only once in a population. This criterion excluded three maximum hibernation season data: 8 months for the little pocket mouse (*Perognathus longimembris*; Kenagy and Bartholomew, 1985); 6 months for the long-tailed pocket mouse (*Chaetodipus formosus*; Kenagy and Bartholomew, 1985); and 11 months for the Eastern chipmunk (*Tamias striatus*; Munro et al., 2008).

The availability or absence of data (longevity and hibernation season duration) in the literature for the 152 species examined is specified in Electronic Supplementary Materials (see Table S1). In total, our literature search allowed inclusion of 82 hibernating mammal in the analyses including 80 placental mammals, 27 bats, one marsupial (the mountain pygmy possum) and one monotreme (the short-beaked echidna (*Tachyglossus aculeatus*)). Longevity, body mass and hibernation season duration data for these species are available in Electronic Supplementary Materials (see Table S2).

2.4 Phylogenetic data

We downloaded 100 phylogenetic mammalian trees from http://vertlife.org/phylosubsets/ (see (Upham et al., 2019), focusing on the 82 species in our data set (see Electronic Supplementary Material, Table S2). These trees were used to construct strict consensus trees for the hibernating species of our study, where the included clades were those present in all the 100 phylogenetic mammalian trees (Paradis, 2011). Because we ran subsequent analyses on different subsets of the data (see section 2.5 below), we constructed separate phylogenetic trees on (1) the full hibernator data set (N = 82 species), (2) the data set excluding bats (N = 55 species), (3) the data set with only deep hibernator (see below) excluding bats (N = 46 species) and (4) the data set excluding bats and hibernators > 1.5 kg (N = 44 species) (see Electronic Supplementary Material, Fig S1).

The rationale for eliminating bats from some analyses was to compare the specific effect of hibernation season duration on longevity between bats which have very distinct characteristics (*i.e.*, flight capacity, highly gregarious behavior during hibernation (Austad and Fischer, 1991)) and other hibernators.

The metabolic rate during torpor is not known for all hibernating species studied (Ruf and Geiser, 2015). To test the prediction that the effect of hibernation season duration on longevity should increase with metabolic reduction, we compared the effect of hibernation season duration on the longevity of two groups including (all hibernators excluding bats) or excluding (only deep hibernators without bats) species reducing their energy expenditure during hibernation by less than 90% compared to the euthermic state. These comprise *Ursidae* species and the European badger (*Meles meles*) that reduce their total energy expenditure from 33 to 75% during hibernation compared to the euthermic state (Hellgren, 1998; Ruf and Geiser, 2015; Tøien et al., 2011; Watts and Jonkel, 1988) and small tropical hibernators such as *Cheirogaleidae* and *Tenrecidae* species, which show a 70% reduction (Dausmann et al., 2009; Wein, 2010). Thus, the 'deep hibernator' group includes the species capable of reducing their total energy expenditure by about 90% or more during hibernation as compared to the euthermic state and reaching a body temperature during torpor below 10°C (mainly small Holarctic species; Heldmaier et al., 2004)

In addition, the analyses of Turbill et al. 2011 indicated a body mass threshold of 1.5 kg, below which the benefits of hibernation (compared to non-hibernation) for longevity increased. To test the effect of hibernation season duration on longevity between hibernators < 1.5kg and larger ones, we used the data set excluding bats and hibernators > 1.5 kg.

Branch lengths for respective consensus trees were calculated with the ‘compute.brlen’ function from the ‘ape’ package based on Grafen's (1989) computations, and were used to compute PGLS models with the ‘caper’ package in R (see section 2.5 below).

2.5 Statistics

We tested for a significant relationship between hibernation season duration and species maximum longevity, using phylogenetic generalized least squares (PGLS) models using the ‘ape 5.0’, ‘apTreeshape 1.5’ and ‘caper 1.0’ packages in R v. 3.6.2 (Orme et al., 2013; Paradis, 2011; Paradis and Schliep, 2019; R Core Team 2014). We thus statistically “controlled” for the influence of the phylogenetic relationships among species on the variables before evaluating relationships. In addition, the relative effect of the phylogenetic tree on the linear model could be estimated as a λ parameter, ranging between 0 (covariation among species measurements is independent of co-ancestry) and 1 (covariance entirely explained by co-ancestry). Testing the models with $\lambda = 0$ allowed comparison to λ-positive models, and thus the extent to which phylogeny influenced analyses of the models examined. In addition to phylogeny, our model evaluated the influences of average body mass (of adults) of the different species, bats and arboreality lifestyle, and the fact that some data were acquired from captive and wild populations (see below).

We ran PGLS models for the 4 different conditions listed above (Table 1). Longevity was our dependent variable in all models, and hibernation season duration and species average body mass were independent variables. In all models, body mass and longevity were log-transformed to normalize their distributions, and all independent variables were standardized (using *z-scores*), so that their coefficients are directly comparable as estimates of effect sizes (Abdi, 2007). In the original models, we included the interaction *hibernation season duration x body mass* to test for the possibility that the effect of hibernation season duration on longevity was more important for species of small body mass (see Fig 2 in Turbill et al., 2011), as well as a ‘captive/wild’ factor to account for captivity-related variation in longevity (Tidière et al., 2016). However, these factors were parsimoniously dropped in the final models based on Akaike’s Information Criterion (AIC). Among the models within ΔAIC <2 ($\Delta AIC_i = AIC_i - AIC_{min}$), we kept the model with the lowest number of terms (see Electronic Supplementary Materials Table S3). Nevertheless, body mass was retained throughout our models, because of the dominance that it shows as a primary axis of energetics and life history (Brown et al., 2004; Stearns, 1992). In order to control for higher longevity due to particular lifestyles, we added a 'bat (yes/no)' factor in the full model (Turbill et al., 2011; Wilkinson and South, 2002) and an 'arboreality (yes/no)' factor in each model (Healy et al., 2014; Kamilar et al., 2010; Shattuck and Williams, 2010).We limited the number of additional predicators in order to maintain sufficient statistical power with respect to the sample size (table 2; Mundry, 2014).

For the final models, the level of covariation in maximum longevity among species was estimated by maximum likelihood (λ_{ML}).

Within bats (individuals from wild populations only), we were not able to estimate the effects of body mass and hibernation season duration on longevity, while controlling statistically for phylogeny. We had too few species of bats (N = 27; Münkemüller et al., 2013) for properly evaluating the phylogenetic signal (the lower CI bound for the phylogenetic signal could not be estimated; see Electronic Supplementary Material, Fig S2). Thus, we present simple linear regressions for this group later indicated as model 5 (Table 1 and 2)

Model	**1**	**2**	**3**	**4**	**5**
Model type	PGLS	PGLS	PGLS	PGLS	Linear model
Hibernators > 1.5 kg	x	x			
Hibernators < 1.5 kg	x	x		x	
Deep hibernators	x	x	x		
Bats	x				x
Sample size	82	55	46	44	27
Arboreal and semi-arboreal species	16	16	11	15	0
Hibernation season duration range (day)	105-296	105-296	105-296	105-296	120-255
Longevity range (year)	3.5-49.5	3.5-49.5	3.5-49.5	3.5-29	6-41
Body mass range (g)	4.6-227500	8-227500	8-7300	8-958	4.6-28.55

Table 1. Summary of models and datasets. The category known as ‘deep hibernator’ includes the species capable of reducing their total energy expenditure by about 90% or more during hibernation as compared to the euthermic state and reaching a body temperature during torpor below 10°C (mainly small Holarctic species; Heldmaier et al., 2004). Crosses indicate group(s) included in each model

3 Results

The characteristics of the models and data used are summarized in Table 1. For each model, hibernation season duration and longevity were similar in range between the different datasets (Table 1). Naturally, the range of body mass was much smaller when considering only deep hibernators, small species and bats.

Model 1(N = 82): Accounting for the effect of phylogeny, variation in longevity was positively associated with hibernation season duration and body mass across all hibernating mammals (Table 2, Fig 1 and 2). On average, bats had significantly longer lifespans (79%, $\overline{x}$ = 21 years, N = 27) as well as species with an arboreal lifestyle (11%, $\overline{x}$ =13 years, N =16), than other mammals ($\overline{x}$ = 11.8 years, N = 55) (Table 2).

Model 2 (N = 55): Removing hibernating bats from the analyses showed that hibernation season duration had a significant positive effect on longevity (Table 2, Fig 1 and 2). The positive effect of higher body mass and arboreality lifestyle on longevity remained, mammals with greater body mass or arboreality lifestyle exhibiting significantly longer lifespan (Table 2, Fig 1 and 2).

Models 3 and 4 (N= 46 and N = 44 respectively): When only deep hibernators (model 3) and small hibernators < 1.5 kg (excluding bats) were considered (model 4), we found a positive effect of hibernation season duration on longevity (Table 2, Fig 1 and 2). The positive effect of arboreality lifestyle on longevity only remained for small hibernators (model 4).

Among the above models, the effect of hibernation season duration was slightly higher for small hibernators < 1.5 kg and highly significant (Table 2, Fig 1 and 2). These models showed a strong influence of phylogeny on the results (Table 2). Ignoring the effect of phylogeny by constraining λ to 0 removed the effect of hibernation season duration on longevity (Table 2).

Model 5 (N = 27): Because our sample size for bats alone was too small, we could not perform an analysis controlling for phylogeny. Instead, we ran simple linear models to test for the effects of hibernation season duration and body mass on longevity. Here as well, hibernation season duration, but not body mass, was positively and significantly related to maximum longevity (Table 2, Fig 1 and 2). Hibernation season duration had an effect on bat longevity up to two times higher than in previous models excluding bats. This significant effect without accounting for phylogeny was probably due to a lower level of phylogenetic differences among bat species, compared to other models including up to eight different orders.

			λ_{ML}				$\lambda = 0$		
			λ_{ML}	β ± SE	t	P	β ± SE	t	P
Phylogenetic correction (PGLS)	Model 1: All hibernators (82 species)	Intercept	*λ_{ML} = 0.736* *CI_{95} = [NA-0.924]*	0.986 ± 0.111	8.847	< 0.001***	0.834 ± 0.032	25.778	< 0.001***
		z-Hibernation duration		0.051 ± 0.020	2.484	0.015 *	0.028 ± 0.020	1.343	0.183
		z-log (Body mass)		0.163 ± 0.043	3.800	< 0.001***	0.216 ± 0.026	8.409	< 0.001***
		bat		0.531 ± 0.170	3.131	0.002**	0.656 ± 0.060	10.903	< 0.001***
		arboreality		0.163 ± 0.075	2.175	0.033*	0.182 ± 0.054	3.387	0.001**
	Model 2: Hibernators without bats (55 species)	Intercept	*λ_{ML} = 0.849* *CI_{95} = [0.238-0.969]*	0.970 ± 0.112	8.682	< 0.001***	0.841 ± 0.031	27.439	< 0.001***
		z-Hibernation duration		0.058 ± 0.022	2.645	0.011*	0.004 ± 0.022	0.200	0.842
		z-log (Body mass)		0.171 ± 0.038	4.442	< 0.001***	0.217 ± 0.024	8.920	< 0.001***
		arboreality		0.191 ± 0.070	2.738	0.008**	0.173 ± 0.051	3.409	0.001**
	Model 3: Deep hibernators without bats (46 species)	Intercept	*λ_{ML} = 0.850* *CI_{95} = [0.480-0.960]*	1.025 ± 0.107	9.611	< 0.001***	0.876 ± 0.026	33.483	< 0.001***
		z-Hibernation duration		0.051 ± 0.022	2.279	0.028*	0.008 ± 0.023	0.342	0.734
		z-log (Body mass)		0.100 ± 0.054	1.833	0.074.	0.173 ± 0.034	5.120	< 0.001***
	Model 4: Small hibernators (< 1.5 kg) without bats (44 species)	Intercept	*λ_{ML} = 0.740* *CI_{95} = [0.293-0.924]*	0.867 ± 0.084	10.240	< 0.001***	0.820 ± 0.029	28.543	< 0.001***
		z-Hibernation duration		0.061 ± 0.020	2.994	0.005**	0.024 ± 0.021	1.148	0.258
		z-log (Body mass)		0.014 ± 0.053	0.264	0.793	0.121 ± 0.042	2.864	0.007**
		arboreality		0.204 ± 0.069	2.937	0.005**	0.191 ± 0.048	4.002	< 0.001***
No phylogenetic correction (Linear model)	Model 5: Bats only (27 species)	Intercept	NA	1.453 ± 0.168	8.619	< 0.001*	NA		
		z-Hibernation duration		0.101 ± 0.045	2.215	0.036*			
		z-log (Body mass)		0.141 ± 0.179	0.785	0.440			

Table 2. *Z*-standardized model estimates (β) for the effects of hibernation season duration and body mass on species maximum longevity. The phylogenetic effect is estimated by λ_{ML}. Both body mass and longevity were log-transformed before the analyses. For comparison, we have provided estimates for λ constrained to zero (no effect of phylogeny). The model for bats was a simple linear model not controlling for phylogeny, due to limited sample size in this group. In the model with all hibernators, the NA value in the confidence interval for λ_{ML} indicates that the caper package could not calculate the full confidence interval. An NA value is considered as

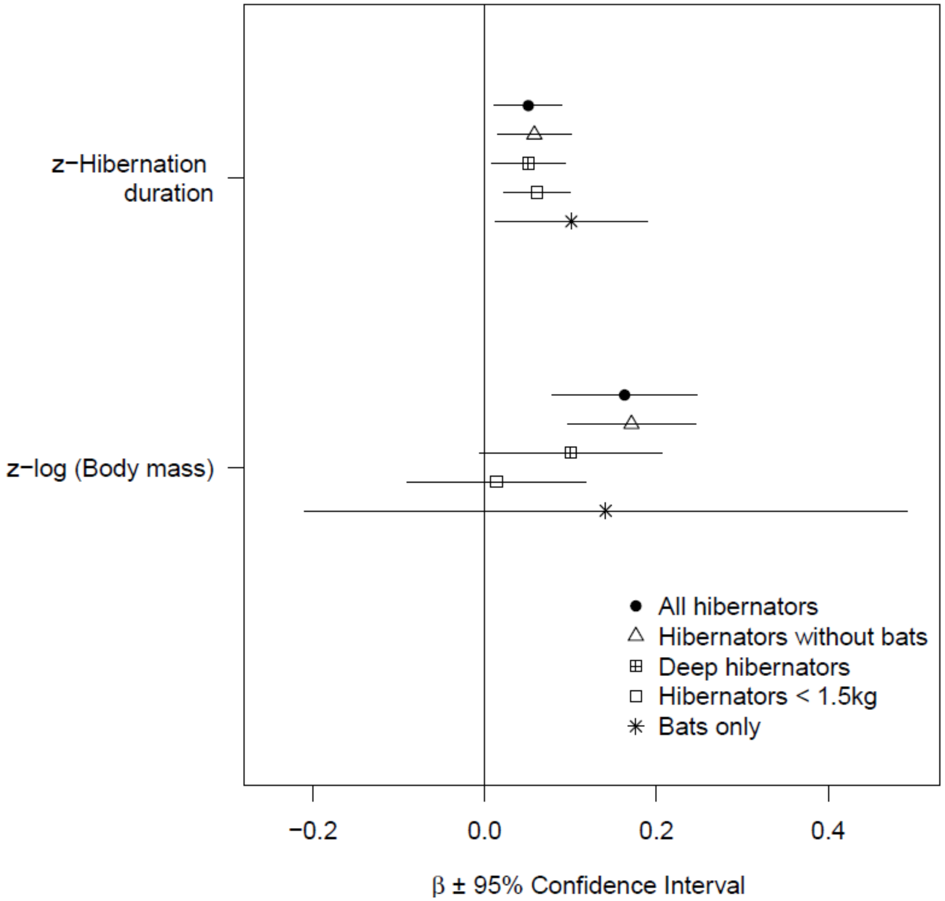

Figure 1. Effects of hibernation season duration and body mass on longevity. Z-standardized model coefficients are presented ± 95% Confidence Interval (1.96xSE). Both body mass and longevity were log-transformed before the analyses. The effect sizes are presented for PGLS models for all mammals (N = 82), mammals without bats (N = 55), deep hibernators without bats (n=46) and small mammals without bats (N = 44). For comparison, effect sizes from a simple linear model not accounting for phylogeny are presented for bats only (N = 27).

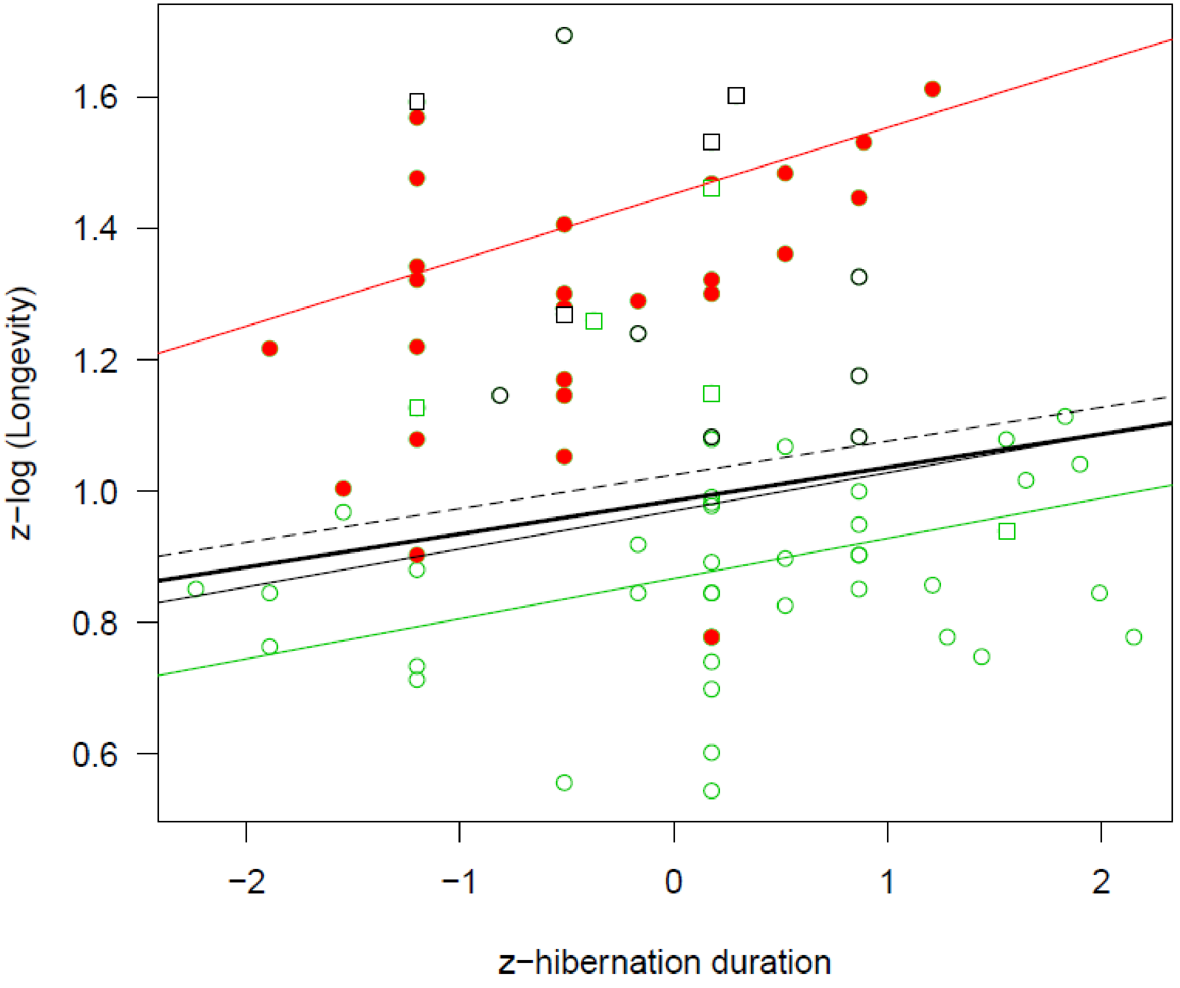

Figure 2. Relationship between hibernation season duration (standardized) and longevity (log-transformed and standardized). The regression lines are presented for PGLS models for all mammals (bold black line, N = 82, *p*=0.015), all hibernators without bats (black line, N = 55, *p*=0.011), deep hibernators without bats (dashed line, N = 46, *p*=0.028) and small hibernators without bats (green line, N = 44, *p*=0.005). For comparison, effect sizes from a simple linear model not accounting for phylogeny are presented for bats only (red, N = 27, *p*=0.036). Full red circles highlight bat species, the squares highlight species reducing their energy expenditure during hibernation by less than 90% compared to the euthermic state, green item highlight species below 1.5kg, and black circle highlight all remaining hibernators above 1.5kg in the data set. Please note that some dots referring to bat species are superimposed because the corresponding species have exact same hibernation season durations and longevities.

4 Discussion

4.1 Influence hibernation season duration on longevity

Our purpose was to examine the extent to which the activity time budget explains variation in life history traits in mammals. We investigated this question in hibernating species because of their marked seasonal cycle of activity/inactivity, which is associated with very different risks of mortality (Turbill et al., 2011). While controlling for phylogeny, our study highlighted a positive influence of hibernation season duration on longevity in mammalian hibernators. These results were in agreement with an early study that tested the effect of hibernation duration on longevity in captive Turkish hamsters (Lyman et al., 1981). In agreement with Dobson (2007) and Sibly and Brown (2007), the two major axes of life histories of mammalian hibernators are body mass and lifestyle, with lifestyle contributing to the slow-fast continuum. The bat lifestyle (*e.g.*, aerial) had the greatest influence on longevity, with a positive effect on longevity that was three times greater than the arboreality lifestyle. The effect of hibernation season duration, in addition to these lifestyles, appeared to be roughly one-third of the effect of body mass on longevity (see model estimates in Table 2).

Our results show that the effects of hibernation season duration on longevity were consistent across a wide range of body sizes, and became stronger with the limitation in body mass to small species (species < 1.5 kg), especially for bats (Figure 1). Interestingly, hibernation season duration appeared to be more important than body mass in explaining longevity in the latter species. These results support the idea that hibernation (1) is an efficient strategy that limits mortality in periods of energy scarcity for some larger species facing strong energy constraints during part of the year (*e.g.*, *Marmota* species), and (2) may be an especially effective strategy for small mammals that are expected to suffer from both higher predation rate (Cohen et al., 1993; Sinclair et al., 2003), and increased loss of energy expenditure during winter (Ruf and Geiser, 2015). In either case, increased hibernation season duration may increase both annual survival rates (Turbill et al., 2016) and overall longevity. Note that in some cases, the lack of relationship between body mass and longevity in our study could also be due to a smaller range of body mass variation than reported in other studies (for instance in bats; Wilkinson and South, 2002).

In our study, the effect of hibernation season duration on the longevity for bats was twice that of small non-flying terrestrial mammals, though this result should be considered with caution since we were not able to control for phylogeny when considering only bats (Table 2, Fig 2 and 3). Bats stand somewhat apart from other mammals, distinguished notably by their ability for sustained flight, an important lifestyle characteristic (Sibly and Brown, 2007). Flying is an energy-intensive activity, considerably more than terrestrial locomotion (Thomas and Suthers, 1972; Tucker, 1968). Thomas and Suthers (1972) estimated that the greater spear-nosed bat (*Phyllostomus hastatus*) increases its resting metabolic rate more than 34 times during flight, while rodents of similar size increase it only by 8-fold during terrestrial locomotion. Thus, in bats the reduction of metabolism during hibernation is particularly important compared to their period of activity (Wilkinson and South, 2002).

The marked effect of hibernation season duration on longevity in bats may also be explained by some extreme physiological adaptations to hibernation having evolved in response to specific ecological and anatomical constraints (Willis, 2017). For instance, several bat species are capable of very long torpor bouts (up to 60 days; reviewed in Ruf and Geiser 2015), perhaps in response to their limitation on accumulation of internal or external energy reserves (Willis, 2017). In addition, the little brown bat (*Myotis lucifugus*), for instance, is capable of performing "heterothermic arousals", corresponding to shallow torpor bouts ($T_{skin} > 20°C$), during arousal phases, and thus reduce the cost of euthermia (Czenze et al., 2017; Jonasson and Willis, 2012). This particular adaptation may be present in other bat species as well. Finally, bats are highly gregarious during hibernation and can cluster in colonies of up to thousands of individuals (Clawson et al., 1980). Huddling could enable them to reduce energy costs and water loss during hibernation, making hibernation a particularly profitable strategy (Boratyński et al., 2012, 2015; Boyles et al., 2008; Gilbert et al., 2010).

Comparisons between of models either including (model 2) or excluding (model 3) species with lowest metabolic reduction during hibernation did not reveal significant differences. These results suggest that the effect of hibernation season duration on longevity remains consistent whatever the rate of metabolic reduction reached during hibernation compared to the active state (between 70 to 90%). This finding should pave the way for future studies to specifically test this effect of metabolic reduction during hibernation.

Interestingly, in all PGLS models, removing the effect of phylogeny by constraining λ to 0 also removed the effect of hibernation season duration on longevity. This suggests that the effect of hibernation season duration on longevity is masked by the phylogenetic pattern. Thus, hibernation season duration might be a stronger explanation of variation within species or between closely related species, as shown in Turkish hamsters (Lyman et al., 1981). For instance, studies comparing populations of golden-mantled ground squirrels (*Callospermophilus lateralis*) and Columbian ground squirrels (*Urocitellus columbianus*) living along an altitudinal gradient show that populations with longer hibernation season duration generally have higher annual survival and longevity (Bronson, 1979; Dobson and Murie, 1987; Murie and Harris, 1982).

Although our results highlight an association between hibernation season duration and longevity, they do not provide a causal mechanism through which such an association might arise. Periods of prolonged inactivity are likely to increase longevity through the integration of multiple factors affecting both intrinsic and extrinsic mortality, as discussed below.

4.2 Factors affecting extrinsic and intrinsic mortality and the evolution of hibernation

Energetic stress, when energy demand is greater than energy availability in the environment, has a proximate role in the regulation of hibernation pattern (Vuarin and Henry, 2014). However, few studies have focused on the causal link between energetic stress, and the timing of hibernation immergence and emergence (*e.g.*, Humphries et al., 2002). Thus, the hypothesis that hibernation occurs primarily as a response to an energetic stress has not been completely studied (focusing on torpor bouts frequency, depth and duration). To the best of our knowledge, the only study having measured both energy availability in the environment and individual energy expenditure before immergence in hibernation shows in eastern chipmunks (*Tamias striatus*), that immergence occurs while food is still plentiful and climatic conditions are still favorable for maximizing energy storage (Humphries et al., 2002). Other observations also suggest that immergence into hibernation while food is still available seems common, at least in sciurids (Humphries et al., 2003) and for the little pocket mouse (French, 2004). Thus, food availability and ambient temperature alone may not be sufficient to explain the phenology of immergence.

Other evidence suggests that hibernation is not initiated solely in response to deficiencies in energy, water, or poor food quality. Many observations suggest that early immergence (before energetically stressful periods start) occurs when the benefits of reproduction are low. For instance, in years of low beech seed abundance, the edible dormouse (*Glis glis*) skips reproduction, quickly accumulates fat reserves, and is able to hibernate for up to 11 months (Hoelzl et al., 2015). This occurs even if food in the environment is sufficient to allow the edible dormouse to remain active but not to reproduce. Similarly, Eastern chipmunks skip reproduction and cease foraging for almost a full year when food availability is particularly low (Munro et al., 2008). It seems that at that time, chipmunks rely on large amounts of food hoarded during the preceding year; but there is no evidence of torpor expression. This kind of behaviour is also observed in several hibernating ground squirrel species. Females that fail to reproduce may immerge up to several weeks before the others (Bintz, 1988; Choromanski-Norris et al., 1986; Michener, 1978; Neuhaus, 2000). An experiment in semi-natural conditions shows that female European ground squirrels (*Spermophilus citellus*) that were separated from males (and thus did not breed) entered into hibernation 4 to 6 weeks before females that were not separated (Millesi et al., 2008). These results support the view that hibernation phenology is influenced by a trade-off between reproduction and survival, where hibernation seems to provide benefits other than surviving periods of energetic stress. This trade-off may also explain differences (up to 1 month) in the timing of immergence and emergence between gender and age observed in rodents (Siutz et al., 2016; Sheriff et al., 2011; Kawamichi, 1989; Kart Gür and Gür, 2015; Snyder et al., 1961; Holekamp and Nunes, 1989) and bats (Decher and Choate, 1995; Norquay and Willis, 2014; Stebbings, 1970; Thomson, 1982).

So far, most studies have focused mainly on temperate hibernating species. However heterothermy that occurs during daily torpor and hibernation, is taxonomically and geographically widespread (Ruf and Geiser, 2015). A surprisingly large proportion of mammals, including a monotreme, several marsupials, and placental species regularly enter daily torpor and seasonal hibernation in the southern hemisphere (Grigg and Beard, 2000). For some species in these regions, the use of torpor may not be related to low environmental temperatures or limited food availability (Nowack et al, 2020). For example, the short-beaked echidna hibernates (Grigg et al., 1989) while ants and termites, which constitute the main part of its diet, remain available throughout the year (Grigg and Beard, 2000). Short-beaked echidnas are heavily armored, perhaps rendering avoidance of predation an unlikely adaptive benefit for hibernation. These observations suggest that some species may use hibernation because of the energy advantages provided by lack of activity, even though it is not an energy necessity for survival during a period of energetic stress (Grigg and Beard, 2000). Such case studies broaden the scope of possibilities for understanding the evolution of hibernation (Grigg and Beard, 2000; Ruf et al., 2012), and open up exciting perspectives for future research.

5 Conclusion

Hibernation is considered an adaptation to seasonal, hence predictable decrease in food resources and ambient temperatures. However, hibernation is also observed in mild climates and when ambient conditions are still favorable for activity (Nowack et al., 2020). If remarkable physiological aspects of hibernation have been widely studied, fewer studies have focused on its ecological and evolutionary significance in the field. Our study provides evidence that there may be a relationship between activity time budgets, and hence the time dimension of allocation trade-off, and life history traits.

Our phylogenetic analyses shows that variations in hibernation season duration can partially explain variations in longevity in hibernators. The models show a strong influence of phylogeny on this relationship and highlight the need for in-depth studies at an inter- and intra-population scales. For example, future studies may attempt to consider activity time budgets in the context of the pace of life syndrome by examining variations in hibernation with other physiological and behavioral traits. Our results, combined with information available in the literature, suggest that, in addition to its survival benefits during a period of energetic stress, hibernation season duration may have evolved to reduce the effects of other sources of extrinsic and intrinsic mortality.

6 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

7 Author Contributions

T.C.: conception and drafting the manuscript

S.G., C.H.: development of the concept and writing of the manuscript

T.C.: data collection

T.C., V.A.V., F.S.D.: data analyses

V.A.V., M.L.T., P.B., F.S.D., C.H., S.G.: substantial contributions to the conception

F.S.D.: English composition with many revisions of the text

All authors contributed to the revisions.

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Chapter 2

Yongqing Bao received the first prize of Wildlife Photographer of the Year in 2019 for this photo of a marmot scared by a fox on the Tibetan plateau of Qinghai.

Maybe the marmot wondered “Wouldn’t it have been better to hibernate?”

This is what we tried to understand in this next chapter

Running head: Trade-offs in dormancy phenology

Title: Trade-offs in dormancy phenology in endotherms and ectotherms

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Data accessibility statement: if the manuscript is accepted, the data and computer code supporting the results will be archived in an appropriate public repository and the DOI of the data will be included at the end of the article.

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Abstract

Seasonal dormancy (*e.g.*, diapause, hibernation) is widely interpreted as a physiological response for surviving energetic challenges during part of the year. Under this "energy limitation" hypothesis, the timing of initiation and termination (*viz.*, the phenology) of seasonal dormancy is a response to the energy limitation of the environment. However, the selective pressures acting on dormancy phenology are poorly studied. An underappreciated common aspect is the high survival rate during dormancy compared to the active period, perhaps due to the reduced risks of predation and competition. We propose an alternative hypothesis that dormancy phenology is influenced by a trade-off between the reproductive advantages of being active and the survival benefits of being dormant (thus, the "life-history" hypothesis). Using a phylogenetic comparative method and more than 20 hibernating mammal species, we predicted that the sex variation in hibernation phenology should be correlated with sex differences in reproductive investment, independent of an individual's energetic status. Consistent with life-history hypothesis to explain hibernation phenology, the sex that spends more time in an activity directly associated with reproduction (*e.g.*, testicular maturation, gestation) or indirectly (*e.g.,* recovery from reproductive stress) spends less time in hibernation. Some of the tested parameters such as testes maturation or a late mating period during the active season also influence the sex difference in dormancy phenology among ectotherms (*e.g.,* reptiles, invertebrates). Moreover, we found evidence across both endotherm and ectotherm species that dormancy sometimes takes place at times when the environment would allow the maintenance of a positive energy balance. Dormancy during non-life-threatening periods that are unfavorable for reproduction may be more widespread than previously thought. As phenological shift is one of the major responses to climate change, future estimates of its impact on dormant species should take this new hypothesis into account.

Keywords: overwintering adaptations, phylogenetic analysis, climate change, annual cycle, body mass change, reproductive investment, risk spreading, metabolic suppression, seasonality, protandry.

1) Introduction

A large number of species across the tree of life enter prolonged dormancy each year (Gregory 1982, Hand 1991, Cáceres 1997, Ruf and Geiser 2015, Wilsterman et al. 2021). From an evolutionary perspective, dormancy improves survival while waiting for better conditions when they can reproduce (Watts and Tenhumberg 2021). From a physiological point of view, dormancy occurs under a combination of high energy reserves and a significant reduction in energy demand, thus allowing prolonged inactivity for several months to several years (Côme and Corbineau 1989, Hoehler and Jørgensen 2013, Staples 2016). Dormancy has been studied independently within different phylogenetic groups (Wilsterman et al. 2021), which limits the development of a global evolutionary framework to explain dormancy.

The dormancy of plants, micro-organisms and some invertebrate animals has been extensively studied from an evolutionary point of view. In these species and in addition to energetic benefits, dormancy occurs in a large number of situations limiting competition and predation (Ellner 1987, Danks 1992, Williams 1998, Satterthwaite 2010, Guidetti et al. 2011, Ratcliff et al. 2013, Blath and Tóbiás 2020). In some cases, dormancy may be associated with the colonization of new habitats (Ricci 2001, Mahdjoub and Menu 2008). This broadening of knowledge has allowed the development of many different approaches to explain the evolution of dormancy as based, for example, on a “evolutionarily stable strategies” (Hairston Jr and Munns Jr 1984, Satterthwaite 2010, Kortessis and Chesson 2019), “life history theory” (Ji 2011, Shefferson et al. 2014, Watts and Tenhumberg 2021), or as a “bet hedging strategy” (Hopper 1999, Menu et al. 2000, Joschinski and Bonte 2021).

On the contrary, in most animals, prolonged dormancy has been mainly studied in an (eco)physiological context. It has been widely demonstrated that when energy constraints increase (*e.g.,* increased annual fluctuation in temperature or shifting timing of food availability), changes in the dormancy period are observed (Pianka 1970, Bronson 1979, Wilsterman et al. 2021). Thus, theories and models have focused mainly on energetic demands to explain dormancy and its timing (Bronson 1979, Sexton and Hunt 1980, Humphries et al. 2002b, 2003). Although, a reduction in the risk of predation or competition during animal dormancy has been suggested (Turbill et al. 2011, Ruf et al. 2012), no study to date has revealed an influence of these factors on the evolution of prolonged dormancy. This raises the question of whether the timing of animal dormancy over time, *i.e.*, the phenology of dormancy, might be best or even exclusively explained by the hypothesis of energy limitation or, as in other organisms, alternative advantages may be involved.

In animals, a distinction is made between heterothermic endotherms (mammals and birds) that are able to actively control their metabolic rate *via* oxidative metabolism (*e.g.*, full activity versus hibernation and aestivation) and ectotherms (invertebrates, fish, amphibians, and reptiles) whose metabolic rates are more subject to microclimatic fluctuations (Milsom and Jackson 2011, Staples 2016). In both cases, although dormancy drastically reduces energy expenditure, however some energy is yet lost in the absence of an external input. As a consequence, if dormancy phenology is explained solely by energetic issues (the energy limitation hypothesis), selection may favor remaining active until a positive energy balance (in endotherms) or thermal window favorable for activity (in ectotherms; see (Gunderson and Leal 2016)) is no longer possible (Fig. 1a). To the contrary, if there are other benefits such as improved survival due to a reduction of predation risk, these survival benefits may produce a trade-off between being active while investing in reproduction versus being dormant to increase survival (the life-history hypothesis). Within species, this trade-off may be reflected in sex differences in dormancy phenology.

Males often emerge from dormancy and arrive at mating sites some days or weeks before females (termed “protandry”), and mating occurs shortly after female emergence from dormancy (Wang et al. 1990, Morbey and Ydenberg 2001, Winck and Cechin 2008, Nicol and Morrow 2012). For females, emergence phenology may promote breeding and/or care of offspring during the most favorable annual period (*e.g.*, at the peak of food availability, Fig. 1). Although males are active above ground before females, the latter sex may not emerge until later to limit mortality risks (see the "waiting cost hypothesis," Morbey and Ydenberg 2001). For males, sexual selection is assumed to favor early emergence relative to females, because it provides mating advantages (see the mating opportunity hypothesis,” Morbey and Ydenberg 2001). Males that are physiologically prepared to mate (Breedveld and Fitze 2016) and have established intrasexual dominance or territories (Hibbitts et al. 2012) prior to mating are likely to have greater reproductive success (Michener 1983). Thus, greater protandry is assumed to have evolved with longer periods of mating preparation. During the rest of the year, both sexes are expected to prepare and enter dormancy for survival benefits when they are no longer investing or recovering from reproduction.

In the present study, we investigated the “life-history hypothesis”, a relatively new alternative hypothesis to the “energy limitation hypothesis” for explaining the phenology of dormancy, especially sex differences within species. To begin with, we predicted from the former hypothesis that the sex that invests the most time in reproduction, will spend less time in dormancy (Fig. 1d). On the contrary, according to the latter hypothesis, investment in reproduction and dormancy phenology might be independent (Fig. 1c). To examine these predictions, we use two complementary approaches:

First, using phylogenetic comparative analyses, we compared reproductive and hibernation traits that might tradeoff and coevolve in more than 20 promiscuous and polygynous hibernating mammals. We examined types of sex-specific physiological constraints that have been suggested to influence the sex difference in the trade-off between reproduction and survival. At emergence from hibernation, we expected that at the interspecific scale (1) males of species with longer mating preparation would exhibit greater protandry. Mating preparation might increase with the maturation of higher testes mass or higher body mass gain. We tested whether these parameters are correlated with greater protandry. We also expected that (2) the species with higher sex differences in the time spent in activity post mating (maternal effort for female; Levesque et al. 2013) and recovery from mating stress for male; Millesi et al. 1998) would have a greater sex difference in immergence, with the sex that spends more time in their post-mating reproductive activity would also be the one that immerges the latest.

Secondly, there is a need to unify ectotherms and endotherms in the study of dormancy for answering fundamental questions (Wilsterman et al. 2021). While there are insufficient data on dormancy phenology and reproductive investment for ectotherms to allow a comparative analysis, we examined, as a second step, the information already available in the literature for ectotherms and compared it to our results for endotherms. Finally, we discussed some evidence of the "life-history hypothesis" at other scales (*e.g.*, interindividual, interspecific) and broadened the evolutionary causes of animal dormancy.

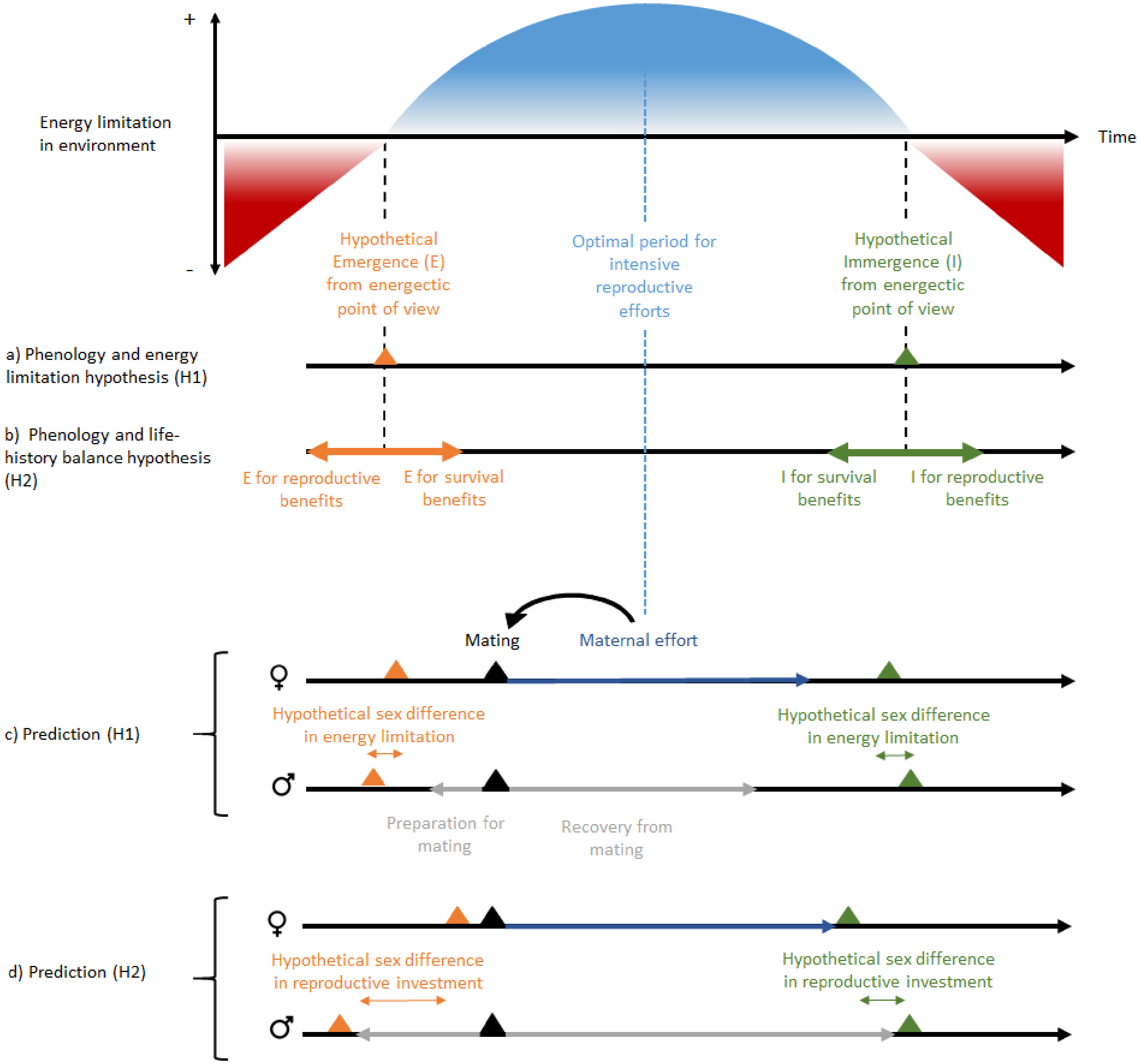

Figure 1 Schematic representation of "the phenology and energy limitation hypothesis" and "the phenology and life-history balance hypothesis" and their predictions. The energetic limitation in the environment refers to the variation over time of the energetic balance (mainly for endotherms) and the thermal window favorable to activity (mainly for ectotherms). Hypothesis H1 assumes that dormancy phenology occurs at the time of transition between favorable and unfavorable energetic conditions or vice versa. It predicts that the sex difference in dormancy phenology is assumed to

be explained by differences in energy limitation, and reproductive investment would be independent of this sex difference in phenology. In contrast, hypothesis H2 predicts that a phenology that would occur before or after this energetic transition may be associated with benefits to survival or reproduction. It predicts that the sex difference in dormancy phenology is associated with a sex difference in reproductive investment. This pattern corresponds to the pattern expected for species without paternal effort examined in this study. But the concept can be applied to other types of mating strategies. The hibernation phenology presented for prediction (H1) correspond to those expected for hibernating mammals. Note that the magnitude and order of sex differences in phenology is not an expected general trend because it is assumed to vary between species according to energy demand (prediction H1) and reproductive investment (prediction H2). Nevertheless, the sex difference is assumed to be smaller with the H1 prediction because there are less sex differences in energy demand than in reproductive investment. Black, grey and dark blue horizontal arrows represent respectively time over the year, reproductive investment in males and reproductive investment in females.

2) Materials and methods

a) Review Criteria

Our literature review was based on the list of 152 hibernating mammals (see supplementary materials 1 in Constant et al., 2020). We excluded non-seasonal hibernating species that do not have a consistent seasonal hibernation phenology (elephant shrew and marsupial species except *Burramys parvus* (the mountain pygmy possum)). We did not include species from the order *Carnivora* and *Chiroptera* because of a difference in reproductive phenology compared to the majority of other hibernators, especially due to delayed embryo implantation (Sandell 1990). For example, bears are the only mammals with gestation, parturition and lactation during hibernation (Friebe et al. 2014). This implies different trade-offs between hibernation and reproduction that require separate analyses. As well, little information was available to analyze the phenologies of bat species. Each of the following literature reviews was conducted using the search engine Google Scholar with specific keywords and considered articles up to and including January 2021.

b) Sex difference in hibernation phenology

We searched for hibernation phenology for each sex based on average date of emergence and immergence in the same population. When these types of data were not available, we accepted the date at which first/last individuals of each sex were observed or the approximate sex difference available in the text. The search criteria were based on combining the following terms: (scientific OR common names of species) AND (phenology OR annual cycle OR hibernation). Because of their imprecision, we excluded the studies for which hibernation season phenology was deduced from the presence of active individuals on a monthly basis. This excluded four studies (Dunford 1974, Gashwiler 1976, Randrianambinina et al. 2003, Mouhoub sayah et al. 2009). As the data were averaged for each species (see section "Statistics") we did not use data with exceptional variation between years within the same study site. This excluded data from (Munroe 2011) on the sex difference in immergence date (55 days difference between the two years) for *Xerospermophilus tereticaudus* (the round-tailed ground squirrel). *Otospermophilus beecheyii* (the California ground squirrel) appeared to be a species with great variation in hibernation phenology and whether males and females hibernated (Dobson and Davis 1986, Holekamp et al. 1988). These data were therefore not included in this study.

From the remaining data, we calculated protandry and the sex difference in immergence as female Julian date – male Julian date.

c) Sex differences in reproductive investment

i. Emergence

As the female emergence is assumed to be selected so that the highest energy investment in reproduction matches with the peak of food availability, it is assumed that the difference between the sexes is explained by the preparation of males for reproduction. As we are comparing sex difference in investments of time in reproduction, we assume that higher relative testes mass (see table 4 in Kenagy and Trombulak, 1986) and a higher accumulation of body mass (Humphries et al. 2002a) take more time and energy.

For relative testes mass, a search was conducted by combining the following terms: (scientific OR common names of species) AND (testes mass OR testes size). The data on testes mass corresponded to the maximum mass reached during the mating season. We favored data measured at the same study site as the hibernation phenology data. Otherwise, the different data obtained for the same species were averaged. Relative testes mass was calculated as follows: testes mass/body mass.

For males, relative body mass change between emergence and before mating hereafter referred to as "Δ body mass before mating" was calculated as follows: ((Body mass before mating - Body mass at emergence) / Body mass at emergence). "Δ body mass during mating" was calculated as follows: ((Body mass at the end of mating - Body mass at the beginning of mating) / Body mass at the beginning of mating).

ii. Immergence

Since males and females have very different activities after mating, the duration of these activities may be related to the sex difference in immergence.

In *Spermophilus citellus* (the European ground squirrel), the most actively mating males delay the onset of post-mating accumulation of body mass and also delay hibernation, presumably due to the long-term negative effects of reproductive stress (Millesi et al. 1998). Thus, the recovery period from reproductive stress is defined as the time between the end of mating and before immergence hereafter referred to as "post-mating activity time" (see "Statistics" and "Results" sections for its validation as a proxy and below for mating period determination).

Some males have already lost body mass before females emerge from hibernation, which may contribute to their stressful situation. Thus, in order to reduce the variable to one measure of change in body mass during the stress period for males, we calculated relative body mass change between emergence and the end of mating, hereafter referred to as "Δ body mass through the end of mating” as follows: ((Body mass at the end of mating - Body mass at emergence) / Body mass at emergence).

For all data on changes in body mass, the search was conducted by combining the following terms: (scientific OR common names of species) AND (body mass change OR annual body mass). To be as accurate as possible, we have obtained data only when measured at the same or nearby the study site that was used for hibernation data. In cases where information were not directly available in the text or table, we used the software Plot Digitizer (Huwaldt and Steinhorst 2015) to extract the data from graphs. This software has recently been validated for this use (Aydin and Yassikaya 2021). The start and end dates of mating were estimated from information available in the text or from other studies at the same study site. When the mating period could not be clearly determined, studies were omitted from analyses.

Maternal effort duration is calculated as the sum of the gestation and lactation periods. We obtained data on the length of gestation and lactation from the AnAge database (The Animal Aging and Longevity Database; Magalhães and Costa, 2009), and complemented these data with information from the PanTHERIA database (Ecological Society of America; Jones et al., 2009) and from a specific search combining the following terms: (scientific OR common names of species) AND (lactation duration OR gestation duration). Since we were interested in the time invested in post-mating activities that differ between the sexes, then for females having several litters per season, we have only taken into account the duration of maternal effort provided to the last litter and not the total time spent over the entire mating season.

d) Climate data

Species living in harsh conditions may be more time constrained by a short active season that might influence the sex differences in hibernation phenology. To take this into account in the models (see section “Statistics”), the location (latitude and longitude) of hibernation study sites were taken from the publication, or when not available we determined their location using Google map from the available information. Then the location data were used to extract values of the minimum temperature of the coldest month (hereafter referred to as minimum temperature) from an interpolated climate surface (BIOCLIM) with 1 km^2 resolution (30 sec) based on data for the period 1970-2000 (Hijmans et al. 2005).

e) Statistics

We used phylogenetic generalized least squares (PGLS) models to account for the non-independence of phylogeny-related species with the “ape 5.0,” “apTreeshape 1.5,” and “caper 1.0” packages in R v. 3.6.2 (Orme et al., 2013; Paradis, 2011; Paradis and Schliep, 2019; R Core Team, 2019). For each model tested we downloaded 100 phylogenetic mammalian trees (see Upham et al., 2019). Then, strict consensus trees for which the included clades were those present in all the 100 phylogenetic mammalian trees were constructed (Paradis 2011). For each consensus trees (see Appendix S1), branch lengths were calculated with the “compute.brlen” function from the “ape” package based on Grafen’s (1989) method, and were used to compute PGLS models with the “caper” package in R. The effect of phylogeny on the linear model could be estimated as a λ parameter, ranging between 0 (no phylogeny effect) and 1 (covariance entirely explained by co-ancestry). By comparing the best models with a similar model but constrained to have a lambda = 0, we evaluated the extent to which phylogeny influenced analyses of the best models.

The PGLS models used an average datum per species for each factor. For hibernation phenology, body mass change, post-mating activity time data and minimum temperature, we first averaged by study when data were available over several years and then we averaged the data for the species. This produces equal weighting between studies on the same species.

We also tested whether the males of species that gain body mass before mating (as dependent variable) are associated with greater competition between males (as reflected by relative testes mass) or body mass loss during mating (as independent variables) as might be expected from capital breeders which use storred energy to finance the mating period. We used the factor "body mass gain before mating" for which all the species had a positive value.

To validate the post-mating activity time as a proxy of the recovery period from reproductive stress for males, we tested whether changes in body mass during mating or changes in body mass before and during mating (as independent variables) increased the post-mating activity time (as the dependent variable). We expected that the more body mass males lose before the end of the mating (as a measure of high stress), the more time they spend active afterwards.

To test for a sex difference in hibernation phenology, protandry and sex difference in immergence were the dependent variables in all our models and each variable presented in the section "Sex differences in reproductive investment" were independent variables. Several parameters may decrease the sex differences in hibernation phenology. We tested for lower protandry with decreasing temperature as species living in harsh conditions may be more time constrained (Blouin-Demers et al. 2000). We also tested for lower protandry when mating was delayed longer after the onset of the annual activity period, as has been shown for reptiles (Olsson et al. 1999) hereafter referred to « delay in mating ». And finally, we tested for lower protandry for species that store food in a burrow and consume it after the last torpor bouts, which may allow them to prepare for the reproduction without emerging above ground (Williams et al. 2014). Food-storing species have been identified in several studies (Kenagy et al. 1989, Vander Wall 1990, Michener 1992, Bieber and Ruf 2004). These parameters may also soften the effects of reproductive parameters on hibernation phenology. Thus, we tested for a “two factor interaction” between either temperature or delay in mating or food-storing with the Δ body mass before mating or relative testes mass.

All full models tested are described in Table 1 with their respective sample sizes (see Appendix S2 for datasets). In the case of multi-factor models, we used the dredge function of the MuMIn package (version 1.43.17; Barto 2020) to select the best model based on corrected Akaike information criterion (AICc). Normality and homoscedasticity were checked by graphical observation. We tested for multicollinearity using the variance inflation factor (we required VIF < 3) on linear models including the factors of the best models. PGLS models do not include calculations of VIFs (Wartel et al. 2019, Ancona et al. 2020). Relative testes mass was log-transformed in all models to obtain the normality of the residuals. All independent variables were standardized (using *z-scores*) in multi-factor models, so that their coefficients are directly comparable as estimates of effect sizes (Abdi 2007).

Table 1 Summary of full models tested and sample size. Crosses indicate variables included in the models. Stars indicate factors for which interactions were tested with log transformed relative testes mass (model 5) or Δ body mass during mating (model 6). The abbreviation “Diff” and "Bmc", stands respectively for “Difference” and “Body mass change”.

	Model number	1	2	3	4	5	6	7	8
	Sample size	11	11	19	15	22	19	14	20
Dependent variable	Protandry					X	X	X	
	Sex diff in immergence								X
	Body mass gain before mating	X	X						
	Post-mating activity time			X	X				
Independent variable	Log(Relative testes mass)		X			X			
	Δ body mass before mating						X	X	
	Δ body mass during mating	X		X					
	Δ body mass through the end of mating				X				
	Post-mating activity time								X
	Maternal effort								X
	Minimum temperature					X*	X*	X*	
	Food-storing					X*	X*	X*	
	Delay in mating [Mean mating delay (week)]					X* [1.52]	X* [1.82]	Without	

3) Results

a) Preliminary assumption

There was no significant relationship between body mass gain for males before mating and Δ body mass during mating, as would be expected for capital breeder species (model 1 in table 2). However, body mass gain before mating increase significantly with higher relative testes mass (model 2 in table 2). In these models, there was little or no influence of phylogeny.

Male Δ body mass during mating did not have a significant influence on the time spent active after mating (but approached significance, model 3 in table 2). However, the time that males spent active after mating increased significantly with body mass lost from emergence until the end of reproduction by males (model 4 in table 2). This result is consistent with the assumption that the post-mating activity time could be used as a proxy of the recovery period from reproductive stress for males. In these models, the influence of phylogeny is strong. Nevertheless, similar results were found when influences of phylogeny were not considered (lambda = 0 in table 2).

b) Emergence

The relationship of protandry and testes mass was complicated, with protandry decreasing with relative testes mass only at the lowest temperatures (Fig. 2). This trend was reversed at relatively high temperatures, for which protandry increased with relative testes mass (model 5 interaction term, Table 2 and Fig. 2).

Protandry increased significantly with the increase in body mass before mating (model 6 in Table 2 and Fig. 3). At the same time, this pattern was strongest for species that had mating soon after emergence from hibernation, and a single outlier caused a significant pattern of decreased protandry with a strongly delayed mating period.

The two explanatory models for protandry show different influences of covariates. After model selection, the delay in mating period was not included in model 5, but was included in model 6. This may be explained by the fact that the mean delay in the mating period is lower in model 5 compared to model 6 (Table 1). Minimum temperature was not included in model 6 (Table 2), where a more delayed mating period was associated with decreased protandry. At the same time, protandry increased with the increase in male body mass before mating. If we exclude species with delayed mating period (more than the minimum value of one week between female emergence and the mating period) from this model, then the best model includes an interaction between male Δ body mass before mating and minimum temperature but this effect is non-significant (model 7, Table 2). The trend shows that the effect of body mass gain before mating decrease with decreasing temperatures.

The influence of phylogeny varied greatly among models, with lambda ranging from 0 to 1. By constraining the model to remove the influence of phylogeny (lambda=0), variable estimates are preserved in the model 5; only the explanatory power of the models increases slightly (Table 2). Nevertheless, the explanatory power in the model 6 is twice as high with phylogeny as without. In addition, the influence of Δ body mass before mating and delay in mating are weaker in the model with phylogeny taken into account, which may imply that a part of these influences is explained by phylogeny.

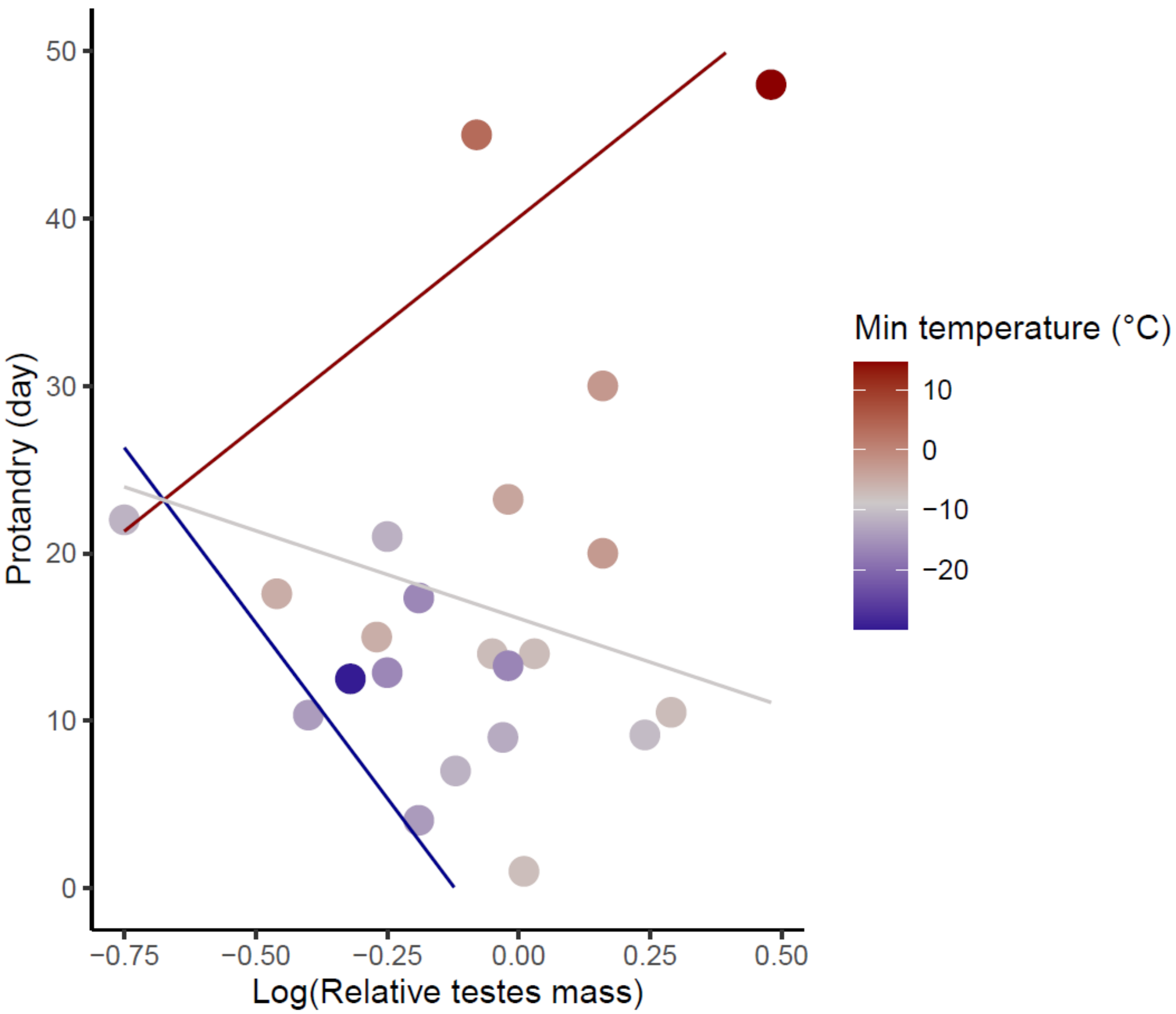

Figure 2 Effects of relative testes mass (log-transformed) on protandry. The minimum temperatures of the study sites are indicated by a color gradient with the warmest temperatures in red. The regression lines in red, light grey and blue indicate respectively the effect of log-transformed relative testes mass on protandry when the annual minimum temperature is equal to the max, mean and min value among study sites.

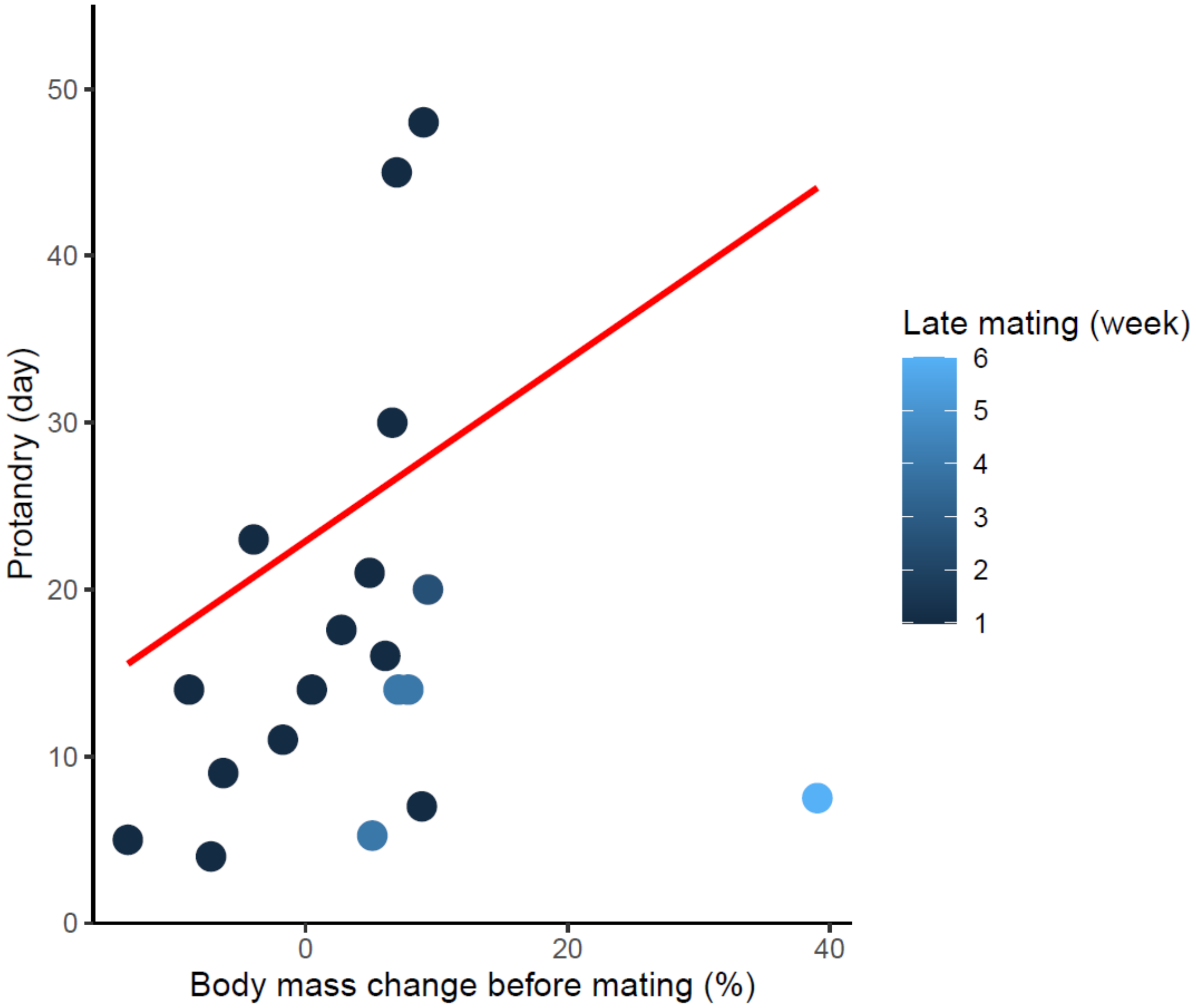

Figure 3 Effects of Δ body mass before mating on protandry. The delay between female emergence and the beginning of the mating period is represented by a color gradient with the greatest delay in light blue. The regression line in red indicates the effect of Δ body mass before mating for the mean mating delay. Δ body mass before mating was represented as a percentage of body mass at emergence.

c) Immergence

The sex difference in immergence date was correlated with post-mating activity time for males and maternal effort (Fig. 4, Table 2). The sex that spends the most time in these activities immerges last. This pattern was also influenced by an outlier, a species for which gestation and lactation for females was an extremely long period. Maternal effort only approached significance when the outlier was removed (Appendix S3). Finally, phylogeny has no influence on this model.

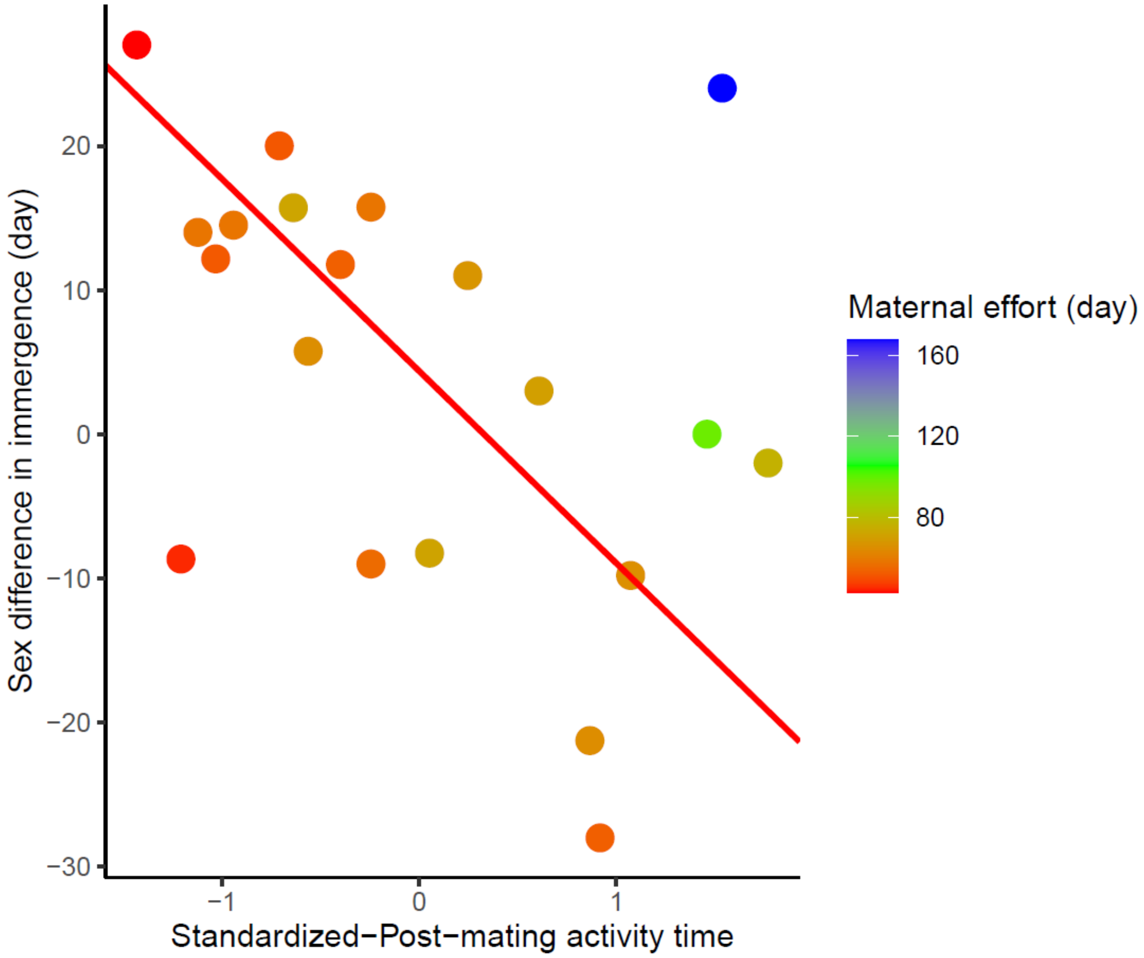

Figure 4 Effects of active time spent by males after mating (standardized) on the sex difference in immergence date. The regression line in red indicates the effect of post-mating activity time for the mean maternal effort. The duration of the maternal effort is represented by a color gradient with the longest effort in blue. A negative value on the y-axis indicates that males immerge after females and a positive value indicates that males immerge before females.

Table 2 Regression results for the best models explaining variation in protandry and sex difference in immergence. The Z standardized model estimates and the phylogenetic effect are reciprocally estimated by β and γ_M. The abbreviations “Diff”, “rel” and “Min temper” stands respectively for “Difference”, “relative” and “Minimum temperature”. The factor “body mass gain before mating” corresponds to all the species that have a positive value for the factor “Δ body mass before mating”. A negative value for the sex difference in immergence indicates that males immerge before females and a positive value indicates that females immerge before males. "Without" in model 7 indicates that species for which the time between emergence and the mating period is greater than one week (the smallest value of delay in mating) have been removed from the model 6. Relative testes mass, Δ body mass before mating, Δ body mass during mating, Δ body mass through the end of mating was represented respectively as a percentage of body mass, body mass at emergence, body mass before mating and body mass at emergence.

	γ_{ML}							$\gamma = 0$			
	R^2	γ_{ML}	**Dependent variable**	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**	R^2	**β ± SE**	***t*-value**	***p*-value**
Model 1 (11 species)	0.20	0.000 (NA, NA)	Body mass gain before mating	Intercept	7.97 ± 1.14	7.01	< 0.001***				
				Δ body mass during mating	0.16 ± 0.09	1.86	0.095.				
Model 2 (11 species)	0.56	0.000 (NA, 0.564)	Body mass gain before mating	Intercept	6.79 ± 0.56	12.10	< 0.001***				
				Log relative testes mass	8.06 ± 2.18	3.70	0.005 **				
Model 3 (19 species)	0.14	0.764 (NA, 0.992)	Post-mating activity time	Intercept	98.25 ± 20.38	4.82	< 0.001***	0.13	90.59 ± 11.31	8.01	< 0.001***
				Δ body mass during mating	-1.74 ± 0.88	-1.98	0.064.		-1.96 ± 1.02	-1.92	0.072.
Model 4 (15 species)	0.38	0.69 (NA, NA)	Post-mating activity time	intercept	99.15 ± 16.24	6.10	< 0.001***	0.33	89.76 ± 9.01	9.96	< 0.001***
				Δ body mass through the end of mating	-1.78 ± 0.58	-3.07	0.009 **		-2.07 ± 0.74	-2.79	0.015 *
Model 5 (22 species)	0.47	0.479 (NA, 0.899)	Protandry	Intercept	17.08 ± 3.51	4.87	< 0.001***	0.58	15.34 ± 1.76	8.64	< 0.001***
				z-Log rel testes mass	-2.86 ± 1.79	-1.60	0.126		-2.97 ± 1.97	-1.44	0.167
				z-Min Temper	7.55 ± 2.22	3.40	0.003**		7.88 ± 2.00	3.64	< 0.001***
				z-Log rel testes mass : Min Temper	3.54 ± 1.44	2.46	0.024*		3.56 ± 1.42	2.50	0.022*
Model 6 (19 species)	0.47	1.00 (0.841, NA)	Protandry	Intercept	24.97 ± 5.82	4.29	< 0.001***	0.23	17.12 ± 2.48	6.89	< 0.001***
				z-Δ body mass before mating	5.95 ± 1.77	3.37	0.004**		8.39 ± 3.57	2.34	0.032*
				z-Late mating	-7.44 ± 1.77	-4.21	< 0.001***		-9.46 ± 3.57	-2.64	0.018*
Model 7 (14 species)	0.79	0.00 (NA, 0.980)	Protandry	Intercept	-17.34 ± 1.82	-9.53	< 0.001***				
				z-Δ body mass before mating	-6.02 ± 1.81	-3.34	0.008**				
				z-Min temperature	-5.25 ± 2.41	-2.17	0.055.				
				z-Δ body mass before mating : z-Min temperature	-6.30 ± 2.84	-2.22	0.051.				
Model 8 (20 species)	0.47	0.000 (NA, 0.333)	Sex diff in immergence	Intercept	4.38 ± 2.42	1.81	0.130				
				z-Post-mating activity time	-13.34 ± 3.18	-4.20	< 0.001***				
				z-Maternal effort	11.20 ± 3.18	3.53	0.003**				

4) Discussion

a) Sex difference in dormancy phenology

i. Trade-off between dormancy and reproduction

In this study, we challenged the traditional view of dormancy phenology based on energy limitation by contrasting it with a life-history hypothesis. The sex difference in hibernation phenology is a good opportunity to confront these hypotheses because the sexes are faced with somewhat different life-history challenges. The energy limitation hypothesis should predict relatively little variation in sex difference phenology and independent from reproductive investment among species. The life-history hypothesis, however, predict that the sex with greater investment of time and energy in reproduction should have a longer active season, and thus a shorter dormancy season. Using phylogenetic comparative analyses (for endotherms) and information from literature (for ectotherms), we compared reproductive traits and dormancy phenology supposed to trade off and coevolve. We found that parameters that may increase male reproductive success such as high testes mass or body mass before mating seem to favor protandry. But when the time constraint is less important, protandry is no longer persistent. As well, the sex that spent the least amount of time in post mating activity (maternal effort or recovery from reproductive stress) immerges first. Furthermore, we presented evidence that dormancy phenology is independent of energy constraints in some species. Some of the results are consistent in both endotherms and ectotherms and support the life-history hypothesis. We then showed that this hypothesis may also explain dormancy phenology at other scales broadening dormancy's adaptiveness. This comparative method does not allow assignment of causation of one variable on the other; that is, of the causal direction of the selection pressure between the reproductive investment and hibernation phenology.

In response to sexual selection, protandry seems to be higher in species for which mating preparation for males takes longer. To begin, males with higher energy reserve accumulation before mating show higher protandry. Contrary to our expectations, this does not serve to compensate for the loss of body mass during the mating period. In fact, body mass gain before mating increases significantly with relative testes mass, a proxy for sperm competition (Harcourt et al. 1995). Thus, in addition to being used as a reserve, a large body mass could also have a competitive advantage in gaining access to mating females. Further, those males that lose mass before mating might have important costs if they emerge long before females, probably due to harsh conditions. In ectotherms, very few data are available on the body mass variation before emergence and thus do not allow to evaluate this hypothesis.

Protandry increases with the relative testes mass of males in species living in warm environments. Indeed, gonadal maturation requires euthermic conditions and can start during interbout arousals during hibernation (Pra et al. 2022) a pre-emergence euthermic period (early physiological departure from hibernation before behavioral emergence above ground; Barnes et al., 1988; Millesi et al., 2008; Shvareva and Nevretdinova, 1989; Strauss et al., 2008) . The duration of testes maturation might increase with relative testes mass (see table 4 in Kenagy and Trombulak, 1986). Thus, a greater difference in gonadal maturation time between males and females in species where males have a large relative testes mass may explain this result. Unfortunately, only few data are available, but it seems that gonadal maturation for either sex can take up to several weeks (Barnes et al. 1986, 1987, Millesi et al. 2008b, Morrow et al. 2009). Since relative testis mass is also a proxy for sperm competition (Harcourt et al. 1995), it is possible that physiological and behavioral preparation of this mating strategy explains this result. However, the relationship is reversed for species living in cold environment, such that species with higher relative testes mass have less difference with females in emergence date. This could indicate a constraint on investment in testes maturation or maintenance in a harsh environment. To avoid this, males of some fat-storing species hoard some amounts of food in their burrows. This energetic supply would support a return to euthermia of up to a few weeks prior to behavioral emergence and allow for testes maturation and fat accumulation (Michener 1992, Williams et al. 2014), while remaining sheltered in the burrow. Thus, males might gain energy benefits without paying survival costs of above-ground activity.

In ectotherms, testes maturation has also been proposed as a driver of protandry. *In Zootoca vivipara* (the viviparous lizard), male lizards generally emerge earlier than females (Breedveld and Fitze 2016). The sex difference did not seem to be explained by a difference in the maturation duration of the reproductive organs, but rather in timing. Indeed, in this species, females do not have developed follicles at emergence and ovulation occurs several weeks after mating (Bauwens and Verheyen 1985). In addition, by experimentally manipulating the emergence from dormancy of males but not females, it was shown that the degree of protandry affected the sperm presence in males but not the probability of copulation. Thus, protandry may increase the chances of fertilizing eggs for males and decrease the probability of copulating with an infertile male for females (Breedveld and Fitze 2016). In *Gonepteryx rhamni* (the common brimstone), butterfly males emerge from dormancy 3 weeks before females. They are quickly ready to reproduce, but this delay would allow them to increase the amount of sperm before mating and thus reproduce more successfully (Wiklund et al. 1996)

As for lizards and snakes (Graves and Duvall 1990, Olsson et al. 1999), mammals for which reproduction occurs several weeks after female emergence show little difference in emergence date between sexes despite a substantial accumulation of fat in some of them (*e.g.*, *Ictidomys parvidens*, Schwanz, 2006). According to life history hypothesis, it is suggested that the benefits for males to emerge before females decreases with the delay in the mating period (relative to female emergence), because they are less constrained by time for mating preparation. But a low protandry may also imply that both sexes are waiting for favorable energetic conditions to emerge, as assumed by the phenology and energetic limitation hypothesis. A measurement of energy balance at the time of emergence for these species is therefore necessary to discriminate the hypotheses.

Back to the results from mammalian species, minimum temperature reduced the effect of relative testes mass on protandry. The pattern of results seemed to confirm a constraint to emergence from harsh environmental conditions. Although food storage in the burrow may have evolved to overcome these costs, model selection did not retain the food-storing factor. Thus, the ability to accumulate food in the burrow alone was not likely to prevent males of some species from emerging earlier (*e.g.*, *Cricetus cricetus*, Siutz et al., 2016), perhaps to consume higher quality food or to compete with other males (*e.g.*, territory establishment).

Unlike emergence, the sex that immerges first varies among species. Body mass loss in males before and during mating increases the post-mating activity time which is associated with a delay in male immergence (for the same date of female immergence). Thus, the need to accumulate and defend supplementary food reserves (Williams et al. 2014) or the need to confirm the location of the burrows of females before hibernating (Kawamichi 1996) do not seem to adequately explain the late male immergence of some species. For females, the longer the duration of maternal effort, the later the females immerge for the same date of male immergence. Therefore, it is the sex difference in time spend in reproduction or recovery from reproduction which is correlated with the order of immergence. In ectotherms, very few data are available on sex difference in immergence date and therefore do not allow to evaluate this hypothesis.

These results are consistent with the assumption that dormancy phenology of ectotherms and endotherms seems to be in trade-off with reproductive investment at the intraspecific level. In addition, other elements from the study and the literature based on energy balance are inconsistent with “the energy limitation hypothesis”.

ii. Dormancy and energy balance independence

If from an energetic point of view, it is favorable to remain active as long as the energy balance is stable or positive, or conversely to remain in hibernation as long as the environment does not allow for a positive energy balance, then any deviation from this principle may highlight a balance rather in favor of reproduction (by sexual or “other” natural selection) or survival (Fig. 1). Presumably, reducing the risk of extrinsic mortality favors dormancy while the environment allows a positive energy balance. In contrast, preparation for reproduction promotes activity while the environment does not allow a positive energy balance. Thus, a dormancy phenology staggered with respect to the harsh season (earlier emergence and immergence than expected) illustrates the selection pressure exerted by the trade-off between reproduction (earlier emergence than expected) and survival of adults (earlier immergence than expected).

In our study, several elements might suggest that hibernation occurs even when environmental conditions allow for a positive energy balance. Gains in body mass, such as mass gain for males between emergence and mating, may indicate that an environment allows a positive energy balance for individuals that can be assumed to have comparable energy expenditures, such as different sexes or age groups. In several species, females stay in hibernation (up to almost 2 months more) while males were gaining body mass of up to 9% after emergence, or one sex immerges while the second continues to accumulate energy reserves (Table 3). Sexual dimorphism may be responsible for sex differences in energy expenditure (Kenagy et al. 1989, Key and Ross 1999, Scantlebury et al. 2006) and therefore energy balance. However, these observations concern species with a sexual size dimorphism biased towards both males or females (Table 3). Moreover, in some species, all adult individuals immerge whereas juveniles continue to accumulate reserves during several weeks or months (*e.g.,* *Urocitellus richardsonii*, Michener, 1998). Nevertheless, further studies are needed to verify whether changes in energy expenditure between sexes and cohorts induce differences in energy balances that are large enough to explain these disparities. On the contrary, males of some species emerge under unfavorable conditions (*e.g.*, snow cover, food unavailable) that may result in a greater loss of body mass after emergence than during hibernation (Snyder et al. 1961, Morton and Sherman 1978). In this case, the energy reserves accumulated before hibernation might also be selected to survive these harsh post-hibernation conditions.

Species	*Body size dimorphism*	*Male body mass gain before mating (% of emergence body mass)*	*The end of reserve accumulation before hibernation for females*
Cricetus cricetus	1.14 (1)	9.35 (2)	27 day after male (3)
Cynomys leucurus	1.04 (4)	4.89 (5)	11 day after male (6)
Glis glis	0.97 (7)	6.63 (8)	14 day after male (9)
Microcebus murinus	0.96 (10)	9.01 (11)	Same time as male (12)
Urocitellus parryii	0.97 (13)	0.49 (14)	35 days before male (15)

Table 3 Species with dimorphisms biased in favor of males or females and their body mass gain during the year. Body size dimorphism is calculated as male body size divided by female body size. See section “Sex differences in reproductive investment” for the determination of the body mass gain before mating. References : (Kryštufek et al. 2020) (1) (Lebl and Millesi 2008) (2) (Siutz et al. 2016) (3) (Hayssen 2008) (4) (Bakko and Brown 1967) (5) (Clark 1977) (6) (Matějů and Kratochvíl 2013) (7) (Bieber 1998) (8) (Bieber and Ruf 2004) (9) (Rakotondranary et al. 2011) (10) (Schmid and Kappeler 1998) (11) (Schmid 1999) (12) (Hayssen 2008) (13) (Buck and Barnes 1999) (14) (Sheriff et al. 2011) (15).

In ectotherms as well, some observations confirm similar link between energy balance and sex difference in dormancy phenology. Females *Gonepteryx rhamni* delay emergence 3 weeks after males despite "ample nectar supply" to coincide with the phenology of the host plant consumed by the larvae. For *Vipera berus* (the common European adder), males emerge before females in thermally unfavorable periods, leading to significant mass loss. These possible survival-related costs may be outweighed by the important benefits to reproductive success of having mature testes prior to the brief and highly synchronized mating period (Herczeg et al. 2007). These elements seem to show that in some both ectotherms and endotherms, the emergence and immergence of each sex are independent of their energy constraints.

The trade-off between investment in reproduction and dormancy phenology as well as the independence of the latter with energy balance seems to validate the life-history hypothesis to explain the sex difference in dormancy phenology of up to several months (this study, Van Damme et al., 1987; Wang et al., 1990; Winck and Cechin, 2008). Taking into account the survival benefits of dormancy, these sex differences may have important consequences on other life-history traits, especially in short-lived species such as insects. We first focused on the sex difference pattern, considered to be a widespread example of this trade-off, but this new hypothesis may also apply at other scales and may broaden our view of the adaptive nature of hibernation.

b) Life history hypothesis at other scales

In mammals, individuals (males and females) that invest less or not at all in reproduction advances energy reserve accumulation and immergence for up to several weeks while members of the same group continue their activity (Michener 1978, Choromanski-Norris et al. 1986, Millesi et al. 1998, 2008a, Neuhaus 2000, Nicol and Morrow 2012), suggesting a positive energy balance. To our knowledge, the only study that measured energy balance at the time of immergence shows that *Tamias striatus* (the eastern chipmunk) immerge while a positive energy balance could have been maintained (Humphries et al. 2002a). Observations of other species suggest immergence when little food is available, but supposedly enough to support activity (Grigg and Beard 2000, Munro et al. 2008, Hoelzl et al. 2015, Karanewsky et al. 2015). On the contrary, low productivity can lead to later immergence (Alcorn 1940, O'Farrell et al. 1975, Harris and Leitner 2004), probably due to a delay in the accumulation of reserves. This contradicts the view that hibernation duration should necessarily increase with energetic constraints. In *Urocitellus mollis* (the Piute ground squirrel), food-poor years can either result in a delay (Alcorn 1940) or in an early immergence when reproduction is skipped (Smith and Johnson 1985). Another surprising example of this trade-off is *Glis glis* (the edible dormouse), for which emergence became earlier with age. The authors posited that as younger individuals have a greater chance of reproducing in subsequent years, they delay their emergence for survival benefit at the expense of their immediate reproductive success (Bieber et al. 2018).

In ectotherm, the reduction of extrinsic mortality such as avoiding predators (Slusarczyk 1995, Kroon et al. 2008, Ji 2011) or intra- (Tougeron et al. 2018) and interspecific competition (Dyugmedzhiev et al. 2019) has been proposed to influence dormancy phenology. For example, in reptiles, some observations show that individuals enter dormancy while ambient temperature is still high enough to promote activity (Jameson Jr 1974, Jameson and Allison 1976). Adult lizards *Aspidoscelis sexlineatus* (the six-lined racerunner) enter in dormancy while food is still plentiful and the climate enables the maintenance of its temperature preference for activity (Etheridge et al. 1983). In addition, the young of this species remain active for another two months to grow and accumulate energy reserves, demonstrating the possibility of a positive energy balance at the time of adult immergence. Another example favors the life history hypothesis over the energy limitation hypothesis. In *Elaphe obsoleta* (the black rat snake), it seems that part of the variation in emergence date is explained by the fact that smaller and younger individuals emerge later than others (Blouin-Demers et al. 2000). This result would be the opposite of what is expected from a thermoregulation perspective, since small individuals should reach their preferred temperature for activity more quickly (due to their low inertia) and should be the first to emerge (Stevenson 1985). The authors propose, on the contrary, that small individuals, subjected to a higher predation rate in spring, privilege survival. Other large inter-individual differences may also be explained by the occurrence of both risk-taking and risk-averse strategies within a population (Nussear et al. 2007).

In the same way, it might be quite common for insects to adopt a risk spreading strategy associated with dormancy. Indeed, it is clearly established that the majority of insects enter into dormancy long before environmental conditions deteriorate, and remain dormant sometimes long after favorable conditions return (Tauber and Tauber 1976, Košťál 2006, Tougeron et al. 2020). This strategy has been called "temporal conservative bet-hedging" (Hopper 1999). Temporal bet-hedging strategies reduce fitness variation across the years in a temporally fluctuating environment and result in higher average long-term fitness. In this case, all individuals in a population (conservative because of low phenotypic variability) reproduce only during the period that is always favorable through the years and avoid the period with adverse conditions in some years at the expense of possible reproductive benefits in years with favorable conditions. Temporal diversified bet-hedging exists in species for which the duration of dormancy varies within a single cohort (diversified because of high phenotypic variability) from one to several years (*i.e.*, prolonged diapause), regardless of external conditions. Thus, whatever the environmental conditions, a small proportion of the progeny will experience optimal conditions to reproduce (Danks 1992, Hopper 1999, Menu et al. 2000). Another example of the influence of reproduction on insect dormancy phenology is that of species whose larvae develop only on one or a few specific host plants. In this case, emergence is largely influenced by the phenology of those plants (Pratt and Ballmer 1993, Diamond et al. 2011, Navarro-Cano et al. 2015).

The independence of ectotherm dormancy towards harsh environmental conditions is in contradiction with the vision of a passive inactivity induced by suboptimal temperature. Several physiological and behavioral thermoregulation mechanisms may facilitate entering into dormancy when ambient temperature above ground is still high. Indeed, some ectotherms enter dormancy in summer (*i.e.,* estivation or summer dormancy) and use deep burrows or crevices where the ambient temperature is much colder. Thus, by exploiting their habitat, some ectotherms are able to reduce their energy consumption (Pinder et al. 1992). On the other hand, some species are capable of an active reduction in metabolism below that required under the simple passive effect of ambient temperature on metabolism (Q10 effect) (Boutilier et al. 1997, Hahn and Denlinger 2011, Lin et al. 2020, Mayhew 1965, Storey 1996, Speers-Roesch et al. 2018, Staples 2016). Ectotherm dormancy could therefore be less temperature dependent than previously thought and would allow survival under a wider spectrum of biotic and abiotic pressures.

Finally, it is questionable whether the phenology and life-history hypothesis applies to all dormant species. For example, the reduction of extrinsic mortality risk during hibernation, is assumed to apply only to small hibernators (Turbill et al. 2011, Ruf et al. 2012). However, a recent study shows that competition between *Ursus americanus* (the black bear) and mesocarnivorous species (*e.g., Canis latrans*) decreases when bears hibernate (Moll et al. 2021). This should prompt further studies to determine the extent to which interspecific competition influences the hibernation phenology of the bears. In addition, our study included two non-Holarctic species that occur in tropical and subtropical habitats. Although they represent a very small minority of hibernating species tested, the results obtained seem to be consistent with Holarctic species. Hibernation in non-Holarctic species is supposed to have evolved in response to other environmental factors than food shortage, such as water shortage (Nowack et al. 2020). However, similar selection pressures may therefore exist and should encourage further comparative research on hibernation between non-Holarctic and Holarctic species. Finally, since similar survival benefits is recorded during ectotherm dormancy, this raises the question of whether this hypothesis may also apply to any dormant species.

4) Conclusion

The sex difference in dormancy phenology observed in endotherms and ectotherms may be a widespread consequence of the trade-off between the benefits of being active for reproduction and the benefits of dormancy for survival (*viz*., the life-history hypothesis). Other non-exclusive hypotheses have also been proposed (Morbey and Ydenberg 2001) and further studies are needed to test them. Energy constraint explain a part of dormancy phenology in both endotherms and ectotherms (Bronson 1979, Sexton and Hunt 1980, Strain et al. 2012, Wilsterman et al. 2021) but a large body of evidence from this study shows some independence of energy balance at the specific time of immergence and emergence. Thus, we can assume that dormancy phenology may have multiple evolutionary causes. The occurence of dormancy at high altitude and latitude where no energy resources are available over part of the year appears to be a support for energy limitation hypothesis (Ruf et al. 2012), although this hypothesis may be of limited importance in explaining the phenology of the transition from dormancy to activity and the reverse. Dormancy in energetically benign periods, but unfavorable for reproduction, may be more widespread than previously thought. Such research highlights the opportunities of studying dormancy across a broad spectrum of species (Wilsterman et al. 2021). Expanding the research to other phylogenetic groups would allow us to take advantage of and build on the progress made from more taxonomically restricted studies. Moreover, it offers a challenge to unify different fields of dormancy research such as ecophysiology, evolutionary biology and chronobiology. Finally, it may have considerable implications for understanding the variety of species' responses to climate change and their impacts on ecosystems.

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Chapter 3

A male Brandt's bat (*Myotis brandtii*) was recaptured in the wild after 41 years. This corresponds to a longevity 9,8 times greater than that expected for its size. Its prolonged hibernation is suspected to be a cause of this longevity (Podlutsky et al., 2005). But by what mechanism does hibernation increase longevity?

We have tried to understand it in the next chapter.

Experimental study confronting aging theories in a hibernating mammal

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Abstract

Several hypotheses have been formulated to explain the higher longevity of hibernators compared to non-hibernating species of the same size. These hypotheses assume that longevity is explained either by 1) reduced physiological damage due to the depressed metabolism during winter, 2) a high investment in maintenance during hibernation, and/or 3) over the entire year regardless of the period. To date, no consensus has been reached on any of these hypotheses. This study examines for the first time these non-exclusive hypotheses through an experimental design under controlled laboratory conditions. Fifty juvenile female common hamsters (*Cricetus cricetus*) were divided into four groups placed in conditions favoring a mix of either long or short hibernation and either deep or shallow torpor. These individuals were then followed until the end of the active season when half of the individuals from the four groups were bred. The influence on longevity was estimated through the effect on relative telomere length (RTL), a biomarker of aging. The results show that increased total time spent in torpor is the most important factor to explain telomere elongation during the hibernation period suggesting that the low metabolic rate may have an effect on the slowing down of aging especially with a high torpor body temperature. In addition, the time spent in torpor reduces the investment in growth and reproduction, which may also favor an investment in maintenance and telomere elongation during hibernation. However, hibernation conditions are also not more favorable to an investment in maintenance than the active period. Indeed, the investment of energy in maintenance seems limited, so that telomere elongation during one period (hibernation or active season) is associated with erosion during the other one, regardless of initial RTL. Thus, hamsters would be able to invest in somatic maintenance regardless of the time of the year, in a trade-off with the investment

of energy in growth and reproduction. These results do not show a greater contribution of one of the three hypotheses to explain the greater longevity of hibernators.

1) Introduction

One striking characteristic of hibernators is their higher longevity compared to non-hibernating species of the same size (Turbill et al., 2011). Several non-exclusive hypotheses, have been formulated to explain this higher longevity but no consensus has been reached so far. These hypotheses relay on concepts (reduction of metabolism, reduction of extrinsic mortality or investment in maintenance) that may apply to non-hibernating species. Thus, their examination should broaden our understanding of the aging process of species living in a seasonal world.

Hibernation is a succession of multiday bouts of hypometabolism and hypothermia (*i.e.*, deep torpor as opposed to daily torpor) interspersed with periods of arousal to euthermia. The body temperature in torpor (T_b torp) is usually a few degrees above the ambient temperature (Min T_b torp of 16.9°C for daily torpor and 3.9°C for hibernation; Ruf and Geiser, 2015) and the deeper the T_b torp, the greater the energy sparing (Ruf and Geiser, 2015). The metabolic rate in torpor can decrease up to 5% of the basal metabolic rate in mammalian hibernators (Ruf and Geiser, 2015). This is one of the proposed mechanisms that may increase the longevity of hibernators. In the perspective of the free radical theory of aging, it has been proposed that hibernation slows down aging by reducing the accumulation of reactive oxygen species and thus the associated cellular damage (Wu and Storey, 2016). Furthermore, mechanisms involved in metabolic depression (*e.g.*, suppression of the insulin signaling pathway) and stress resistance (*e.g.*, antioxidant production) during torpor are also responsible for increased longevity in non-seasonal heterotherms (Wu and Storey, 2016). Thus, according to the hypothesis of reduced metabolism, it is predicted that longer and deeper torpor leading to greater energy saving should further slow cellular aging.

Another hypothesis assumes negative effects of hibernation and rewarming from deep torpor at regular intervals during winter. Deep torpor is associated with costs such as reduction of the immune system or accumulation of metabolic waste (Humphries et al., 2003). Although physiological processes are up-regulated during inter-torpor euthermia, arousal from a low T_b torp is highly energetically costly and responsible for a high ROS production (Orr et al., 2009). Torpor use seems to be optimized by a trade-off between the energetic benefits of torpor and its physiological costs (Humphries et al., 2003). Thus an alternative hypothesis (*i.e.*, maintenance during hibernation hypothesis) proposes that hibernation period would be propitious to a shift in the allocation of energy from growth and reproduction to somatic maintenance (Humphries et al., 2003). This hypothesis has been developed and validated under certain conditions in a mathematical life-history model (Shanley and Kirkwood, 2000). Humphries et al, proposes this hypothesis as an alternative to the metabolic reduction hypothesis. Nevertheless, it seems possible to consider that these two hypotheses are non-exclusive with both a slowing down of aging with the decrease of metabolism and an important investment in maintenance during inter-torpor or arousal bouts.

The effect of hibernation patterns (*e.g.*, duration, depth, frequency of torpor) on cellular aging has been studied through their influence on telomere length dynamics. Telomeres are non-coding regions of DNA at the end of eukaryotic chromosomes (Greider, 1996). Telomere length is considered as a biomarker of aging (Haussmann et al., 2003; Horn et al., 2010) as it shortens with chronological age (time since birth) and under the effect of oxidative stress (Chatelain et al., 2020). The first results showing an acceleration of aging with the time spent in euthermia or with the frequency of arousal suggest a slowing of aging with torpor (Giroud et al., 2014; Hoelzl et al., 2016a; Turbill et al., 2011, 2013, Nowack et al. 2019). Nevertheless, the increase in delta temperature between torpor and euthermia, relative to deep torpor, seems to accelerate aging (Hoelzl et al., 2016a; Turbill et al., 2011). Furthermore, several species have shown the ability to lengthen their telomeres probably during inter-torpor bout euthermia (Nowack et al., 2019; Turbill et al., 2013, Ragger et al. 2020), likely achieved *via* the enzyme telomerase or DNA recombination mechanisms (Greider and Blackburn, 1985; Neumann et al., 2013). The latter would be in agreement with the hypothesis of a higher maintenance of the organism during hibernation.

However, telomere elongation does not seem to be restricted to the hibernation period, and therefore would not be specific to the physiological conditions of hibernation. Indeed, in edible dormice (*Glis glis*), an increase in telomeres is observed at the beginning of the active season when sufficient food is available (Hoelzl et al., 2016a). Elongation of telomeres with chronological age has also been demonstrated in edible dormice and Eastern chipmunks (*Tamias striatus*) (Hoelzl et al., 2016b; Tissier et al., 2021). According to the theory of life history trait, a low mortality rate should promote a redirection of energy allocation from reproduction and growth to somatic maintenance (Healy et al., 2019). A high annual survival, probably explained by a reduction of predation during hibernation, may therefore explain an important investment in maintenance in hibernators that is not specific to hibernation period (Hoelzl et al., 2016b; Ruf et al., 2012). To date, no study favors one of these three non-exclusive hypotheses.

In this study, we set up an experimental design to confront for the first time these different hypotheses. The hypotheses were tested on the common hamster (*Cricetus cricetus*) a food-storing hibernator (that feed during inter-torpor bouts) that shows the ability to elongate its telomeres (Constant et al, in prep). Fifty juvenile female hamsters were divided into four groups, which differed in hibernation duration (long *vs*. short) and were submitted to different ambient temperatures (8°C *vs*. 20°C) influencing the possibility to perform deep torpor bouts (read below for more details). Half of the individuals from each group were bred with males at the subsequent reproductive period. According to the hypothesis of reduced metabolism, it is expected that the group that hibernates the longest at 8°C, would have the lowest rate of telomere erosion. For the maintenance investment hypothesis, we assume that the group that hibernates the longest at 20°C, would have the highest investment into maintenance. Finally, regarding the "reduced extrinsic mortality" hypothesis, we assume that telomere elongation is independent of the time of year, but should be less prevalent in individuals allowed to breed because of the trade-off in energy allocation between reproduction and maintenance. To evaluate these predictions, we recorded hibernation patterns and measured RTL, plasma estradiol levels, and body size at the beginning and end of hibernation and at the end of the breeding period.

2) Materials and Methods

a) Ethical statement

The experimental protocol followed the European Union Directive 2010/63/EU for animal experiments and the care and use of laboratory animals, and was approved by the Ethical Committee under the agreement number (APAFIS#20715-2019040116252316).

b) Animals and housing conditions

This study was carried out from October 2020 to October 2021. During the whole experiment, hamsters were provided with *ad libitum* access to food and water with a conventional diet (pellets 105, from Safe, Augy, France, composed of 19.3% protein, 54.9% carbohydrates, 5.1% lipids, 4.2% cellulose, 5.0% minerals, and 11.5% water). Hamsters were housed individually (W × H × D: 265 × 237 × 420 mm) until breeding and marked with miniature subcutaneous PIT tags of the following dimensions (Ø x L): 1.4 x 10.3 mm, weight: 35±6mg (ALLFLEX PROTRAQ mini, France).

c) Experimental design

Fifty hamsters were implanted with body temperature loggers in October (iButton, DS1922L model, Maxim Integrated Products, Sunnyvale, CA, weighing 3.2±0.1 g after paraffin ELVAX inclusion, temperature accuracy of ±0.5°C from -10°C to +65°C, temperature resolution 0.0625°C). The surgical protocol and data acquisition for hibernation pattern were the same as in Constant et al (2022 in prep). We measured the total time spent in torpor as the total duration of all torpor bouts (multiday periods of reduced body temperature below 30°C) and T_b torp as average of the 4 lowest values for each torpor bouts. Hamsters were separated into four groups (two groups of 13 females and two groups of 12 females) taking into account two constraints. The first was to limit the number of sisters within the same group (maximum of two sisters in only two groups). Second, we grouped the females so that there was no significant difference in body mass between the groups (Anova test, p= 0.661) since it influences hibernation patterns. The four groups were placed under conditions triggering either short (SH) or long (LH) hibernation, shallow torpor (ST) or deep torpor (DT) in order to test the different conditions (SH-ST, SH-DP, LH-ST, LH-DP). Before the beginning of the experiment in November, individuals were placed at 20°C in short photoperiod (10L: 14D; favorable for hibernation). The two ST groups were maintained at this temperature while the room temperature of the DT groups was progressively decreased (2°C per day) to 8°C from

November 5, inducing the beginning of deep torpor. The end of hibernation for the SH groups was achieved by a switch to long photoperiod (14L: 10D; favorable to reproduction) and a gradual return (2°C per day) to a temperature of 20°C for the DT group on 16 December. The change of these conditions was carried out on 25 January 2021. In total, individuals spent 40 days in conditions favorable for hibernation for the SH group against 80 for the LH group.

On May 4, half of the individuals in each group were breed according to the protocol used in Constant et al (2022 in prep). Ear tissues were collected for telomere measurement and plasma for estradiol concentration determination before and after hibernation as well as before the second hibernation, according to the methodology used in Constant et al (2022 in prep). Relative telomere length (RTL) change was calculated as follows: RTL_{t+1}- RTL_{t0}. Over the same period the body length was measured with a caliper to the nearest.

d) Statistics

Statistical analysis was performed using R v. 3.6.2 (R Core Team, 2019). We first verified that the experimental design created the expected differences in the time spent in torpor and torpor depth between groups by analysis of variance (ANOVA) with the aov() function from the stats package (version 3.6.2; R core Team et al., 2018). Hibernation duration and T_b torp were placed as dependent factors in separate models with group as an independent factor. Then, we used Tuckey tests with the TukeyHSD() function from the stats package to test for specific differences between groups.

For the rest of the statistics (unless mentioned), we used linear mixed-effect models with the lme() function from the nlme package (version 3.1-152; Pinheiro et al., 2017) including the kinship (sisters only) placed as a random factor in each model. For all models we performed a model selection using the dredge() function of the MuMIn package (version 1.46.0; Barton and Barton, 2015) based on AICc comparison We limited to four the number of factors retained in the final model allowing to maintain a ratio of data to explanatory factors ≥ 10 for all our models, thus limiting overfitting. We reported the best model with standardized explanatory factors in order to compare effect sizes. Model using lme() function ware fitted based on "maximum likelihood" method, as it is preferred when comparing models with the same random effects.

The maintenance hypothesis (Hypothesis 2) assumes that hibernation is a period associated with a redirection of energy allocation away from reproduction and growth. We investigated this prerequisite by evaluating how growth and reproduction investments measured over the same period of time is affected by different hibernation patterns (long or short hibernation, deep or shallow torpor). We tested the effect of T*b* torp and total time spent in torpor as independent factors on body growth over the long hibernation period (5 November to 25 January) as well as estradiol concentration at the end of hibernation period, each placed as a dependent factor.

We also used glm() function from the package stats (version 3.6.2; R core Team et al., 2018) with a binomial distribution to test the influence of hibernation patterns (independent factors) on the probability of vaginal opening at hibernation emergence (dependent factors). Vaginal opening is a physiological sign of an individual's ability to reproduce.

We confronted in the same model 1) the hypothesis of reduced metabolism by testing the effects of T_b torp and time spent in torpor and 2) the hypothesis of maintenance during hibernation by testing the effects of body growth over hibernation period, estradiol concentration and vaginal opening at the end of hibernation period (independent factors) on telomere change (dependent factor) over the long hibernation period (5 November to 25

January). Telomere length at the beginning of the hibernation period was placed as an factor because longer telomeres are susceptible to greater erosion (Bauch et al., 2014). We presented and compared the best models within a delta AICc<1.

To test the hypothesis of reduced extrinsic mortality (hypothesis 3), we compared in a first model the differences in RTL change between the active and hibernation periods by distinguishing the hibernation of the four groups. For this model only, we used the lmer() function of the package lme4 (version 1.1-30; Bates and Sarkar, 2007) to include, as random factors, a kinship and individual factors (to account for repeated measurements). Furthermore, hypothesis 3, assumes an investment in maintenance at any time of the year but subject to the energy allocation trade-off between fitness components such as reproduction, growth and maintenance. Thus, we run a model testing the effects of (1) reproductive effort during the active period represented (reproduction or not), the number of live pups, and estradiol concentration before reproduction; (2) change in body size, *i.e.*, growth; and (3) previous maintenance investment represented by RTL change over hibernation (all as independent factors) on the telomere change over the active season (dependent variable).

For each model, we checked the multicollinearity thanks to the vif() function of the car package (version 3.1-0; Fox et al., 2012) while the normality and the homoscedasticity were checked graphically.

3) Results

a) Differences in hibernating patterns between the experimental groups

As expected, a significant difference in the T_b torp is observed between the LH-ST and LH-DT groups and between the SH-ST and SH-DT groups, but no difference is observed inside the ST and DT groups (Fig. 1). By contrast, contrary to what we expected, the total time spent in torpor is significantly different between the two LH groups as well as between the two SH groups. In addition, all groups show significant differences between each other in terms of total time spent in torpor except between the two ST groups (Fig. 2). This shows that we failed to induce a LH-ST hibernation behavior in common hamsters with our experimental protocol

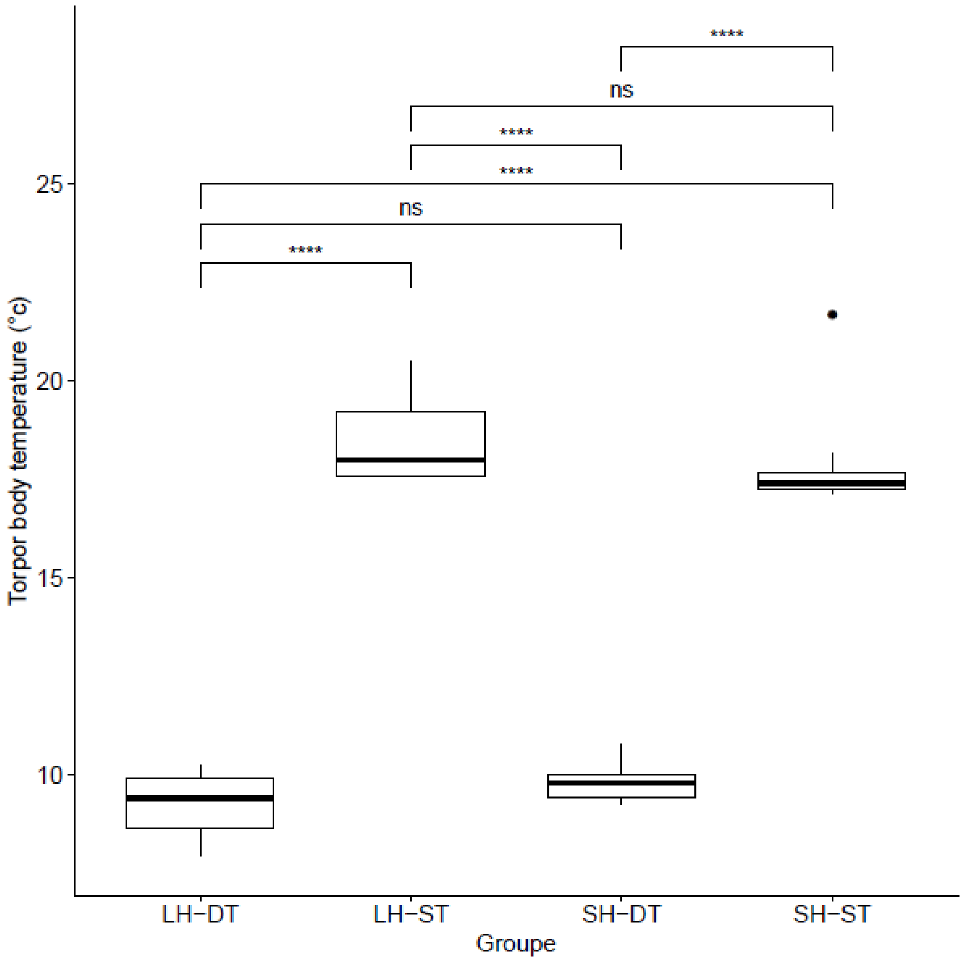

Figure 1. Boxplot of torpor body temperature between groups.

Significant results are represented by *p<0.05, **p<0.01, ***p<0.001. “ns” stands for "not significant". “LH”and “SH” stand respectively for “long hibernation” and “short hibernation”. “DT” and “ST” stand respectively for “deep torpor” and “shallow torpor”.

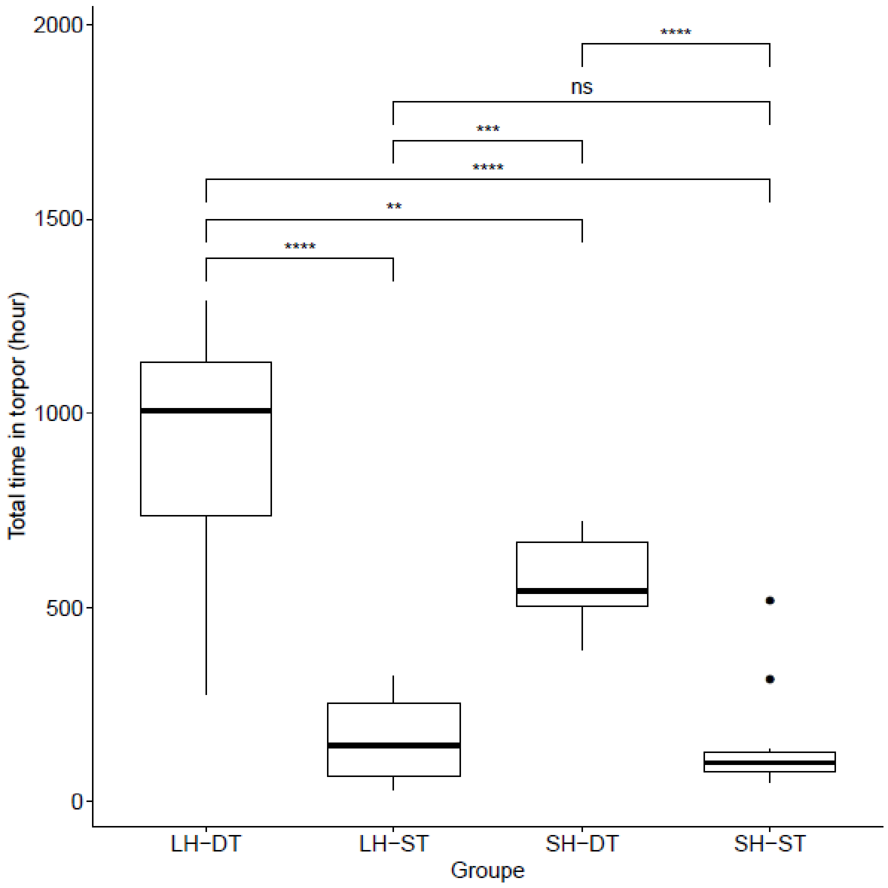

Figure 2. Boxplot of total time in torpor between groups. *

Significant results are represented by *p<0.05, **p<0.01, ***p<0.001. “ns” stands for "not significant". “LH”and “SH” stand respectively for “long hibernation” and “short hibernation”. “DT” and “ST” stand respectively for “deep torpor” and “shallow torpor”.

b) Effect of hibernation pattern on growth and reproduction

Increasing the total time spent in torpor significantly decreased body growth over hibernation (p=0.006**) and the probability of vaginal opening (p=0.003**). Estradiol concentration tended to increase with the total time spent in torpor at the end of hibernation although this effect was non-significant (p=0.089). Low T_b torp also decreased the probability of vaginal opening (p=0.017*). There was a trend of slower growth with low temperature but this effect was non-significant. (p=0.06).

c) Hibernation pattern, growth and reproduction effect on RTL change over hibernation

Increasing the total time spent in torpor reduced telomere erosion and even significantly increased RTL during hibernation (Fig. 3) in three of the five best models (models 1, 2 and 5; Table 1). In addition, a 4th model showed a similar trend of a positive link of total time spent in torpor on RTL but this effect was non-significant (model 3; Table 1). Also, increasing T_b torp reduced erosion and even increased telomere length during hibernation in the first two best models, but this effect was weakly significant (model 1 and 2; Table 1). Increased body growth during hibernation significantly increased telomere erosion in a model including only RTL before hibernation (model 5; Table 1; Fig. 4). Another model including in addition the total time spent in torpor showed a trend towards increased telomere erosion with increased body growth but the effect was non-significant (model 3; Table 1). Finally, in the first best model, there was a trend of increased telomere erosion during hibernation with increasing estradiol concentration at the end of hibernation period, but this effect was non-significant (model 1; Table 1).

In each of these models, longer telomeres at the beginning of hibernation significantly increased telomere erosion during hibernation and conversely, shorter telomeres at the beginning of hibernation showed elongation during hibernation.

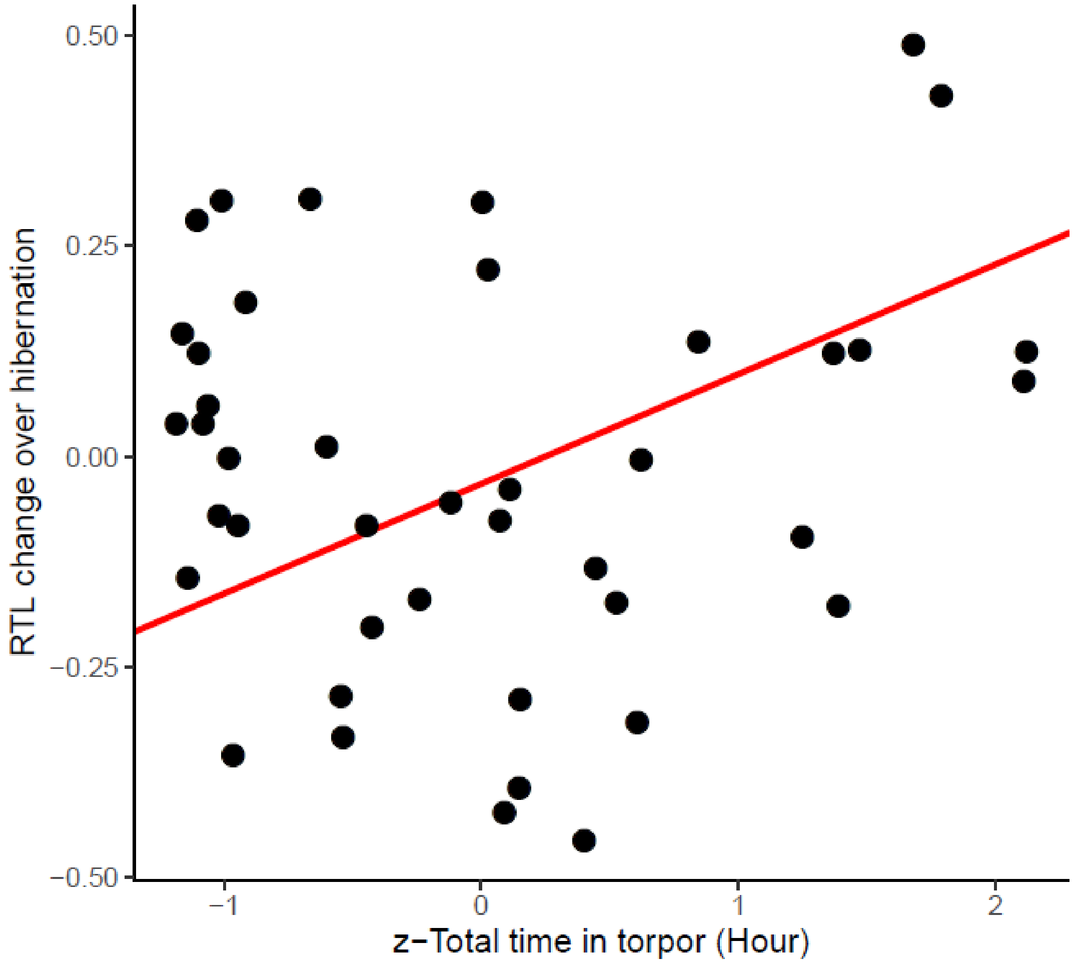

Figure 3. Effects of total time spent in torpor (standardized) on RTL change over hibernation period. The regression line in red is based on the results of model 1. The abbreviation “z” stands for standardized.

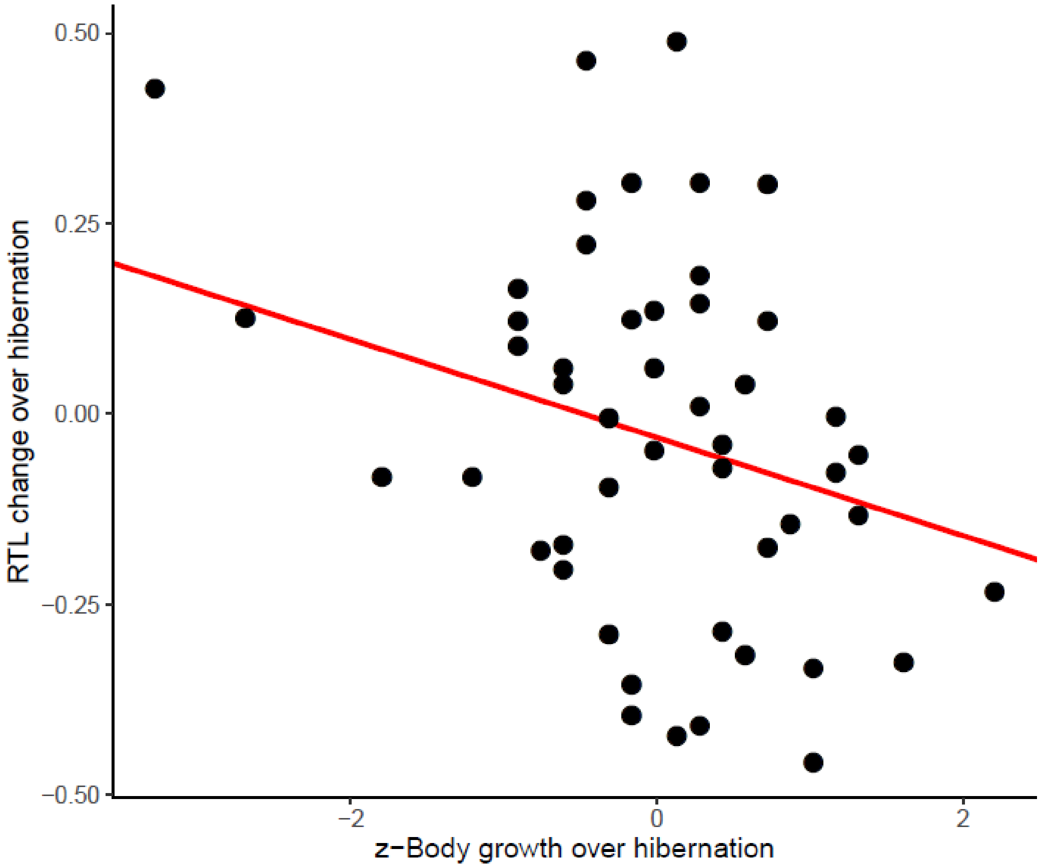

Figure 4. Effects of body growth over hibernation period (standardized) on RTL change over hibernation period. The regression line in red is based on the results of a model including all individuals with body growth data (see supplementary materials). Statistical results are identical to the model 4 that does not include individuals with missing hibernation pattern data. The abbreviation “z” stands for standardized.

Table 1 Best models resulting from model selection to explain RTL variation over hibernation. Models are ranked according to delta AICc, starting with the best model. The model estimates are presented by β. The abbreviation “z” stands for “standardized”.

	R^2	Dependent variable	Independent variable	β ± SE	*t*-value	*p*-value	delta AICc
Model 1	0.86	RTL change over hibernation	Intercept	-0.03 ± 0.03	-0.92	0.36	0
			z-Estradiol concentration after hibernation	-0.04 ± 0.02	-1.68	0.10	
			z-RTL before hibernation	-0.18 ± 0.02	-7.83	< 0.001***	
			z-Total time spent in torpor	0.13 ± 0.03	3.30	0.003**	
			z- T_b torp	0.07 ± 0.03	2.05	0.05.	
Model 2	0.82	RTL change over hibernation	Intercept	-0.03 ± 0.03	-0.96	0.34	0.08
			z-RTL before hibernation	-0.17 ± 0.02	-7.21	< 0.001***	
			z-Total time spent in torpor	0.11 ± 0.04	2.85	0.01*	
			z- T_b torp	0.06 ± 0.03	1.75	0.09.	
Model 3	0.83	RTL change over hibernation	Intercept	-0.03 ± 0.03	-0.96	0.34	0.12
			z-RTL before hibernation	-0.17 ± 0.02	-7.37	< 0.001***	
			z-Total time spent in torpor	0.04 ± 0.02	1.84	0.08.	
			z-Body growth over hibernation	-0.04 ± 0.02	-1.72	0.10	
Model 4	0.77	RTL change over hibernation	Intercept	-0.03 ± 0.03	-0.91	0.37	0.55
			z-RTL before hibernation	-0.16 ± 0.02	-6.63	< 0.001***	
			z-Body growth over hibernation	-0.05 ± 0.02	-2.36	0.02*	
Model 5	0.82	RTL change over hibernation	Intercept	-0.03 ± 0.03	-0.95	0.34	0.56
			z-RTL before hibernation	-0.18 ± 0.02	-7.58	< 0.001***	
			z-Total time spent in torpor	0.05 ± 0.02	2.55	0.01*	

d) Comparison of RTL change between hibernation and active season

After taking into account the initial RTL of each period, we did not find any significant difference in RTL change between the hibernation of the four groups and the active period. Only the SH-DT group showed a trend of a greater telomere erosion than the other groups and compared to the active season, but this effect was non-significant (*p*= 0.056).

The only model retained (with delta AICc<1) to explain RTL change during the active season included RTL at the beginning of the active season and RTL change over hibernation. There was a trend of more erosion during the active season with longer telomeres at the end of hibernation but this effect was non-significant (p=0.08). Nevertheless, after taking this effect into account, an increase in telomere elongation during the active season significantly increased telomere erosion during the active season (p=0.003) and conversely, an erosion during the hibernation period led to an elongation during the active season (Table 2; Fig. 5).

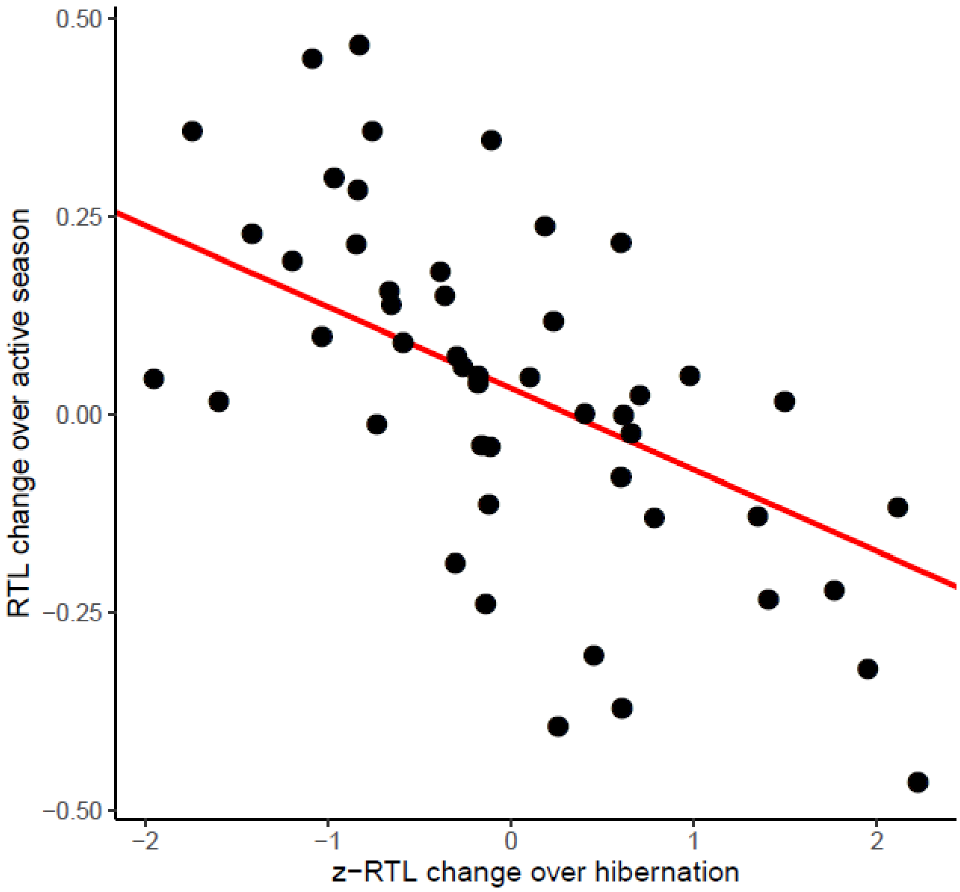

Figure 5. Effects of RTL change over hibernation (standardized) on RTL change over active season with the regression line in red based on the results of model 1. The abbreviation "z" stands for standardized.

Table 2 Best model resulting from model selection to explain RTL change over active season hibernation. The model estimates are presented by β. The abbreviation “z” stands for “standardized”.

	R^2	**Dependent variable**	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 6	0.45	RTL change over active season	Intercept	0.03 ± 0.02	1.43	0.34
			z-RTL before active season	--0.05 ± 0.03	-1.76	0.08.
			z-RTL change over hibernation	-0.10 ± 0.03	-3.24	0.003**

4) Discussion

This study confronts for the first time several hypotheses to explain the greater longevity of hibernators. These hypotheses assume that longevity is explained by either 1) reduced physiological damage during hibernation, or 2) a high investment in maintenance during hibernation, or 3) over the entire year regardless of the period. To test these hypothesis, 50 juvenile female hamsters were placed in an experimental design to modify torpor depth and hibernation duration. The results show that increased total time spent in torpor is the most important factor to explain telomere elongation during the hibernation period suggesting that the low metabolic rate may have an effect on the slowing down of aging especially with a high t_b torp. However, torpor reduced the investment in growth and reproduction, which may also favor an investment in maintenance. Hibernation conditions were not more favorable to an investment in maintenance than the active period. Indeed, the investment of energy in maintenance seemed limited and subject to a time allocation trade-off.

The common hamster shows a large inter-individual difference in hibernation patterns (Siutz and Millesi, 2017; Waßmer and Wollnik, 1997) making it an interesting model to test these hypotheses even if the experimental design did not allow to create all different hibernation patterns expected. Indeed, individuals placed in conditions favoring long hibernation with shallow torpor showed a short hibernation similar to the group SH-ST. This may be explained by the fact that the common hamster exhibits an endogenous circannual rhythm of hibernation (Monecke et al., 2014), inducing a cessation of hibernation even under short photoperiod conditions. The LH-DT group stayed longer in hibernation than the others, assuming that the circannual rhythm may be temperature dependent in the common hamster as it has been assumed in other species (Körtner and Geiser, 2000).

Our results show that a long hibernation slows or delays the development of reproduction and growth. A similar effect on reproduction is observed with deep torpor. This is consistent with studies showing that torpor tends to inhibit the development of the reproductive system (Barnes et al., 1986; Millesi et al., 2000). Nevertheless, this development may start during the inter-torpor bouts at euthermia (Dai Pra et al., 2022; Millesi et al., 2000). Our study was carried out on juveniles that had not completed their growth before the beginning of hibernation. Surprisingly, to our knowledge, this is the first study to show a slowing of body growth with increasing time spent in torpor. Of course, other results point in the same direction, such as the slowing down of teeth growth in hibernating rodents (Klevezal and Anufriev, 2013) and the inhibition of somatic growth factors like insulin-like growth factor during torpor (Schmidt and Kelley, 2001).

The total time spent in torpor was the factor the most present in the best models explaining RTL change over hibernation and the second one that showed the most important influence on RTL change (after the effect of RTL before hibernation). This positive effect of torpor persisted when T_b torp was not taken into account in the model, which implies that this effect is not only related to metabolism reduction. We can therefore assume that this effect might come from a change in energy allocation favoring somatic maintenance at the expense of reproduction and growth, both inhibited during torpor. Our results seem to support this hypothesis, since the two most parsimonious explanatory models (*i.e.*, with the fewest explanatory factors) included only time spent in torpor or growth over hibernation (in addition to RTL before hibernation) with an identical effect (absolute value of the estimates) on telomere change during hibernation. Moreover, the effects of growth and time spent in torpor became non-significant when these two variables were present in the same model suggesting a common explanation of the data. Interestingly, when the negative non-significant trend of deep torpor on RTL was taken into account in the model (thanks to the T_b torp factor), the positive effect of time spent in torpor doubled or even tripled. This result seems to support the trade-off between the energy-saving benefits of deep torpor and the costs of arousals (Nowack et al., 2019).

Our results are in agreement with previous studies showing a negative effect of the time spent in euthermia during hibernation period on telomere length in garden dormice (Giroud et al., 2014; Turbill et al., 2013). However, they differ from another study on edible dormice in the wild that shows RTL shortening in all animals after a prolonged hibernation of 7.5 to 11.4 months. Although the frequency of periodic arousal seems to be the main factor explaining this erosion in edible dormice, the immediate net effect of hibernation is RTL shortening (Hoelzl et al., 2016a). These differing results could be related to the different energy storage strategies of these species: edible dormice are fat-storing animals, whereas common hamsters are food-hoarders that consume food during inter-torpor bouts. A recent study even showed telomere elongation during hibernation in garden dormice (*Eliomys quercinus*) a fat-storing hibernator, when individuals were supplemented with food during hibernation (Ragger et al. 2020, Giroud et al. in prep). Moreover, this result is independent of the ambient temperature (3°c or 14°c), supporting the results obtained in the present study. The provision of food during the inter-torpor bouts may compensate for the negative costs of arousal from deep torpor. Nevertheless, a negative effect of the duration of long and deep hibernation on annual RTL change was reported in common hamsters submitted to different temperature and photoperiod conditions than in this study, suggesting a complex influence of environmental factors during hibernation on telomere dynamics (Constant et al. In prep).

Our results appear to be consistent with the hypothesis suggesting that physiological condition during hibernation would explain the greater longevity of hibernators (Humphries et al., 2003). However, we did not observe any significant difference between RTL change other hibernation and the active period. Furthermore, RTL change over hibernation influenced RTL change over the active period such that telomere erosion over hibernation led to telomere elongation during the active period, whereas elongation during hibernation led to erosion during the active period. This result was independent from RTL at the beginning of the active period, suggesting that hamsters may have a limited energy capital to invest in maintenance throughout the year, not just over hibernation. From an evolutionary perspective, the life-history trait theory suggests that reduced extrinsic mortality during hibernation leading to higher annual survival than in same-sized non-hibernating species (Turbill et al., 2011), may favor the evolution of a greater investment in somatic maintenance in hibernators (Healy et al., 2019).

Surprisingly, the parameters of reproductive investment were not retained as explanatory parameters for RTL change over the active period. However, a few individuals gave birth to pups and among these, none produced more than one litter, which is far from the reproductive capacity of the species (Franceschini-Zink and Millesi, 2008). Furthermore, a positive effect of reproductive investment on RTL variation has been demonstrated in this species (Constant et al, in prep). This phenomenon may be explained by a higher investment in maintenance such as antioxidant response before or during the breeding period to avoid stress impact (shielding hypotheses; (Blount et al., 2016). Thus, the weak reproductive investment and its potential compensation to maintain telomere length may explain the lack of influence on RTL change.

5) Conclusion

In conclusion, these results do not show a greater contribution of one of the three hypotheses to explain the greater longevity of hibernators. Indeed, it is likely that the slowing of metabolism during torpor reduces telomere erosion, especially when the cost of rewarming is reduced with higher T_b torp. The decrease in T_b torp, and even more the increase in the total time spent in torpor decreased the energy investment in growth and reproduction and may favor an investment in somatic maintenance causing an elongation of telomeres. However, physiological conditions during hibernation would not only explain the greater longevity of hibernators (Wu and Storey, 2016). Indeed, our findings seem to indicate that hamsters would be able to invest in somatic maintenance regardless of the time of the year, in a trade-off with the investment of energy in growth and reproduction. These results may be consistent with the hypothesis of reduced extrinsic mortality. Nevertheless, the ability to lengthen telomeres is not specific to hibernators and has been demonstrated in other species (Criscuolo et al., 2020; Fairlie et al., 2016; Haussmann et al., 2003; Olsson et al., 2018).Thus, to further investigate this hypothesis, it would be necessary to compare the investment capabilities in somatic maintenance in both hibernating and non-hibernating species according to their risk of extrinsic mortality.

6) Author Contributions

TC conceived and drafted the manuscript. TC, HC, SZ collected the data. SG and CH contributed to development of the concept and writing of the manuscript. TC carried out the data analyses. All authors contributed to the revisions.

7) Funding

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8) Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

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Chapter 4

In roach (Rutilus rutilus), individual differences in boldness influence migratory tendency (Chapman et al., 2011). In view of some similarities in the evolutionary causes and consequences of migration and hibernation phenology, one may ask: what about hibernation?

Hibernation and early life condition in the context of Pace of life Syndrome

Short title: Hibernation and Pace of life

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Abstract

The pace of life syndrome (POLS) predicts covariation between behavioral, physiological, and life history traits along a fast-slow continuum at both interspecific and interindividual levels. Energy metabolism is thought to be a key component of the POLS (with energy sparing supposed to be at the slow end of the continuum). Surprisingly, species that experience seasonal variation of their metabolism have never been tested so far in this context. Among hibernators, an increase in hibernation duration and thus energy sparing is associated with a slower life history. In this study, we tested the hypothesis that longer and deeper hibernation is also associated with a slow POLS at the interindividual scale. Furthermore, early life conditions are expected to influence POLS *via* developmental plasticity. We therefore hypothesized that individuals reared under suboptimal conditions (large litter size, male biased sex ratio and late birth date) would develop a fast POLS as they have less chance of survival in the future. These hypotheses were tested in 34 juvenile male and female common hamsters followed under laboratory conditions from birth until the end of their first reproduction. Contrary to our hypothesis, we found that i/ longer hibernation was associated with faster POLS, ii/ individuals born under suboptimal conditions (large litters with reduced growth rate and high cortisol levels) showed a slower pace of life. In fact, some studies explain that individuals born under stressful but not critically poor conditions, may develop a reactive coping style associated with a slow POLS. Regarding hibernation, a long and deep hibernation is generally explained by lower energy reserves that may lead to decreased chances of future survival, and could thus be linked to the development of a fast POLS. We therefore propose that hibernation should not be integrated into the POLS of the common hamster because its

expression is not explained by a tradeoff between reproduction and survival. Nevertheless, it may be an indicator of an individual pace of life by reflecting its chances of future survival.

1) Introduction

Phenotypic variation within a population is a prerequisite for natural selection (Darwin, 1859) and is thus a major issue in evolutionary biology. The Pace of Life Syndrome (POLS) attempts to explain the covariation, along a slow-fast continuum, of life history, behavioral, physiological, hormonal or immune traits at the inter-specific/population/individual scales (Réale et al., 2010). The slow end would correspond to trait favorable for the survival in contrast to the fast end that would prioritize investment in reproduction. Traits covariation may be explain by similar environmental pressures on these traits (*i.e.*, correlated selection) or by mechanistic links (Réale et al., 2009, 2010). At the inter-individual level, although some results are consistent (*e.g.*, Krams et al., 2014; Mugel and Naug, 2020), it would appear that some of the predictions of POLS, especially the integration of behavioral traits, are rarely verified (Niemelä and Dingemanse, 2018; Royauté et al., 2018). A lack of POLS detection may be explained by differences in environmental conditions encountered by individuals that shape it. In particular, it has been suggested that environmental conditions may alter POLS when they occur early in life but not in adulthood, as irreversible developmental plasticity acts early in life (Hämäläinen et al., 2021). POLS is a recent theory that receives a significant interest (several hundred collective citations; Dammhahn et al., 2018), but for which there is a need for new approaches to be validated at the inter-individual scale.

Among the various POLS parameters, energy metabolism seems to play a key role (Arnqvist et al., 2017; Biro and Stamps, 2010; Brown et al., 2004; Careau et al., 2008; Mugel and Naug, 2020). Indeed, individuals with a higher metabolic rate have the ability to generate more energy to sustain energy consuming activities, *e.g.*, foraging (Huntingford et al., 2010) or physiological processes, *e.g.*, growth (Yamamoto et al., 1998) and early reproduction

(Arnqvist et al., 2017). However, it is also hypothesized that a high metabolic rate is associated with a more proactive temperament such as exploration, boldness, or high aggressiveness (Biro and Stamps, 2008; Careau et al., 2011; Mathot et al., 2015) and thus increased extrinsic mortality risks (*e.g.*, predation, conflict, environmental hazards; meta-analysis : Smith and Blumstein, 2008; but see Bergeron et al., 2013). Furthermore, at an intrinsic level, intense metabolic activity is accompanied by the production of reactive oxygen species (ROS) that can lead to oxidative domage and accelerate aging (*i.e.*, free radical theory (Wickens, 2001)). Thus, according to POLS, a high metabolic rate is assumed to be on the fast end of the continuum in coevolution with other traits such as proactive behavior (Réale et al., 2010). Surprisingly, although energy metabolism is assumed to be a key parameter of POLS, species experiencing significant variation of their energy metabolism (*i.e.*, endothermic heterotherms) have not been studied in this context. In addition, heterothermy expression can vary widely between individuals (Dammhahn et al., 2017; Schmid and Kappeler, 1998; Waßmer and Wollnik, 1997). Thus, the POLS predicts high inter-individual differences in life history, behavior or immune response associated with this heterothermy expression.

Hibernation represents the most effective strategy to spare energy in endotherms (van Breukelen and Martin, 2015). It is characterized by multiday torpor bouts with reduced metabolic rate and body temperature. Energy sparing is significant with a metabolic rate in torpor that can drop up to 5% of the basal metabolic rate (Geiser, 2011). Each torpor is interrupted by an arousal to euthermia which is energy consuming but crucial for the survival of hibernators (Karpovich et al., 2009). Torpor is suggested to slow the aging process (Kirby et al., 2019; Lyman et al., 1981) and allows to remain hidden for several months reducing other mortality risks such as predation (Ruf et al., 2012; Turbill et al., 2011) or interspecific competition (Moll et al., 2021). As a consequence, increasing hibernation duration increases longevity/survival at the inter-specific (Constant et al., 2020), inter-population (Turbill and Prior, 2016), and inter-individual (Lyman et al., 1981) scales. On the contrary, arousal frequency (Hoelzl et al., 2016; Wilbur et al., 2019) and the time spent in euthermia (Giroud et al., 2014; Nowack et al., 2019; Turbill et al., 2013) increase telomere erosion, which has been proposed as one of the hallmarks of cellular stress and aging in mammals (Whittemore et al., 2019). In addition, torpor inhibits the development of the reproductive system (Barnes et al., 1988; Millesi et al., 2000) whereas early immergence from hibernation may increase male reproductive success (Constant et al, in prep; Michener, 1983). Thus, many trade-offs between reproduction and survival seem to occur for both hibernation pattern (depth, duration and frequency of torpor) and phenology, which makes hibernation an interesting phenomenon for integration into the POLS theory.

In this study we tested whether inter-individual differences in hibernation expression may be spread along the slow-fast continuum in line with POLS. We predicted that a longer and deeper hibernation is at the slow end of the continuum (*i.e.*, slow growth, low reproduction rate, higher survival and thorough exploration). To account for differences in early life conditions experienced by individuals, we also tested the hypothesis that suboptimal conditions such as limited food availability in early life should favor faster POLS, because it decreases the probability of future survival (Vincenzi et al., 2013). We predict that individuals born late in the year, from larger litters and with a biased sex ratio in favor of males should exhibit a faster POLS as they will have less time to grow before hibernation and/or lower access to food (Mahlert et al., 2018; Vincenzi et al., 2013). To this end, we focused on the common hamster (*Cricetus cricetus*), a food-storing hibernator, that exhibits large inter-individual differences in hibernation patterns and phenology (Siutz and Millesi, 2017; Siutz et al., 2016; Waßmer and Wollnik, 1997) as well as in life history traits (Franceschini-Zink and Millesi, 2008; Millesi et al., 2004). Both males and females were considered because sex differences in POLS have been highlighted especially in polygynous species such as the common hamster (Tarka et al., 2018). We monitored from birth to onset of second hibernation, under controlled laboratory conditions, 34 juvenile hamsters (18 males and 16 females) born at different times during the breeding season. Then, 14 mating pairs were formed and followed until the end of their first reproduction. Open field tests were conducted to determine the exploratory temperament of individuals, and relative telomere length (RTL) was measured and used as a proxy for aging process and future survival.

2) Materials and Methods

a) Ethical statement

The experimental protocol followed the European Union Directive 2010/63/EU for animal experiments and the care and use of laboratory animals, and was approved by the Ethical Committee under the agreement number (APAFIS#20715-2019040116252316).

b) Animals and housing conditions

This study was carried out from March 2019 to October 2020. In total, we monitored 34 juvenile common hamsters during 18 months, from birth to the beginning of their second hibernation, including first hibernation and subsequent reproduction. Hamsters were maintained under controlled laboratory conditions with a photoperiod of 10L: 14D from July to the end of December to promote hibernation, and 14L: 10D from January to the end of June to promote reproduction (Monecke and Wollnik, 2004). The room temperature was set at 20±2°C from March to October, then decreased gradually over 20 days to 12±2°C to induce deep hibernation and maintained at 12±2°C from November to the end of February. Hamsters had *ad libitum* access to food (pellets 105, from Safe, Augy, France, composed of 19.3% protein, 54.9% carbohydrates, 5.1% lipids, 4.2% cellulose, 5.0% minerals, and 11.5% water) and water throughout the experiments. After separation from the mother five weeks after birth, juveniles were housed individually (W × H × D: 265 × 237 × 420 mm) until breeding and marked with miniature subcutaneous PIT tags (dimensions (Ø x L): 1.4 x 10.3 mm, weight: 35±6mg, ALLFLEX PROTRAQ mini, France).

c) Growth and body mass

Body mass of each animal was assessed once a week from the first week after birth to mother's separation at five weeks after birth and then twice a week during the next ten weeks. As growth is negligible after separation from the mother, we chose to take into account only the growth phase before separation calculated as follows: $\textit{Growth rate} = (\textit{body mass}_{\textit{at five week}} - \textit{body mass}_{\textit{at one week}}) / \textit{Time between measurement}$

d) Hibernation patterns measurements

Body temperature was recorded every 60 minutes at a resolution of 0.0625°C from October 2019 to March 2020 using subcutaneously implanted data loggers (iButton, DS1922L model, Maxim Integrated Products, Sunnyvale, CA, weighing 3.2±0.1 g after paraffin ELVAX inclusion, temperature accuracy of ±0.5°C from -10°C to +65°C, temperature resolution 0.0625°C). The recorders were implanted intraperitoneally in October 2019 and removed one year later, according to the protocol of (Capber, 2011) with the following modifications: the animals were anaesthetized with 5% isoflurane in 1.2 L·min^{-1} oxygen for induction, and maintained under 2.5% isoflurane in 1.2 l/min oxygen during the whole surgical procedure on a warm surgery table (37 °C) to maintain body temperature. Meloxicam 1mg/kg (Meloxidolor® injectable, Le Vet. Beheer B.V., Nederland) was used as anti-infammatory and analgesic agent and injected subcutaneously prior to surgery.

Torpor bouts were defined as multiday periods of reduced body temperature below 30°C between two arousals (Siutz et al., 2018). To analyze hibernation patterns, we defined the following parameters: hibernation onset (date of the first torpor bout), number of torpor bouts, frequency of torpor bouts (number of torpor bouts divided by hibernation duration), mean torpor bout duration (calculated in hours), time spent in torpor (total duration of all torpor bouts, calculated in days), mean inter torpor bout duration (calculated in hours), time spent in inter torpor (total duration of all inter torpor bouts, calculated in hours), hibernation end (date of the last torpor bout), hibernation duration (days from the onset of the first and termination of the last torpor bout) and minimal body temperature in torpor (Average of the 4 lowest values for each deep torpor).

e) Reproductive effort and fecundity

Among all the hamsters we formed 14 breeding pairs taking into account inbreeding rate (< 10%). Before each breeding attempt, we assessed fecundity of hamsters by visual inspection of vaginal opening and testes size under isoflurane anesthesia following the same procedure as stated above. 14 females were included in the two breeding events but two individuals gave birth only once. After two weeks kept together in a cage (W × H × D: 380 × 257 × 590 mm) equipped with a shelter box (W × H × D: 140 × 230 × 230 mm), that corresponds to the time of 3 oestrus cycles, females were separated from males and housed individually (W × H × D: 265 × 237 × 420 mm). At the time of separation, males and females were supplemented with protein-rich food (150g alfalfa pellets and 6g of puppies' kibbles (Virbac Baby Dog Small & Toy) to support the reproductive effort. Then, they were further supplemented with 6g of puppies' kibbles per week (stop after 2 weeks if no birth) and 50g of alfalfa pellets 3 weeks after birth to support the important effort of lactation. For each birth, we recorded litter size, offspring body mass and mother body mass every week until 5 weeks after birth. Thereafter, the offspring and the mother were separated and housed in individual cages.

f) Personality test

Hamsters' exploratory behavior has been quantified using the Open-field test adapted from (Archer, 1973). Each hamster was transferred to a small box (W x H x D: 15 x 15 x 40 cm) with some of its own bedding (wood filament and paper) to limit stress, and placed on the center of an opaque circular arena in PVC (Ø x H: 1.25 x 0.80 m) divided into five zones (4 peripheral zones of equal volume delimiting a central zone). The box was opened after an acclimation period of three minutes and we started filming hamsters for five minutes using a Sony Camcorder. At the end of each session, the arena and the box were washed with 70% ethanol. Animals were tested twice: the first test was carried out between the 15th and 17th September 2020 and the second test was carried out 5 weeks later between the 21th and 23rd October 2020. We recorded (i) the time spent in the center zone (including latency between the opening of the box and the exit of the hamster from the box and time spent in the box), (ii) the number of grooming sequences, (iii) the number of transitions between the different zones, (vi) the number of rearing (*i.e.*, when the hamster raised the upper part of the body). Rearing and transitions are the most used variables to characterize exploration in rodents (Careau et al., 2015; Montiglio et al., 2010; Réale et al., 2007).

g) Relative Telomere Length and hormone measurements

Ear tissue punches (~2mm^2) and blood samples were collected at three time points: 1) at the onset of first hibernation, 2) after first hibernation and just before reproduction and 3) at the onset of second hibernation. Samples were taken under isoflurane anesthesia, always in the afternoon between 1:00 and 7:00 p.m. to limit the effects of the time of the day on hormone levels.

Sublingual blood samples (100 µL) were taken (as described by Heimann et al., 2009) with a heparinized capillary tube. All the blood samples were conserved on ice in heparinized microtubes until centrifugation (3000 g for 15 min) at 4°C to extract plasma. Plasma and ear tissue was conserved at − 80 °C until telomere and hormone analyses.

Telomere measurements were carried out on DNA extracted from the ear tissue punches using the NucleoSpin Tissue Kit, according to the manufacturer's protocol (Macherey Nagel, France). The Relative Telomere length measurements were conducted by quantitative real-time amplification (Cawthon, 2002) adapted for ear tissues and for the common hamster. This measurement is based on the determination of a number of amplification cycles necessary to detect a lower threshold of fluorescent signal. It estimates the quantity of telomere repeated DNA sequences relative to a reference gene (c-Myc) that was predetermined to be non-variable in copy number (non-VCN) among the sample genomes (Smith et al., 2011). Primer sequences for the non-VCN gene (5’-GAG GGC CAA GTT GGA CAG TG-3’, and 5’-TTG CGG TTG TTG CTG ATC TG-3’) amplified a 54 bp portion of the c-Myc proto-oncogene. Forward and reverse telomeric primers were 5’- CGG TTT GTT TGG GTT TGG GTT TGG GTT TGG GTT TGG GTT-3’ and 5’- GGC TTG CCT TAC CCT TAC CCT TAC CCT TAC CCT TAC CCT-3’, respectively.

The hormone levels were assessed by ELISA with competitive immunoassay using specific commercial kits (Enzo Life Sciences International Inc., PA, USA). For all assays, samples were measured in duplicate or triplicate. The intra-assay coefficient of variation CV was 14% (n = 108) for cortisol and 15% (n = 57) for testosterone.

h) Statistics

Statistical analysis was performed in R v. 3.6.2 (R Core Team, 2019). First of all, we investigated for an influence of the location of the hamster cages in the room on hibernation feature due to an ambient temperature gradient in the room. To do that, we used the function lme() from the package nlme (version 3.1-152; (Pinheiro et al., 2017)) in order to take into account the relatedness (only brother and sister) as a random factor. Minimum body temperature in torpor was the only hibernation feature that was significantly influenced by the location of the hamster cages. In the following we used a corrected value of the minimum body temperature in torpor, which corresponds to the residuals of the linear regression between this parameter and the cage location in the room. Based on the function ggpairs() from the package GGally (version 2.1.2; Schloerke et al., 2018), we confirmed that all hibernation variable are highly correlated. As a consequence, we used a Principal Component

Analysis (PCA) to derive new non-correlated variables. The different steps of development and validation of the PCA (*e.g.*, eigenvalue, KMO) are presented in the supplementary material S1. We have only retained the first component of the PCA for further analysis with a positive value of the first component corresponds to a long hibernation with high number and long average duration of torpor, a late date of last torpor bouts and a lower average body temperature in torpor. For the following, we used the terms "hibernation PC1" or terms associated with "hibernation duration" to refer to this first component for clarity.

We then investigated whether across the openfield test, individuals show consistent behavioural differences over time, *i.e.*, differences in personalities (Réale et al., 2010). Using the fitdist() function of the fitdistrplus package (version 1.1-8; Delignette-Muller et al., 2015) we identified that the behavioral data followed a negative binomial distribution, which is common for count data (Lindén and Mäntyniemi, 2011). To take into account this type of distribution, we used the method of Nakagawa et al., (2017) based on the function glmer.nb from the package lme4 (version 1.1-29.; Bates and Sarkar, 2007). The model used takes into account the sex and the sessions in fixed effect, as well as the relatedness (brother and sister only) and individual factor as random effect (See section 2.2 in appendix 6 from Nakagawa et al. (2017) for the equations used). Only the number of transitions and the time spent in the center can be considered as personality traits and used thereafter with a respective repeatability of 0.33 and 0.38 (with values between 0.3 and 0.5 considered moderately repeatable; Cohen, 2013).

The list of traits tested for covariation with hibernation PC1 and their respective prediction in the context of POLS are summarized in Table 1. Only the pre-reproduction testosterone measurement was retained as it may be an indicator of investment in reproduction, on the contrary the testosterone values were at their minimum before hibernation. For cortisol, we tested only the measurements before the first and second hibernation in order to take into account its evolution in time at two identical moments of the season. In order to have a comparable measure of juvenile growth between females, we used a growth measure corrected for differences in sex ratio or litter size using the same procedure as for minimum body temperature in torpor (see above). Birth weight was not corrected because it is not influenced by either of these parameters.

To test the covariation of hibernation with biological traits, we used linear mixed models with the function lme() except for behavioral data for which we used the function glmmTMB() of the package glmmTMB (version 1.1.3; Brooks et al., 2022) in order to take into account the negative binomial distribution of this type of data (Kruppa and Hothorn, 2021). These mixed models allowed us to take into account the relatedness between individuals as a random effect. Each biological trait listed was placed as a dependent factor in a model. Hibernation PC1 was tested as a dependent factor, in simple interaction with litter size, sex ratio, birth date (hereafter referred to as early life condition) and sex. The early life conditions were themselves tested in simple interactions with sex. We added a simple interaction between sex ratio and litter size because we assumed that competition within the litter should increase as the number of males increases. In the model with telomere erosion as a dependent variable, we added two covariates to control for potentially greater erosion in reproductively active individuals (Sudyka, 2019) or for individuals with longer telomeres at the beginning of the experiment (Bauch et al., 2014).

We also developed a model to test the effect of early life condition on hibernation. The hibernation PC1 was placed as a dependent factor and early life condition as independent factor in simple interaction with sex and the interaction between sex ratio and litter size. The body mass before hibernation was also in interaction with the sex as a covariate to take into account the influence of energy reserves on hibernation expression.

For each model, we checked the multicollinearity thanks to the vif() function of the car package (version 3.1-0; Fox et al., 2012) while the normality and the homoscedasticity were checked graphically. If the normality of the residuals was not respected, we performed a boxcox transformation on the dependent variable. Cortisol data were log-transformed to obtain normality of the residuals.

For all models we performed a model selection using the dredge() function of the MuMIn package (version 1.46.0; Barton and Barton, 2015) based on AIC comparison. The models with the glmmTMB() function were fitted based on maximum likelihood contrary to the lme() function for which we specified the "maximum likelihood" method. This method is usually preferred when comparing models with the same random effects. When the data include both males and females (n>30) we limited to 4 the number of factors retained in the final model, while for models with data from only one of the two sexes (n=14 for females or n=18 for males) we limited this number to 2 factors. This allowed us to maintain a ratio of data to explanatory factors ≥ 7 for all our models, thus limiting overfitting. We reported the best model with standardized explanatory factors in order to compare effect sizes.

Table 1: List of studied traits and respective predictions in the context of pace of life syndrome

	Traits studied	**Fast POLS**	**Slow POLS**
Life history traits	Growth rate	Fast	Slow
	Total number of offspring	High	Low
	Mean offspring by litter	High	Low
	Offspring growth rate	Fast	Slow
	Offspring body mass at birth	Low	High
Physiology	Hibernation	Short and shallow	Long and deep
	Telomere erosion	High	Low
	Early life cortisol	Low	High
	Cortisol at the end of the experiment	Low	High
	Testosterone before reproduction	High	Low
Behavior	Total number of transitions	High	Low
	Total time spent at the center	Low	High
Early life condition	Litter size	High	Low
	Sex ratio	More males	More females
	Birth date	Late born	Early born

3) Results

a) Early life condition and hibernation

Hibernation PC1 decreased significantly with the body mass before hibernation, with heavier individuals hibernating for shorter periods (Model 1, Table 2). In addition, hibernation PC1 appeared to be explained by an interaction between litter size (early life condition) and sex having an effect as large as body mass before hibernation (Model 1, Table 2 and Figure 1). Thus, hibernation duration increased slightly with litter size in females but decreased in males.

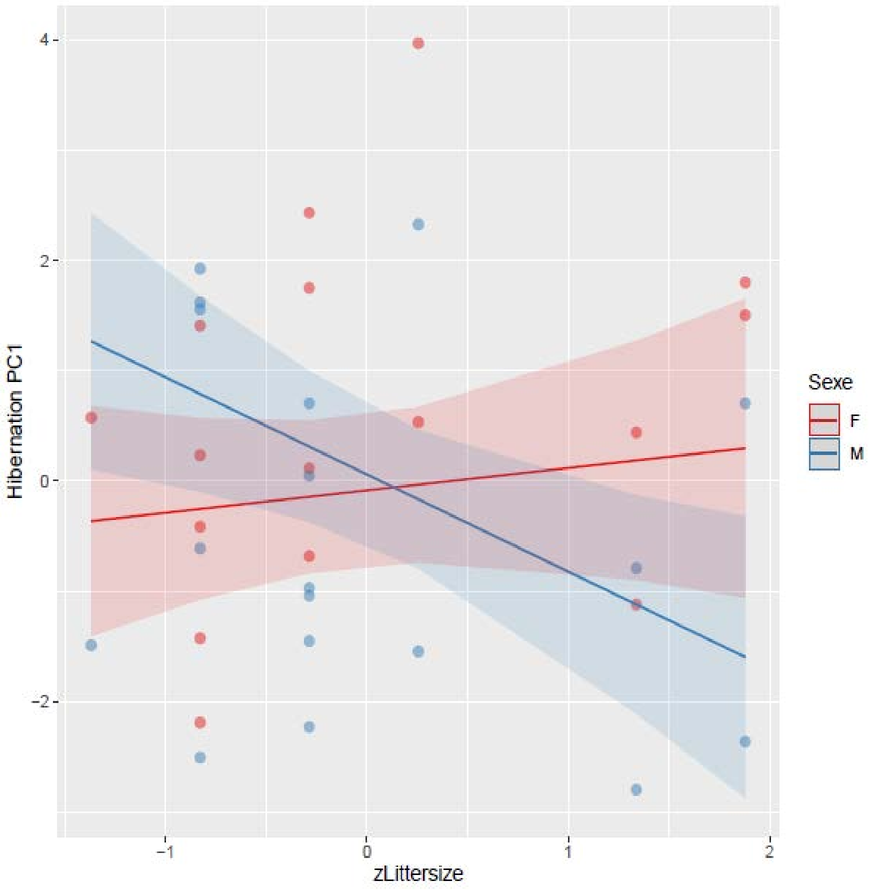

Figure 1. Effects of litter size (standardized) on hibernation PC1. The interaction effect between litter size and sex is represented by two different colors for the regression lines, blue for males (M) and red for females (F).

b) Hibernation, early life condition and life history

Growth rate decreased with litter size (early life condition) with a trend for higher decrease for males but the effect is non-significant (Model 2, Table 2 and Figure 2). There was a significantly positive relationship between hibernation duration and growth rate with an effect that is about half as large as litter size (Model 2, Table 2).

The number of offspring per litter increased with hibernation duration but the effect was not significant (Model 3, Table 2). No factors came up in the best model to explain the total number of offspring (Model 4, Table 2). Corrected offspring growth rate decreased with birth date and the size of the mothers’ early life litters, but both effects were not significant (Model 5, Table 2).

Offspring's body mass at birth increased significantly with the size of the mothers’ early life litter (Model 6, Table 2). On the contrary, offspring's body mass decreased significantly with the increase of the mothers' hibernation duration but this effect was 3 times less important than the one of the sizes of the mothers’ early life litter (Model 6, Table 2).

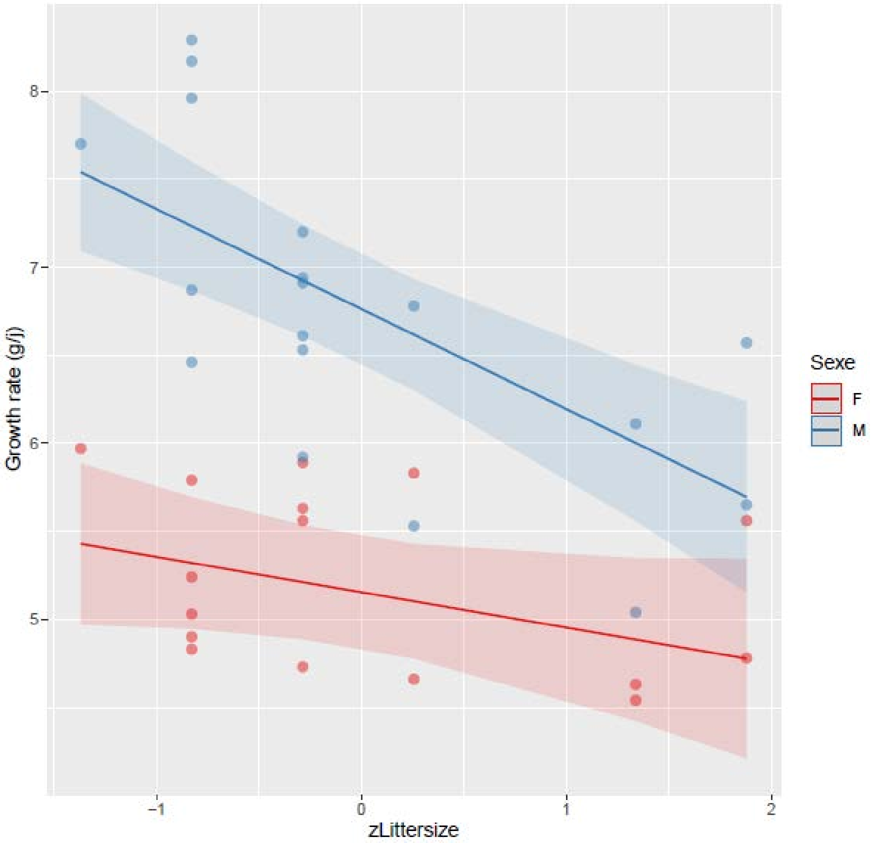

Figure 2. Effects of litter size (standardized) on growth rate. The interaction effect between growth rate and sex is represented by two different colors for the regression lines, blue for males (M) and red for females (F).

c) Hibernation, early life condition and behavior

The total number of transitions increased significantly with the date of birth (Model 7, Table 2). Furthermore, the total number of transitions was explained by a significant interaction between litter size and sex, such that the number of transitions increased slightly with males' litter size whereas it decreased with females' litter size (Model 7, Table 2, and Figure 3).

Total time spent at the center increased significantly with the date of birth (Model 8, Table 2). The total time spent in the center was also explained by an interaction between hibernation PC1 and the sex ratio: longer hibernation had little or no positive effect on the time spent in the center when reared in a litter with a low proportion of males, but quickly had a negative effect when the proportion of males in the litter increased (Model 8, Table 2 and Figure 4).

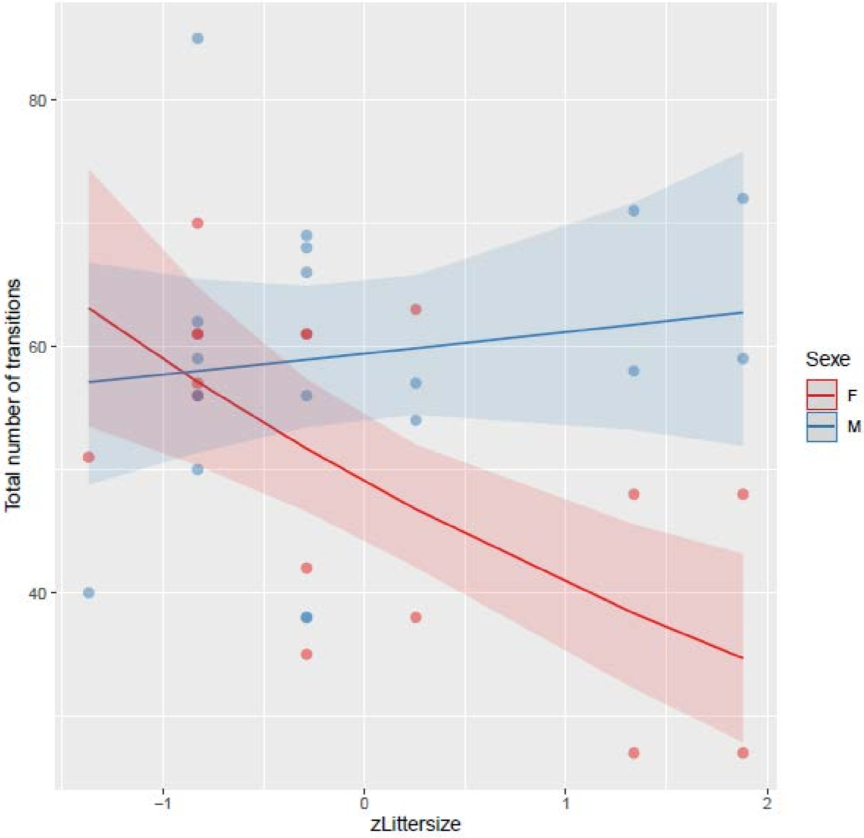

Figure 3. Effects of litter size (standardized) on the total number of transitions. The interaction effect between the total number of transitions and sex is represented by two different colors for the regression lines, blue for males (M) and red for females (F).

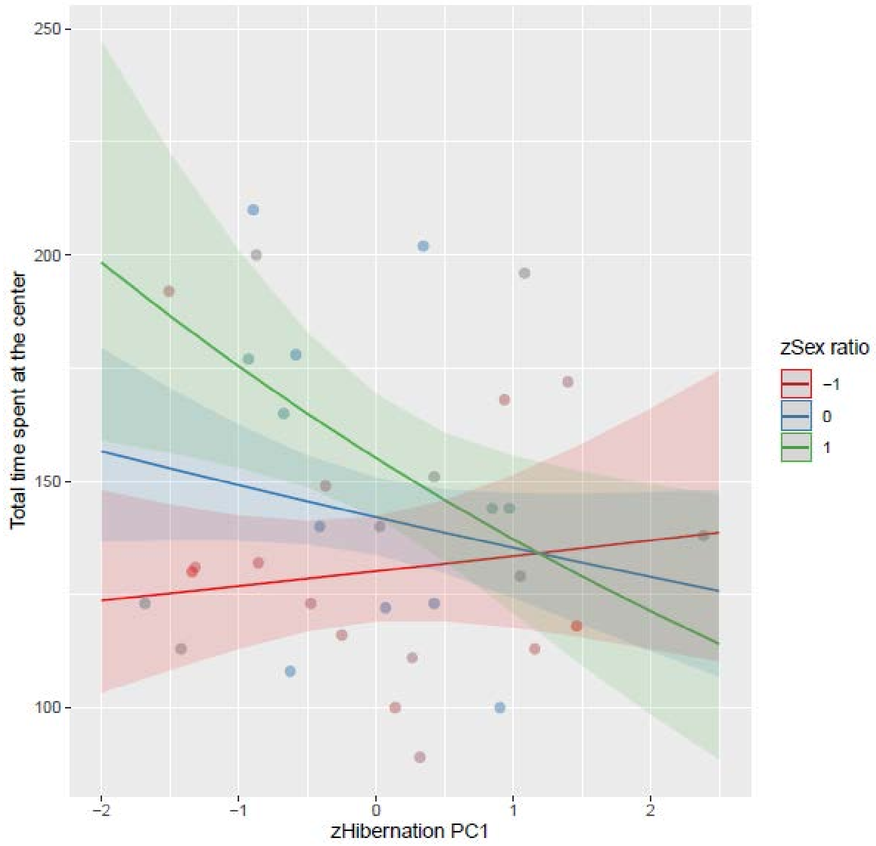

Figure 4. Effects of hibernation PC1 (standardized) on the total time spent at the center. The regression lines in blue, red, green indicates respectively the effect of hibernation PC1 when the sex ratio (standardized) is equal to the mean, one standard deviation below and above mean value.

d) Hibernation, early life condition and physiology

Telomere erosion increased significantly with telomere length at the beginning of the experiment as well as with hibernation duration, but the latter effect was half as important (Model 9, Table 2). On the contrary, telomere erosion was less important for individuals that could reproduce or were raised in a large litter, with a telomere elongation even observed for some (Model 9, Table 2).

Cortisol levels measured in both early and late experiments increased in individuals reared in a large litter size but with less effect and explanatory power at the end of the experiment (Model 10 and 11 and Table 2). In addition, males had lower early life cortisol levels compared to females but this effect was not present in the best model at the end of the experiment (Model 10 and 11 and Table 2).

Pre-breeding testosterone levels were higher in males reared with a high proportion of males but this effect was non-significant (Model 11, Table 2).

Table 2: regression results for the best models explaining covariation between hibernation, physiological, behavioral, life history trait and early life condition. The Z standardized model estimate is estimated by β.

	R^2	**Dependent variable**	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 1 n=34	0.43	Hibernation PC1	Intercept	-0.09 ± 0.37	-0.25	0.79
			zLittersize	0.19 ± 0.33	0.57	0.56
			Sexe (M)	0.16 ± 0.55	0.29	0.77
			zBody mass before hibernation	-1.13 ± 0.30	-3.77	< 0.001***
			zLittersize:Sexe (M)	-1.08± 0.47	-2.29	0.03*
Model 2 n=34	0.84	Growth rate	Intercept	5.15 ± 0.17	29.35	< 0.001***
			zLittersize	-0.20 ± 0.13	-1.47	0.15
			Sexe (M)	1.60 ± 0.18	8.83	< 0.001***
			zHibernation PC1	0.17 ±0.10	1.62	0.11
			zLittersize:SexeM	-0.36 ± 0.17	-2.06	0.05.
Model 3 n=14	0.15	Total number of offspring	Intercept	11.34 ± 0.61	18.56	< 0.001***
			zHibernation PC1	0.69 ±0.47	1.46	0.19
Model 4 n=14		Mean offspring by litter	Null model			
Model 5 n=14	-0.04	Corrected offspring growth rate	Intercept	0.43 ± 0.16	2.60	0.04*
			zDate of birth	-0.02 ± 0.01	-1.95	0.10
			zLittersize	-0.00 ± 0.00	-2.37	0.06.
Model 6 n=14	0.94	Offspring body mass at birth	Intercept	18.97 ± 0.54	34.61	< 0.001***
			zHibernation PC1	-0.85 ± 0.30	-2.84	0.03*
			zLittersize	2.65 ± 0.28	9.28	<0.001***
Model 8 n=34	0.65	Total number of transitions	Intercept	3.89 ± 0.05	75.32	< 2e-16 ***
			zLittersize	--0.18± 0.05	-3.62	< 0.001***
			Sexe (M)	0.19 ± 0.06	3.06	0.002***
			zSex ratio	-0.09 ± 0.07	-2.43	0.015*
			zLittersize:Sexe (M)	0.21 ± 0.06	3.35	< 0.001***
Model 9 n=34	0.38	Total time spent at the center	Intercept	4.89 ± 0.03	162.59	< 0.001***
			zSex ratio	0.08 ± 0.03	2.65	0.008***
			zHibernation PC1	-0.04 ± 0.03	-1.56	0.117
			zDate of birth	0.11 ± 0.03	3.40	< 0.001***
			zSex ratio:zHibernation PC1	-0.07 ± 0.03	-2.19	0.028*
Model 10 n=32	0.87	Telomere erosion	Intercept	-0.28 ± 0.04	-6.11	< 0.001***
			zLittersize	0.06 ± 0.01	3.36	0.003***
			zRTL Early life	-0.10 ± 0.01	-5.86	< 0.001***

			Reproduction (Yes)	0.20 ± 0.04	4.68	< 0.001***
			zHibernation PC1	-0.05 ± 0.01	-3.27	0.003***
Model 11 n=31	0.59	Early life cortisol	Intercept	1.15 ± 0.07	14.84	< 0.001***
			zLittersize	0.12 ± 0.04	2.63	0.01*
			Sexe (M)	-0.12 ± 0.07	-1.54	0.13
Model 12 n=34	0.11	Cortisol at the end of the experiment	Intercept	0.63 ± 0.17	3.68	< 0.001***
			Littersize	0.05 ± 0.02	2.06	0.04*
Model 13 n=18	0.48	Testosterone before reproduction	Intercept	2.15 ± 1.34	1.60	0.14
			zSex ratio	4.40 ± 2.34	1.87	0.09.

4) Discussion

a) Long hibernation and a fast pace of life

Our purpose was to test the hypothesis that energy metabolism is a key component of the POLS syndrome using hibernation as an example with extreme changes of metabolic rate for several months. We tested this hypothesis in the common Hamster (*Cricetus cricetus*), a hibernating species that shows large inter-individual variation in hibernation patterns (Siutz and Millesi, 2017; Siutz et al., 2016; Waßmer and Wollnik, 1997). Hence, we predicted that long and deep hibernation is associated with a slow pace of life, as such a relation is suggested by outcomes from several studies (Blanco and Godfrey, 2013; Constant et al., 2020; Turbill et al., 2011). On the contrary, our results do not support this prediction, but rather a covariation of hibernation with a faster POLS: long and deep hibernation is associated with fast growth, greater telomere erosion, more exploratory behavior (in interaction with a biased sex ratio, see below), more offspring (although not significant, but included in the best model) with low body mass at birth (Figure 5).

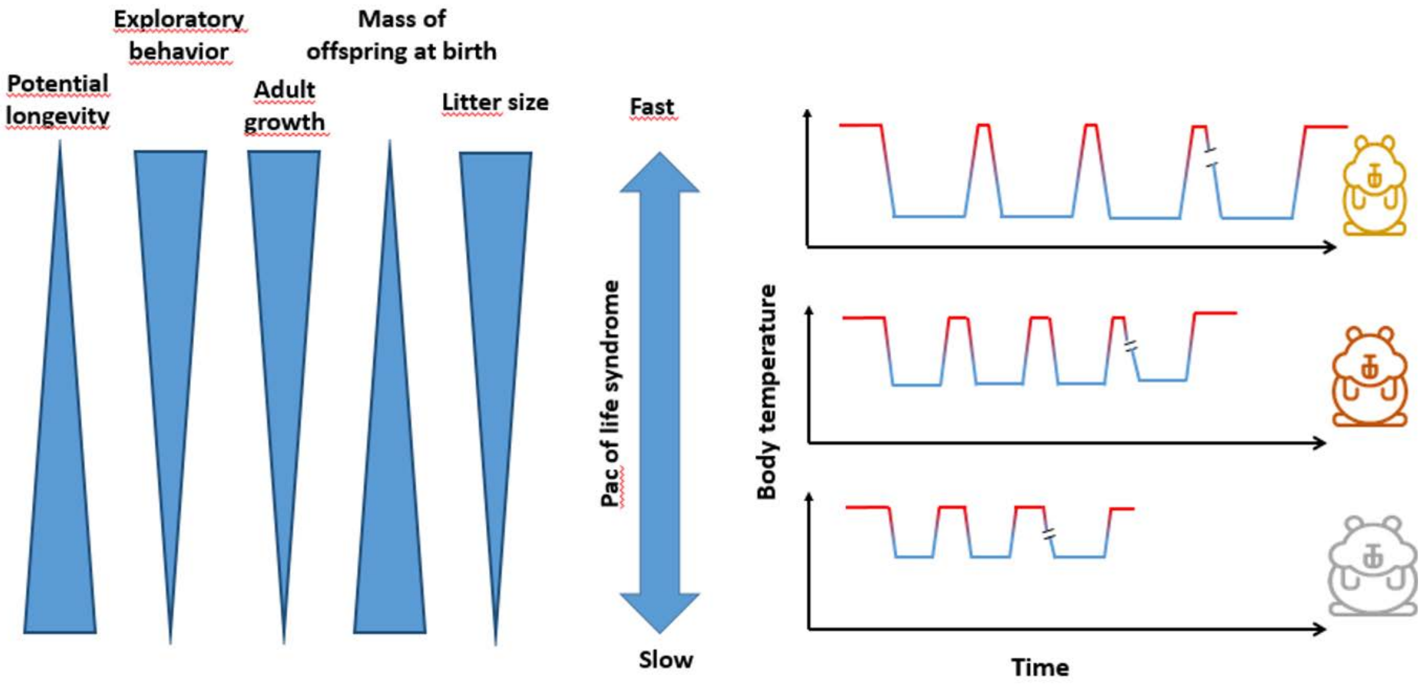

Figure 5. General scheme of the relationship between several biological traits and hibernation patterns. A long and deep hibernation covaries with biological traits located at the fast end of the slow-fast continuum. Contrary to our predictions, long hibernation is not explained by survival benefits, but rather by a lack of energy reserves. The decrease of survival chances associated with the lack of energy reserve, would explain the link with a rapid POLS. Hibernation does not seem to be integrated in the POLS at the inter-individual level in hamsters because its occurrence is not explained by a trade-off between survival and reproduction but is rather an index of future survival chances.

A long hibernation associated with a fast POLS seems at first glance to be contrary to published studies at the population (Turbill and Prior, 2016) and species levels (Constant et al., 2020) that show a longer hibernation associated with higher longevity and/or survival. Moreover, mechanistic links imply opposite functions between a long hibernation and high reproductive investment. Torpor prevents the development of the reproductive system which requires a return to euthermia either during inter torpor bouts at the end of hibernation or after the last torpor (Barnes et al., 1988; Millesi et al., 2000). From a phenological perspective, late emergence from hibernation may reduce both male and female reproductive success (Michener, 1983). Thus, it seems unlikely that the covariation between long hibernation and fast traits is the result of similar selection pressure or mechanistic links.

These contradictions may be explained by the fact that some relationships obtained at a higher scale (population, species) cannot be applied at the individual scale, this misinterpretation is called "the ecological fallacy" (Robinson, 2009). Indeed, at the inter-individual scale, there may be costs or trade-offs that are not perceptible/existent at higher organizational levels. At the individual levels, torpor expression is governed by a trade-off between the benefits of saving energy and the important physiological costs of being torpid such as the production of oxidative stress during arousals, telomere erosion, or sleep inhibition (our study; Humphries et al., 2003). Thus, as observed in this study, individuals with more energy reserves (internal or external) tend to perform less and shallower torpor to avoid physiological costs (Humphries et al., 2003). Based on this principle, long and deep hibernation should be explained by a lack of external or internal energy reserves before hibernation.

Limited fat mass prior to hibernation decreases the chances of survival during hibernation (Ozgul et al., 2010; Rieger, 1996; Stumpfel et al., 2017) and lead to increased telomere erosion due to arousals from low temperature (this study, Hoelzl et al., 2016; Nowack et al., 2019). According to the pace of life syndrome theory, a reduced chance of survival in the future may explain the development of the fast pace of life observed in individuals performing a longer hibernation. We therefore propose that hibernation cannot be integrated into the pace of life syndrome of the common hamster because its expression is not explained by a tradeoff between reproduction and survival. Nevertheless, it could be an indicator of an individual pace of life by reflecting its chances of future survival.

These results may suggest that in the common hamster, a short-lived species relative to its size (up to 3,6 years max for 500g (Magalhães and Costa, 2009)), the internal cost/benefit balance governs the expression of torpor more than the benefits of remaining in hibernation to reduce predation risk. Interestingly, in the edible dormouse, a very long-lived hibernator species relative to its size (up to 13 years max for 125g (Trout et al., 2015)), individuals with excess internal energy reserves do not stop hibernating earlier, but only decrease the depth of torpor, limiting both the costs of deep torpor and the predation risk by remaining in hibernation (Bieber et al., 2014). This comparison must be taken with precaution because our study, contrary to that of the edible dormouse, was carried out under laboratory conditions and thus without predation pressure. Nevertheless, future studies should test whether hibernation expression at the inter-individual level may be explained by different constraints depending on the life history strategy of species.

b) Early life condition and pace of life

To test the integration of hibernation into the POLS, we accounted for differences in early life conditions hypothesized to influence the pace of life syndrome via irreversible developmental plasticity (Dammhahn et al., 2018). We predicted that suboptimal early life conditions (*e.g.*, low food availability within a large litter) may lead individuals to faster POLS (Vincenzi et al., 2013). Early life conditions had little influence on the covariation of traits with hibernation (only one interaction between hibernation and sex ratio, see below). Nevertheless, individuals born and raised in large litters show many traits located at the slow end of the POLS, especially in females, contrary to the hypothesis developed. Females raised in a large litter show slow growth, slightly longer hibernation, larger pups at birth with slower growth (not significant), more exploratory behavior and higher early and late cortisol levels. Some studies proposed that individuals born under stressful, but not critically poor conditions, may develop a reactive coping style associated with a slow POLS (Champneys et al., 2018; Damsgård et al., 2019; Vincenzi et al., 2013). On the contrary, in males, a large litter is associated with a shorter hibernation and a more exploratory behavior. Litter size influence on males is therefore more complex to interpret in the context of the pace of life syndrome with both slow and fast traits.

Hibernation duration is also explained by early life litter size with a different effect between the sexes. In females, hibernation increases slightly with litter size while it decreases in males. It seems unlikely that this sex-dependent effect is related to energy reserves as the model controls for the effect of body mass before hibernation. On the contrary, the effect of litter size may be explained in part by trade-offs between survival and reproduction that differ between the sexes at the end of hibernation (Constant et al., in prep; Michener, 1983). Males have important benefits to emerge early from hibernation to prepare for reproduction (physically or territory establishment/competition) while females have survival benefits to remain in hibernation and wait until conditions are optimal for reproduction (Constant et al., in prep; Michener, 1983). It has been shown that male rodents raised in a large litter tend to store more food and be more competitive and aggressive (Paul and Mendl, 1991; Seitz, 1954 but see Ryan and Wehmer, 1975) than those born in a small litter. Moreover, male rats or mice raised in a large litter would tend to exhibit significantly more mating behavior toward a female in oestrus (Seitz, 1954) and greater sexual signaling investment (Gibson et al., 2015). We can therefore assume that males raised in large litters are better competitors (especially for reproduction) and tend to emerge earlier from hibernation to have a competitive/breeding advantage. If this hypothesis is true, it would be the first time that conditions at birth and notably behavior or personality may influence the duration of hibernation without depending on energetic aspects and would confirm the different trade-offs between males and females observed between different hibernating species (Constant et al., in prep).

Large litter size is also associated with a large number of physiological and behavioral factors at the slow end of the pace of life. Once again, some correlations seem to be explained by mechanistic links (direct links between variables). The reduction in growth rate with litter size is a common life history trade-off explained by increased competition for food resources or access to the mother (Gibson et al., 2015). Increased competition in larger litter size may explain the increase in cortisol with litter size at the beginning of the experiment as already observed in sheep (*Ovis aries*) (Corner et al., 2007). Moreover, cortisol has a growth inhibitory action (Bellamy, 1964) and may contribute to enhance the litter size effect on growth. The litter size effect on cortisol levels is still present at the end of the experiment, showing long-term effects of early life conditions. Litter size also affects the behavior of male and female adult hamsters differently. Males raised in large litters tend to be more exploratory while females are less exploratory. Contrasting effects of litter size at birth have also been shown on the exploratory behavior of several mammals with more (Seitz, 1954) or less exploratory behavior with increasing litter size (Priestnall, 1973; Seitz, 1954). In sheep, litter size has a different effect between sexes on escaping behavior (Hernandez et al., 2010). To summarize, the influence of litter size has already been demonstrated on a large number of biological traits and yet has rarely been integrated or taken into account in the study of POLS.

Litter size appears to have a significant influence on other biological traits that no other study, to our knowledge, has documented, but which remains consistent with the development of a slow pace of life, favoring survival over reproduction. Females born in large litters produce larger, but slower growing young (although not significant). In addition, individuals born in large litters have less telomere erosion or even showed telomere elongation for some of them. Interestingly, the same statistical model shows that individuals that were placed in reproduction have less telomere erosion than those that were not, and may also show telomere elongation. In house mice (*Mus musculus domesticus*), less oxidative stress was also measured in reproductive individuals compared to non-reproductive ones (Garratt et al., 2011). These unexpected result might be explained by a greater investment in maintenance such as antioxidant response before or during breeding stress to avoid breeding stress for the mother and the offspring (shielding hypotheses; Blount et al., 2016).

In this study, sex ratio at birth and birth date are other early life factors that show a significant influence on some biological traits (especially behavior). The increase in sex ratio biased in favor of males tends to decrease the exploratory character of individuals either through a direct influence or in interaction with the effect of hibernation. The influence of sex ratio on adult behavior has already been demonstrated but its effect varies and is different between species (Gracceva et al., 2011; Laviola and Alleva, 1995; Naguib et al., 2011; Namikas and Wehmer, 1978). However, few studies have looked at the correlation over time and with other behaviors (Gracceva et al., 2011). The influence of birth date on behavior, on the other hand, has been little studied despite an influence on physiology and life history traits (Mahlert et al., 2018). In this study, late-born hamsters tended to have less exploratory behavior than others, which is in contradiction with the hypothesis that late-born individuals would have a faster POLS (Mahlert et al., 2018). These results should encourage behavioral studies in species with multiple births during the year (*e.g.*, on early or late born individuals).

Finally, it is important to mention that the effects of early life conditions, such as sex ratio, litter size or birth date are even more complex to explain as they may come from direct effects of competition but also from changes in parental behavior in response to these conditions (Grota, 1973).

The consistency over time of the traits studied in the pace of life syndrome is an important criterion. In this study, few traits could be measured more than once over time, but as hamsters belong to a short-lived species (less than two years (Kryštufek et al., 2020)) they experience only one or two episodes of hibernation and reproduction during their lifetime. So, these measures remain close to their expression in the natural environment. Furthermore, we did not directly test the trade-off between survival and reproduction (Dammhahn et al., 2018), but based our interpretations on trade-offs already highlighted in other species. Thus, we cannot rule out that individual quality interferes with the results (Dammhahn et al., 2018). In addition, since we do not test for covariation of traits influenced by litter size, we cannot conclude that litter size is responsible for a syndrome (Sih et al., 2004). So, we cannot reject that litter size may influence these traits independently of each other.

5) Conclusion

Contrary to our predictions, a long and deep hibernation seems to be associated with a fast pace of life. These results are therefore in contradiction with studies carried out at the population and species levels for which a long hibernation is rather associated with a slow POLS. This study shows that it is important to test the hypotheses of evolutionary ecology at different scales of life since they do not present the same evolutionary constraints. Hibernation's covariation with other biological traits does not seem to be explained by similar selection pressures (especially trade-offs between survival and reproduction) but rather by mechanistic links with several traits. According to the torpor optimization hypothesis, long and deep hibernation would be the result of a lack of fat mass prior to hibernation, conducting to a decrease in future survival probability. Low probability of survival in the future is precisely supposed to lead to a faster POLS. We propose that hibernation cannot be integrated into the pace of life syndrome of the common hamster because its expression is not explained by a trade-off between reproduction and survival. Nevertheless, it may be an indicator of an individual pace of life by reflecting its chances of future survival. Taking the necessary precautions due to the laboratory conditions, these results may suggest that for the common hamster, the internal cost/benefit balance governs the expression of torpor rather than the benefits of reducing the risk of predation by remaining in hibernation. Reduced predation risk may have a greater influence in a species with a slower life history strategy such as the dormouse. If this is the case, then the inter-individual expression of hibernation could have different evolutionary constraints depending on the life history strategy of the species studied. This study also demonstrates the importance of considering early life conditions especially in species with large differences in litter characteristics or parental investment. In particular, it is interesting to note that individuals born under sub-optimal (but not deleterious) conditions, such as large litter size associated with reduced growth, seem to present a slow pace of life.

6) Author Contributions

TC conceived and drafted the manuscript. TC, HC, SZ collected the data. SG and CH contributed to development of the concept and writing of the manuscript. TC carried out the data analyses. All authors contributed to the revisions.

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8) Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

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Chapter 5

"I want to know my biological age! I'm sure I look younger than I really am... I mean younger than my chronological age. Do I need to hibernate longer?"

Oma, 4.5 years (the survivor)

Telomeres, a complex biomarker of aging in a species with telomere lengthening

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Abstract

Relative telomere length (RTL) or RTL change over time has been proposed and used as a biomarker of aging. Although this relationship has been demonstrated in species with lifetime telomere erosion, no studies have tested it yet in species with the ability to lengthen RTL. To address this gap, we conducted a longitudinal monitoring from birth to death in the common hamster (*Cricetus cricetus;* 12 males and 12 females), a hibernating species with the ability to seasonally lengthen telomeres. Telomere measurements were made every year before and after hibernation until the death of the majority of individuals (7 points maximum were collected over more than 3 years). Using the method of within-subject centering, we separated the inter- and within-individual effects of age. Overall, the results showed an erosion of RTL during hibernation that increased over individuals' lifetime. However, smaller telomeres after hibernation were followed by telomeres elongation during the active period, leading to a maintenance of RTL at the end of the active season throughout life. After accounting for the effect of age on telomere, it appeared that RTL and RTL changes were not repeatable over an individual's lifetime and did not predict the remaining life span. In addition to the seasonal and age effect, there was a significant variation in RTL and RTL changes over time. However, when telomeres reached a critical length, the chances of dying the following year increased considerably. Intriguingly, common hamster aging appears to have characteristics of both catastrophic and senescent deterioration of the organism (that is non-linear and age-related linear aging process). Telomeres in hamsters therefore gather some characteristics of good biomarkers but there use in this species must be limited to specific questions. Further studies are needed to determine if these aging characteristics are common to species capable of lengthening their telomeres.

1) introduction

Aging is an intrinsic characteristic of living beings and corresponds to an irreversible and time-related process of the degradation of functions that support survival and reproduction (Dodig et al., 2019). Determining the factors that influence aging is a fundamental question for many fields of biology (*e.g.*, medicine, evolutionary ecology, molecular biology). However, performing studies over the lifetime of long-lived species is highly demanding in time, money, and material and do not provide a quick answer. Consequently, research is often focused on short-lived and experimentally tractable organisms (Poeschla and Valenzano, 2020), but not representative of species diversity. To solve this issue, biomarkers of aging have been developed. These biomarkers are supposed to represent the physiological health or functional status (*i.e.*, biological age) of individuals and thus distinguish individuals by their future risk of mortality related to aging (Mather et al., 2011). Telomere length is proposed as a biomarker of aging and is all the more interesting as this structure is common to all eukaryotes (Fulcher et al., 2014)**.**

Telomeres are highly repetitive, non-coding regions of DNA at the end of linear chromosomes (Greider, 1996). They protect the coding part of DNA, because at each replication, a part of the DNA at the end of the chromosomes is not copied by the DNA polymerase complex (*i.e.*, end replication problem; Greider, 1996). When a critical point is reached, it causes cell senescence or apoptosis (Greider, 1996). Telomeres shortening with chronological age (the time elapsed since birth) has been observed in many phylogenetically distant species (Haussmann et al., 2003; Horn et al., 2010). Moreover, telomeres seem to be sensitive to stressful (*e.g.*, diseases, pollution) or energy-demanding environmental factors (*e.g.*, reproduction, growth) that may accelerate aging (Chatelain et al., 2020). This erosion of telomeres is often induced by oxidative stress, which occurs when the protective system (*e.g.* antioxidants, DNA repair enzymes) is overwhelmed by reactive oxygen species (ROS) (Chatelain et al., 2020). Thus, longer initial telomeres are associated with lower future mortality risk at both the intraspecific and interspecific scales (Fairlie et al., 2016; Pauliny et al., 2006; Wilbourn et al., 2018). For an accurate prediction of longevity, the rate of telomere erosion may be more appropriate than telomere length solely (Whittemore et al., 2019).

However, these links are not universal and telomeres may have other benefits depending on the species group or ecological context (Olsson et al., 2018; Risques and Promislow, 2018). These biomarkers are however questioned in species able to maintain or even lengthen their telomeres presumably thanks to the enzyme telomerase or by DNA-recombination (Greider and Blackburn, 1985; Neumann et al., 2013). This phenomenon has been demonstrated in several phylogenetically distant taxa and in different tissues (*e.g.*, leukocytes, buccal swabs, tail tissue). It is unlikely related to measurement artifact or survivor bias, that is, the death of individuals with small telomeres, which may artificially increase the mean telomere length in the population over time (Criscuolo et al., 2020; Fairlie et al., 2016; Haussmann et al., 2003; Hoelzl et al., 2016a, 2016b; Olsson et al., 2018; Tissier et al., 2021). Elongation and shortening can occur in the same year depending of environmental conditions (Criscuolo et al., 2020; Hoelzl et al., 2016a), or telomeres may increase with age or in older individuals (Hoelzl et al., 2016b; Tissier et al., 2021). Long telomeres may have a "ROS-trap" role to protect the coding parts of the DNA from oxidative damage in anticipation of a high stress period (*e.g.*, reproduction, hibernation or dry season) as long telomeres have many guanine and cytosine bases that are prime targets of oxidative stress (Bauch et al., 2014). However, maintenance or elongation is energetically-costly (Hoelzl et al., 2016a; Nowack et al., 2019). With these new findings, it is therefore necessary to test the validity of telomeres (length and erosion rate) as a proxy for aging in species likely to restore their telomeres.

In this study we followed under laboratory conditions, the telomere dynamics of the common hamster (*Cricetus cricetus*), a hibernating species that is likely to elongate its telomeres at certain times during the year (Constant et al. in prep). A longitudinal monitoring was performed from birth to death of the individuals (maximum of 3.3 years of monitoring with 7 measures for some individuals) in order to test whether telomere length or its change meets the characteristics of an aging biomarker in hamsters. More specifically, we investigated whether telomeres (relative telomere length and/or its change) 1) change with chronological age considering the inter- and within-individual effect. We also tested whether 2) telomeres are suitable to assess past stressful experience by measuring the within-individual repeatability (ranging from 0 to 1) of RTL dynamics over time. Very high within-individual repeatability (close to 1) implies that the environment has little or no impact on telomeres. On the contrary, very low within-individual (close to 0) implies that telomeres may be highly susceptible to environmental stressors and independent on the previous experience (Kärkkäinen et al., 2021). Finally, we assessed 3) to what extent telomeres predict survival in the short (*e.g.*, catastrophic deterioration of organism) or long term (*e.g.*, senescent deterioration of organism). The monitoring was achieved on a cohort of 24 individuals (12 individuals of each sex) born within a short time interval (1 month max) and raised under the same environmental conditions in order to control other mortality risks than aging. Telomere length was measured from ear tissues collected each year before the beginning and after the end of hibernation, using quantitative PCR (‘qPCR’).

2) Materials and Methods

a) Ethical statement

The experimental protocol followed the European Union Directive 2010/63/EU for animal experiments and the care and use of laboratory animals, and was approved by the Ethical Committee under the agreement number (#20715-2019040116252316 v2).

b) Animals and housing conditions

This study was carried out from the birth of the first individuals in May 2018 until the end of 2022 to follow the longevity of all individuals. Hamsters were maintained in controlled laboratory conditions with a photoperiod of 10L: 14D from July to the end of December that promotes hibernation and 14L: 10D from January to the end of June that triggers reproduction. The temperature was 20±2°C from March to October then was decreased gradually over 20 days to 12±2°C to induce hibernation and maintained from November to the end of February. Hamsters had ad libitum access to food and water. They were fed a conventional diet (pellets 105, from Safe, Augy, France, composed of 19.3% protein, 54.9% carbohydrates, 5.1% lipids, 4.2% cellulose, 5.0% minerals, and 11.5% water) during the whole experiment. Hamsters were housed individually (W × H × D: 265 × 237 × 420 mm) and marked with miniature subcutaneous PIT tags (dimensions (Ø x L): 1.4 x 10.3 mm, weight: 35±6mg, ALLFLEX PROTRAQ mini, France). Each year, individuals were placed in reproduction if they were in physiological condition (*i.e.*, developed reproduction organ) for this activity (for more details see section “Reproductive effort and fecundity” in Constant et al, in prep).

c) Relative Telomere Length measurements

Ear tissue punches (~2mm^2) were collected each year before (October) and after hibernation (March) from birth until October 2021 (only 5 hamsters were still alive), following chirurgical procedure (for more details see section “Hibernation patterns measurements” in Constant et al, in prep). In total, we collected 125 samples that were conserved at − 80 °C until analyses. Telomere measurements were carried out on DNA extracted from the ear tissue punches using the NucleoSpin Tissue Kit, according to the manufacturer's protocol (Macherey Nagel, France). The Relative Telomere length measurements were conducted by quantitative real-time amplification (Cawthon, 2002) adapted for ear tissues and for the common hamster. This measurement is based on the determination of a number of amplification cycles necessary to detect a lower threshold of fluorescent signal. It estimates the quantity of telomere repeated DNA sequences relative to a reference gene (c-Myc) that was predetermined to be non-variable in copy number (non-VCN) among the sample genomes (Smith et al., 2011). Primer sequences for the non-VCN gene (5’-GAG GGC CAA GTT GGA CAG TG-3’, and 5’-TTG CGG TTG TTG CTG ATC TG-3’) amplified a 54 bp portion of the c-Myc proto-oncogene. Forward and reverse telomeric primers were 5’- CGG TTT GTT TGG GTT TGG GTT TGG GTT TGG GTT TGG GTT-3’ and 5’- GGC TTG CCT TAC CCT TAC CCT TAC CCT TAC CCT TAC CCT-3’, respectively.

RTL change was calculated as follows: RTL change = $RTL_{t+1} - RTL_{t0}$

d) Statistics

Statistical analysis was performed in R v. 3.6.2 (R Core Team, 2019). RTL data shows a Gaussian distribution and the boxplot method, useful for this type of distribution (Walker et al., 2018), highlights 4 outliers (see figure S1 in supplementary materials). Each of these measurements were performed less than a year before the death of the individuals with 3 of them corresponding to the last telomere measurement. These measurements may be related to disorders related to the end of life (*e.g.*, thymomas appear in many old hamsters). We therefore decided not to take them into account for the rest of the tests.

We started with an exploration of the data by testing differences in RTL or RTL change between sexes and post and pre hibernation periods using anova with the aov() function from the package stats (version 3.6.2; Team et al., 2018). In addition, graphic observations showed significant differences of age effect on telomere dynamics between post and pre hibernation, as a consequence all models were tested for pre- and post-hibernation periods independently. Several studies have shown a quadratic relationship of telomere variation with age (Bize et al., 2009; Burraco et al., 2020; Rollings et al., 2017; Seeker et al., 2018; Ujvari et al., 2017), including hibernating species (Hoelzl et al., 2016b; Ineson et al., 2020). Thus, we compared models including age variables (*e.g.*, mean age, delta age) square root transformed and not transformed using the AICc (corrected Akaike information criterion). As the best models always include square root transformed data, we will only present these models but the linear relationships bring similar results.

An important issue to consider when studying the influence of a factor from a longitudinal monitoring of a group of individuals is to disentangle inter- and within-individual effects. For example, telomeres may vary with age in the population (inter-individual variation) because individuals with a specific RTL have disappeared, *i.e.,* a selective disappearance. On the other hand, telomeres may also vary over the lifetime of an individual (within-individual variation). The method of within-subject centering (Van de Pol and Wright,

2009) is largely employed to differentiate these two effects based on two new variables. The inter-individual effect is measured from the mean age of individuals over telomeres sampling. This measure gives the cross-sectional slope of the relationship between RTL and age. The within-individual effect or delta age is measured from the time difference between the age of the individual at a sampling date (exact age) and the mean age. This measure provides the slope (between RTL and age) based on longitudinal data. Mean and delta age were included as independent variables in the same model to test their respective influence on RTL and RTL change (dependent variables, model 1 to 5 hereafter). In order to determine if the slope between the inter- and within-individual effect is significantly different it is necessary to test in the same model the effect of exact age (includes both intra and inter-individual effect) and mean age on telomeres (includes only inter-individual effect). If the effect of mean age is significant, it means that there is a significant difference between the inter- and within-individual effects and thus a selective disappearance of individuals in the population (van de Pol & Wright, 2009). Since none of the models including exact and mean age show a significant effect of exact age and do not provide additional information compared to the other models, the results of these models will be presented in supplementary materials Table S1. For this method, we used mixed-effects models with the lmer() function from the package lme4 (version 1.1-30; Bates and Sarkar, 2007) to take into account the repeatability of individual measurements and the relatedness between individuals (at the sibling level) by placing ID and relatedness as crossed random factors.

To test whether within-individual variation is consistent over time, we measured within-individual repeatability of telomere measurements using the rptR() function from the rptR package (version 0.9.22; Stoffel et al., 2017). The models were fit by a Gaussian distribution of the data and tested for both RTL and RTL change as a dependent factor. In each model, mean age and delta age were placed as independent factors to account for variation in telomeres with age as well as sex. Individual ID and relatedness were placed as crossed random factors. As recommended by Stoffel et al., (2017), in a second step, we quantified the uncertainty of the estimators by parametric bootstrapping (10,000 iterations).

We then examined whether RTL or RTL change predicted future long-term or short-term survival. We tested whether RTL or RTL change for both period, at a given age, predicts the remaining life of an individual (long-term survival) based on the method developed in Bichet et al., (2020). We performed mixed-effects models with the remaining life as a dependent factor, which corresponds to the time between the age at telomere measurement and the death of the individual. RTL, RTL change, exact age and sexes were placed in independent factor and ID and relatedness as independent factor (model 6 to 11 hereafter). At the time of conducting the analyses, only one individual to date is not yet dead so it was not included in the analyses.

We then investigated whether the last RTL measurement for both periods predict the odds of survival the following year. On average the last RTL measurement was taken about 6 months before the individual's death. We did not test the effect of last RTL change over hibernation or active season because depending on when the individual died, the last hibernation or active season was more than a year ago, and thus no more representative of a short-term effect on survival for a short-lived species. To specifically verify this relationship, we tested whether RTL telomeres increase the odds of dying in the following year by using a logistic model with the glmer() function from the package lme4. Survival was placed as a dependent factor with the value 1 if the individual survives the year following the RTL measurement and 0 if he died during the year. As an independent factor, we tested the effect of RTL measured until the last post or pre hibernation measurement in the year preceding the death of the individual such that the last post or pre hibernation RTL measurement was associated with a survival of 0 (respectively model 12 and 13 hereafter). Chronological age and sex were also included as covariates and ID and relatedness as crossed random factors. No interaction with sex was retained after control based on AICc criterion.

For each of the above models testing the RTL change as a dependent or independent factor, we have placed the initial RTL as a covariate (including for the repeatability test). Indeed, this allows to correct for the fact that longer telomeres tend to erode faster (Bauch et al., 2014). In addition, the inclusion or not of the sex variable in the model was based on the AICc criterion. For each model, we checked the multicollinearity thanks to the vif() function of the car package (version 3.1-0; Fox et al., 2012) while the normality and the homoscedasticity were checked graphically. Finally, all telomere samples were spread on one plate during qPCR, which explains why we do not include a random "plate" factor in our models.

3) Results

a) Age effect on RTL and RTL change

The data did not show any effect of time period (pre or post hibernation) and sex on RTL (sex: *p*= 0.655, period: *p*= 0.131) or RTL change (sex: *p*= 0.513, period: *p*= 0.469). RTL measured before hibernation (pre hibernation RTL) showed neither inter-individual effect of age (measured with “mean age”, model 1, table 1) nor within-individual effect of age (measured with “delta age”, model 1, table 1). After controlling for pre hibernation RTL, the RTL change during hibernation showed a significant increase in telomere erosion within-individual's lifetime (Fig. 1, model 2, table 1). There was a trend of smaller post hibernation RTL within-individual's lifetime but this effect is non significance (model 3, table 1). After controlling for post hibernation RTL, RTL change during the active period did not show any inter and within-individual age effect (model 4, table 1). However, interestingly, the model that did not include post hibernation RTL as a covariate showed a significance elongation of RTL during the active season within-individual's lifetime (Fig. 2, model 5, table 1). All models testing RTL change showed a significant effect of RTL as a covariate with greater erosion of longer telomeres but also elongation of smaller telomeres (Fig. 3 a and b, model 2 et 4, table 1). None of the best models testing the inter- and within-individual effect of age or their combined effect of age had sex as a covariate.

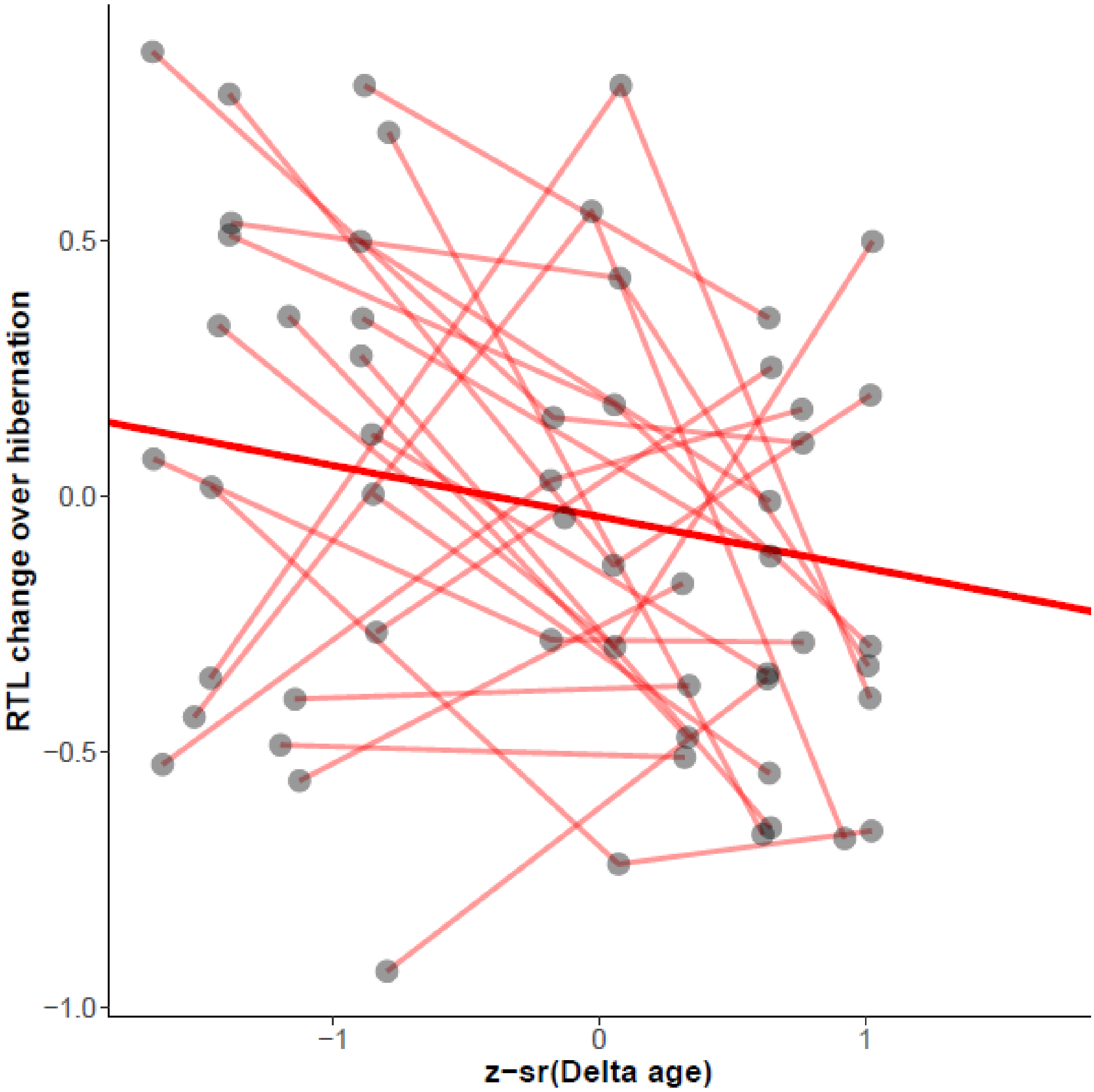

Figure 1. The within individuals' effects of age (delta age standardized and square root transformed) on RTL changes over hibernation with the regression line in dark red. RTL change with delta age for each individual in represented by light red line. The abbreviation "z" and "sr" stand for respectively standardized and the square root transformation.

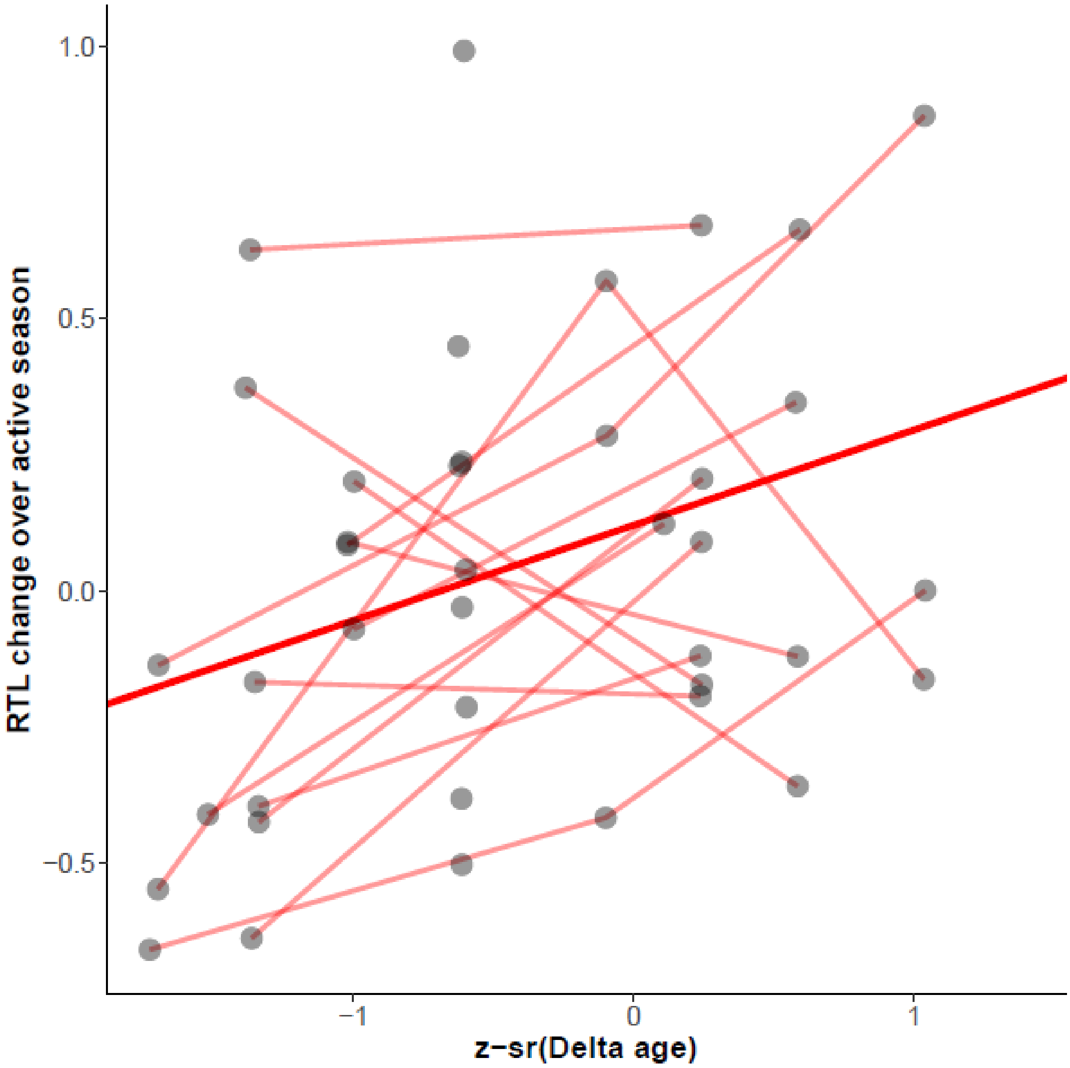

Figure 2. The within individuals' effects of age (delta age standardized and square root transformed) on RTL changes over active season with the regression line in dark red. RTL change over active season with delta age for each individual in represented by light red line. The abbreviation "z" and "sr" stand for respectively standardized and the square root transformation.

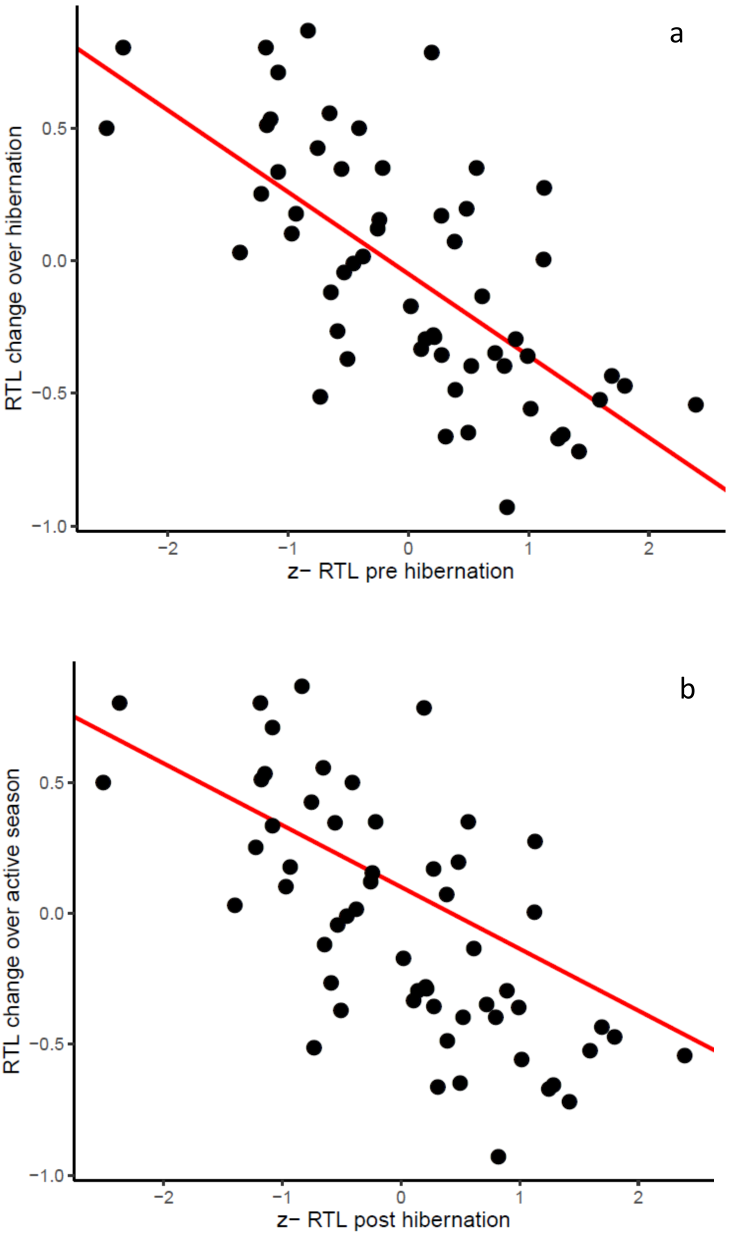

Figure 3. Effects of RTL post and pre hibernation (standardized) on RTL change over a) hibernation and b) active season with the regression line in red. The abbreviation “z” stands for standardized.

Table 1. Regression results for the best models explaining variations in RTL and RTL change with age. The model estimates are presented by β. The abbreviation “sr” stands for “square root”.

	Dependent variable	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 1	RTL pre hibernation	Intercept	2.42 ± 0.49	4.85	< 0.001***
		Mean age (sr transformed)	-0.01 ± 0.02	-0.79	0.43
		Delta age (sr transformed)	0.002 ± 0.005	0.46	0.64
Model 2	RTL change over hibernation	Intercept	1.40 ± 0.48	2.87	0.01*
		RTL pre hibernation	-0.86 ± 0.12	-6.96	< 0.001***
		Mean age (sr transformed)	0.01 ± 0.01	0.63	0.53
		Delta age (sr transformed)	-0.01 ± 0.00	-2.20	0.03*
Model 3	RTL post hibernation	Intercept	1.84 ± 0.44	4.12	< 0.001***
		Mean age (sr transformed)	0.007 ± 0.01	0.36	0.71
		Delta age (sr transformed)	-0.01 ± 0.007	-1.96	0.05.
Model 4	RTL change over active period	Intercept	2.13 ± 0.65	3.26	0.005**
		RTL post hibernation	-0.69 ± 0.15	-4.59	< 0.001***
		Mean age (sr transformed)	-0.02 ± 0.02	-1.12	0.27
		Delta age (sr transformed)	0.01 ± 0.01	1.58	0.12
Model 5	RTL change over active period	Intercept	0.77 ±0.70	1.09	0.282
		Mean age (sr transformed)	-0.02 ± 0.03	-0.95	0.34
		Delta age (sr transformed)	0.03 ± 0.01	2.57	0.01*

b) Intra-individual repeatability

RTL post hibernation (p=0.261), RTL pre hibernation (p=0.306) as well as RTL change over hibernation (p=0.208) and over active season (p=0.294) did not show significant repeatability over individual lifetime. Nevertheless, RTL change over hibernation (R=0.178; CI_{95}=[0, 0.668]) and over active season (R=0.089; CI_{95}=[0, 0.442]) showed slightly greater repeatability than RTL post hibernation (R=0.103; CI_{95}=[0, 0.451]) and pre hibernation (R=0.077; CI_{95}= [0, 0.372]).

c) Telomeres and short and long-term survival predictions

RTL and RTL change at post or pre hibernation did not reveal any effect on remaining survival (long term survival) when controlling for the effect of age (model 6, 7, 8, 9; table 2). In all these models, males showed a significant lower remaining lifespan than females. However, if not controlled for age, telomere erosion during hibernation (model 10, table 2) and small RTL post hibernation (model 11, table 2) decreased remaining lifespan. In addition, there was a trend for a lower remaining life span in males but the effect was non-significant.

RTL had no effect on the odds of survival when considering pre-hibernation telomeres as the last measurement before death of individuals, but there was a significant effect when taking the last telomeres after hibernation as the last measurement (model 12 and 13, table 3). Thus, smaller telomeres after hibernation increased the chances of dying the following year (Fig. 4). In each model predicting the odds of survival the next year, age and sex had significant effects such that older individuals and males were more likely to die the next year (model 12 and 13). Size effect indicated that age and sex had a similar effect, 3 times greater than that of telomeres after hibernation.

Table 2. Regression results for the best models explaining remaining lifespan variation with RTL and RTL change and age. The model estimates are presented by β. The abbreviation "sr" stands for "square root".

	Dependent variable	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 6	Remaining lifespan (sr transformed)	Intercept	42.18 ± 3.30	12.77	< 0.001***
		RTL prehib	0.84 ± 1.39	0.60	0.54
		Sex (Male)	-5.14 ± 1.69	-3.04	0.008**
		exact age (sr transformed)	-0.94 ± 0.05	-17.46	< 0.001***
Model 7	Remaining lifespan (sr transformed)	Intercept	44.78 ± 3.32	13.46	< 0.001***
		RTL posthib	1.52 ± 1.10	1.37	0.17
		Sex (Male)	-6.39 ± 1.81	-3.51	0.002**
		Exact age (sr transformed)	-1.06 ± 0.05	-19.55	< 0.001***
Model 8	Remaining lifespan (sr transformed)	Intercept	41.50 ± 2.59	15.98	< 0.001***
		RTL change hibernation	0.46 ± 0.74	0.62	0.53
		RTL prehib	-0.32 ±1.02	-0.32	0.74
		Sex (Male)	-5.13 ± 1.46	-3.50	0.002**
		Exact age (sr transformed)	-0.74 ± 0.03	-24.7	< 0.001***
Model 9	Remaining lifespan (sr transformed)	Intercept	45.02 ± 2.99	15.05	< 0.001***
		RTL change active season	0.56 ± 1.00	0.56	0.58
		RTL posthib	0.20 ± 1.15	0.17	0.86
		Sex (Male)	- 5.58 ± 1.54	-3.60	0.002**
		Exact age (sr transformed)	-0.92 ± 0.05	-18.24	< 0.001***
Model 10	Remaining lifespan (sr transformed)	Intercept	9.58 ± 5.82	5.83	0.10
		RTL posthib	6.47 ± 2.78	2.74	0.02*
		Sex (Male)	-3.28 ± 1.97	1.90	0.09.
Model 11	Remaining lifespan (sr transformed)	Intercept	18.53 ± 5.95	3.11	0.003*
		Var_RTL hibernation	5.64 ± 2.24	2.51	0.01*
		RTL prehib	3.65 ± 2.84	1.28	0.20
		Sex (Male)	-2.66 ± 1.53	-1.73	0.08.

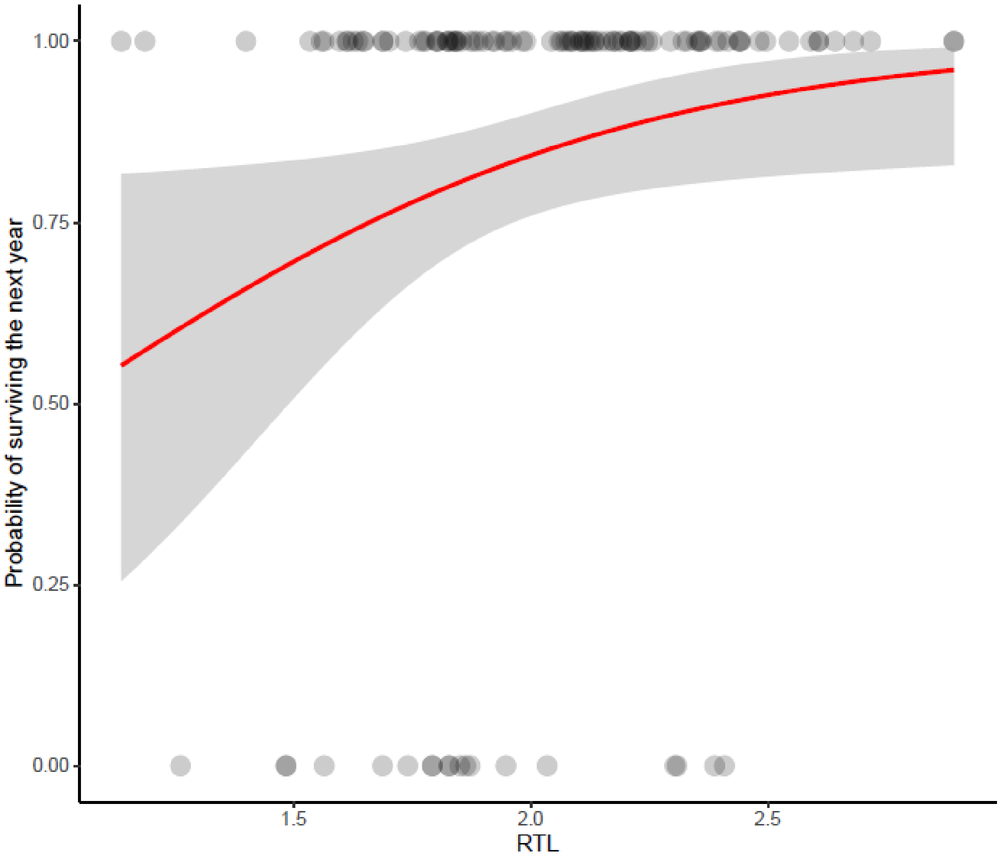

Figure 4. Effects of RTL (standardized) on the probability of survival the next year when considering post hibernation measurement as last measurement before the death of individuals. The logistic regression curve (with 95% confidence bands) is represented with a red line.

Table. 3 Regression results for the best models explaining probability of survival the next year with RTL, sexe and age. The model estimates are presented by β. The abbreviation “sr” stands for “square root”.

	Dependent variable	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 12	Probability of survival the next year (Last pre hibernation measurement)	Intercept	45.25 ± 9.64	4.69	< 0.001***
		z-RTL	-0.81 ± 3.04	-0.26	0.789
		Sexe (Male)	-48.83 ± 9.62	-5.07	< 0.001***
		z- Chronological age (sr transformed)	-44.83 ± 8.84	-5.06	< 0.001***
Model 13	Probability of survival the next year (Last post hibernation measurement)	Intercept	5.92 ± 1.37	2.87	< 0.001***
		z-RTL	1.23 ± 0.51	1.32	0.016*
		Sexe (Male)	-3.60 ± 1.17	-3.06	0.002**
		z- Chronological age (sr transformed)	-3.64 ± 0.87	-4.15	< 0.001***

4) Discussion

This study aimed at testing whether RTL or RTL change can be used as a biomarker of aging in a species that can experience lengthening of their telomeres at certain times of the year. To answer this question, a longitudinal monitoring of telomere dynamics was performed in 24 male and female common hamsters. We found that the RTLs of hamsters shorten with age but this effect was dependent on the time of the year and was added to the seasonal dynamics of telomeres (Fig. 5). Telomeres were not repeatable over time and did not predict long-term survival between same age individuals but did in the short-term (on average 6 months before the death of the individual).

After accounting for RTL prior hibernation, we found evidence for telomere erosion during hibernation that increased over the lifetime of individuals. Although we did not test for a causal link, it is likely that this erosion explained the non-significant trend of smaller RTL post hibernation with age. The effect of age on telomeres at the end of hibernation was no longer apparent at the end of the next active season probably because hamsters with shorter telomeres post hibernation showed telomere elongation during the next active period. This elongation of telomeres during the active season increased over the lifetime of individuals. However, the within-individuals effect of age on telomere elongation during the active season disappeared when post-hibernation telomere length was taken into account in the model. Thus, this process was explained by the reduction of telomeres post hibernation with age and would not be a direct effect of age on elongation unlike the erosion of telomeres during hibernation. To summarize, it may be assumed that increased telomere erosion during hibernation with age led to shorter telomeres at hibernation emergence and telomere elongation during the active period (Fig. 5). Telomere erosion during the unfavorable time of year (here hibernation) and elongation during the active season has been previously demonstrated in a hibernating species (Hoelzl et al., 2016a) and a seasonal non-hibernating species (Criscuolo et al., 2020).

The age effect on telomere erosion during hibernation may be due to an indirect effect of age on hibernation patterns. Indeed, a negative effect of time spent in torpor, frequency of arousal, or hibernation duration on RTL has already been shown in several hibernating species (Hoelzl et al., 2016a; Turbill et al., 2013) including the common hamster (Constant et al, in prep). Additionally, edible dormice show an increase in hibernation duration with age (Bieber et al., 2018). A similar effect in hamsters may explain the observed telomere dynamics with age. Furthermore, telomere elongation upon emergence from hibernation has been demonstrated in several hibernating species (Hoelzl et al., 2016a; Turbill et al., 2013; Viblanc et al., 2022) and at the beginning of the favorable season in a seasonal species (Criscuolo et al., 2020). It has been proposed that elongation may (i) mitigate the negative effects of hibernation on maintenance, (ii) anticipate and protect against the negative effects of future reproduction on maintenance (iii) improve reproductive success as longer telomeres are sometimes associated with better reproductive success (Viblanc et al., 2022).

However, telomeres do not predict long-term survival. RTL and RTL change in common hamsters did not predict the remaining life span when comparing individuals at the same age. Furthermore, it appeared that RTL and RTL change were not repeatable over the lifetime of an individual. Telomeres may be highly sensitive to stressful environmental conditions as suggested by their seasonal variation. The ability of this species to lengthen its telomeres may also compensate for short-term physiological costs and mask the biological age of individuals. These two elements taken together suggest that for the hamster, telomeres did not allow to represent accumulated stress or somatic state at a given time, an important feature for a good biomarker of aging. Therefore, it may be irrelevant to measure the long-term impact of reproductive investment or hibernation patterns on survival from short-term changes in telomere length. Nevertheless, the long-term erosion of telomeres over hibernation and at emergence predicted the remaining life of individuals. Therefore, telomeres are directly or indirectly related to the effect of chronological age on aging leading to the death of the individual. Small telomeres could directly impact survival if they reach a critical size that leads to cell senescence (Kurz et al., 2004) or indirectly by reflecting the cost of other factors such as oxidative stress that damages cellular integrity.

Telomeres may also have an effect on short-term survival. The logistic approach showed that for individuals of the same age and sex, smaller telomeres at the end of hibernation decreased the chance of survival in the following year (odds of survival decreased by 1.42 times for each 0.1 RTL unit less). As explained above, the effect of small telomeres can be direct or indirect. Age and sex showed a threefold effect than telomeres in predicting survival the following year. The odds of surviving the next year for males was 97.3% less likely as compared to females. This observation has already been highlighted in many species and a large number of hypotheses have been proposed (Austad and Fischer, 2016), such as a lower production of reactive oxygen species in females (Vina et al., 2011; Viña et al., 2005) or the influence of sexual selection on the survival of males especially in species with sexual dimorphism like common hamsters (Promislow, 1992).

5) Conclusion

All these results might contribute to a better understanding of the complex aging process in hamsters. Although a seasonal variation in telomere length was observed in hamsters, this species seemed to undergo an age-related linear senescence that only occurred over the successive hibernations and predicted the death of individuals. Nevertheless, after taking into account the age effect, telomeres or their short-term changes were not repeatable over the lifetime of hamster and did not predict the future life span in the long-term. However, in the short-term (on average less than 6 months before death), shorter telomeres predicted future survival. Thus, in addition to the fluctuation of telomeres length with age and season, there would remain an important variation of telomeres over time that prevents the determination of an individual's biological age. This variation might be related to the ability of hamsters to compensate for the effect of stressful environmental conditions by lengthening their telomeres. However, when telomeres reached a critical length, the chances of dying the following year increased considerably. Intriguingly, hamster aging appeared to have characteristics of both catastrophic and senescent deterioration of the organism (that is non-linear and linear aging process). Telomeres in hamsters therefore gather some characteristics of good biomarkers but their use in this species must be limited to specific questions. Further studies are needed to determine if these aging characteristics are common to species capable of lengthening their telomeres.

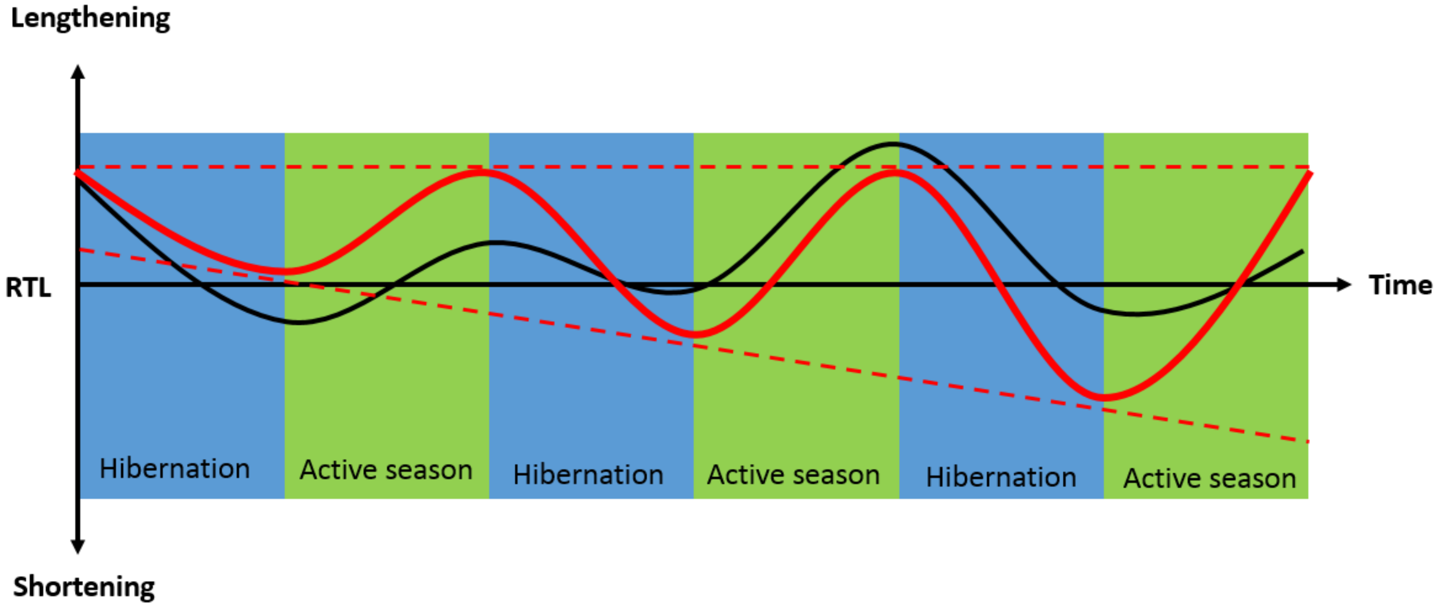

Figure 5. Schematic representation of RTL dynamic within-individual lifespan in common hamsters (*Cricetus cricetus*) including specific seasonal variation and age effect (red curve) and residual variation of age effect (black curve). The black curve showing the residuals variation after accounting for the effect of age illustrates the low reproducibility of RTLs over the lifetime of an individual. Note, the schematic is intended to illustrate the effects obtained in this article and the magnitude of these effect are not to scale.

6) Author Contributions

TC conceived and drafted the manuscript. TC, HC, SZ collected the data. SG and CH contributed to development of the concept and writing of the manuscript. TC carried out the data analyses. All authors contributed to the revisions.

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8) Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interes

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Discussion

I. Cause évolutive de la phénologie de l'hibernation

A. Intégration des résultats dans le contexte actuel des connaissances

Étonnamment, très peu d'études ont tenté d'étudier et surtout de distinguer les facteurs proximaux et ultimes de l'hibernation. L'hibernation a d'abord été décrite comme une adaptation au manque de nourriture et aux températures froides de l'hiver (Lyman, 1982). Néanmoins, l'hypothèse des contraintes énergétique (appelé « energy limitation hypothesis » dans le chapitre 2) se base sur des études qui mettent en évidence un effet proximal et non ultime des contraintes énergétiques (Vuarin and Henry, 2014). Pour démontrer le rôle ultime des contraintes énergétiques, il est nécessaire de tester si le début et la fin de l'hibernation correspondent strictement aux transitions de début et de fin de pénurie énergétique, c'est-à-dire le moment où la disponibilité alimentaire ne permet plus de répondre aux besoins énergétiques de l'organisme. Bien que certaines études suggèrent un effet des contraintes énergétiques sur la durée de l'hibernation (Bronson, 1979; Dobson and Murie, 1987; Dobson et al., 1992), le lien de causalité entre contraintes énergétiques et phénologie de l'hibernation reste peu vérifié. Des études récentes ont suggéré que le risque de mortalité extrinsèque serait une cause ultime de l'hibernation potentiellement très répandue mais néanmoins sous étudiée (Ruf et al., 2012). Jusqu'à ce jour, cette hypothèse a été principalement développée pour expliquer l'hibernation du loir gris (Bieber and Ruf, 2009; Bieber et al., 2018; Hoelzl et al., 2015). Ce rongeur présente des caractéristiques biologiques extrêmes avec notamment une longévité très importante par rapport à sa taille et une capacité à hiberner jusqu'à plus de 11 mois (Hoelzl et al., 2015). Une généralisation aux autres espèces d’hibernants semble donc prématurée et nécessite des recherches complémentaires sur un plus large panel d’espèces.

Les chapitres 1 et 2 de ma thèse ont permis de compiler des faisceaux d’indices qui pourraient suggérer que le risque de mortalité extrinsèque serait une cause ultime de la phénologie de l’hibernation répandue parmi les espèces hibernantes. Les observations ou expériences les plus convaincantes montrent que des individus ou populations anticipent leur début d’hibernation par rapport aux contraintes énergétiques de l’environnement, en raison d’un arrêt ou d’une absence de reproduction (Choromanski-Norris et al., 1986; Michener, 1978; Millesi et al., 1998, 2008; Neuhaus, 2000; Nicol and Morrow, 2012). Ainsi, la phénologie de l’hibernation pourrait s’expliquer par un compromis entre les bénéfices d’être en hibernation pour garantir la survie de l’individu et les bénéfices d’être actif pour optimiser la reproduction. L’hypothèse du compromis (appelé « life-history hypothesis » dans le chapitre 2) a été testée dans le chapitre 2 pour expliquer la différence entre les sexes dans la phénologie de l’hibernation. Ce phénomène est largement répandu et ne semble pas pouvoir être expliqué par l’hypothèse des contraintes énergétique. En effet, chez plusieurs espèces comme le hamster commun, le Microcèbe mignon (*Microcebus murinus*) ou l’échidné à nez court (*Tachyglossus aculeatus*), les femelles restent en hibernation plusieurs semaines (jusqu’à 6 semaines) après l’émergence des mâles alors que le milieu semble favorable à l’activité, puisque les mâles augmentent leur masse corporelle jusqu'à 9% avant l’émergence des femelles (Lebl and Millesi, 2008; Millesi et al., 1999; Nicol et al., 2018, 2019; Schmid, 1999; Schmid and Kappeler, 1998). De la même manière, l’un des sexes entre plus tôt en hibernation tandis que les individus du sexe opposé restent actifs et continuent d’accumuler des réserves énergétiques durant plusieurs semaines voire plusieurs mois après la fin de l’hiver.

Les résultats du chapitre 2 montrent chez plus d’une vingtaine d’espèces hibernantes, que l’hypothèse du compromis entre survie et reproduction permet d’expliquer la différence entre les sexes dans la phénologie de l’hibernation. Alors que les mâles sont déjà actifs, les femelles favoriseraient leur survie en prolongeant l’hibernation et émergeraient de manière à ce que les soins maternels, très énergivores, correspondent à la période exacte de l’année avec le plus de disponibilité énergétique dans l’environnement (Kenagy et al., 1989). Les mâles quant à eux sortiraient d’hibernation en premier pour se préparer à la compétition avant la reproduction. Nous avons pu montrer, chez une vingtaine d’espèces hibernantes, que la variation dans des facteurs explicatifs de la préparation à la reproduction (comme la taille des testicules ou la masse corporelle avant reproduction) permet d’expliquer la variation dans la date d’émergence des mâles par rapport aux femelles.

A l’issue de la période d’accouplement, les mâles et femelles montrent des activités différentes. Les mâles semblent se rétablir du stress physiologique de la reproduction pendant que les femelles sont gestantes puis lactantes (Levesque et al., 2013; Millesi et al., 1998). Les deux sexes accumulent ensuite des réserves énergétiques internes ou externes avant l’hibernation. Ainsi, nous avons pu montrer que pour l’immergence, le sexe qui a investi le plus de temps dans l’activité post accouplement (rétablissement suite au stress physiologique ou soin maternel) est celui qui rentre le plus tardivement en hibernation. Dès lors qu’ils n’ont plus de bénéfice à rester actif pour la reproduction et que la constitution des réserves énergétiques est suffisante, les individus entrent en hibernation, probablement pour limiter les risques de mortalité extrinsèque.

Il est tout de même important de souligner que ce type de méthode comparative ne permet pas d'assigner la causalité d'une variable sur une autre, c'est-à-dire la direction de la pression de sélection entre l’investissement dans la reproduction et la phénologie d'hibernation ou les deux dans le cas d’une coévolution.

À partir des informations développées dans cette thèse, nous suggérons qu’il existe plusieurs causes ultimes de la phénologie de l’hibernation. La pénurie énergétique est probablement un facteur qui explique une partie de la durée de l’hibernation chez de nombreuses espèces hibernantes. Tandis que le moments précis de l’immergence et de l’émergence de l’hibernation semblent être la résultante d’un compromis entre les bénéfices pour la survie d’être en hibernation (la réduction du risque de mortalité) et les bénéfices d’être actifs pour la reproduction. Comme proposé par Ruf et al. (2012), l'hibernation peut être considérée comme une stratégie employée pour augmenter la survie lorsque les conditions environnementales ne menacent pas directement la vie, mais qui sont sous-optimales pour la reproduction. D'un point de vue physiologique, l’hibernation doit être expliquée par une approche globale « coûts/bénéfices » (Willis, 2017), combinant au moins deux compromis majeurs. Le premier compromis entre les bénéfices pour la survie et la reproduction (présenté ci-dessus), devrait être un bon indicateur du temps passé dans l’hibernacula (lieu de l’hibernation) et donc du début et de la fin de l’hibernation. Le second compromis se déroule une fois que les hibernants sont isolés des conditions environnementales dans l’hibernacula avec une quantité donnée de réserves énergétiques. Les profils d’hibernation (nombre, durée et profondeur des torpeurs) seraient expliqués par un compromis entre les coûts et les bénéfices de la torpeur (Humphries et al., 2003a). Les recherches doivent se poursuivre pour vérifier l’existence d'autres compromis.

B. Perspectives des études sur les causes évolutives de l’hibernation

1. La différence entre les sexes dans la phénologie de l’hibernation

Pour tester la validité de l’hypothèse du compromis, il serait intéressant d’étudier des hibernants montrant des caractéristiques de reproduction différentes de ceux étudiés. Par exemple, chez les chauves-souris des régions tempérées, l'accouplement a lieu juste avant l'hibernation, les femelles stockent les spermatozoïdes pendant l'hiver et l'ovulation a lieu peu après l'émergence (Buchanan, 1987). Chez le vespertilion brun (*Myotis lucifugus*), les mâles immergent après les femelles probablement pour augmenter les opportunités d'accouplement et recouvrer la perte de masse corporelle subie pendant l'accouplement (Norquay and Willis, 2014). Par contre, les femelles émergent en premier, probablement parce qu'une mise bas précoce augmente la survie des juvéniles. Ces relations sont cohérentes avec l'hypothèse du compromis mais une étude comparative entre espèces de chauves-souris serait nécessaire pour le confirmer. Un autre exemple est le Chirogale moyen (*Cheirogaleus medius*) qui est une espèce d’hibernant monogame (Fietz, 1999) contrairement aux espèces étudiées jusqu’à présent qui sont majoritairement polygynes. D’après l’hypothèse du compromis, peu de variation entre les sexes dans la phénologie de l’hibernation est attendue du fait d’une faible compétition entre mâles et d’un partage plus équilibré des soins aux jeunes.

2. La prédation comme cause ultime

La relation entre la phénologie de l’hibernation et le risque de prédation reste à être testée avec des données empiriques. Pour cela il serait possible de s’inspirer de l’étude de

Karels et al. (2000) visant à étudier les effets interactifs de la nourriture et de la prédation sur la reproduction et la survie hivernale des écureuils terrestres arctiques (*Urocitellus parryii*). Dans cette étude, les auteurs ont comparé des zones contrôles à des zones expérimentales avec exclusion de prédateur et/ou addition de nourriture dans la zone. Il serait donc intéressant de conduire une étude similaire associée à un suivi précis de la phénologie de l'hibernation, de l'investissement reproducteur et de la valeur sélective. Cela permettrait de confronter dans une même étude, les hypothèses de pénurie énergétique et du compromis entre survie et reproduction pour expliquer les causes ultimes de la phénologie de l'hibernation. Cette étude nécessite de conduire un suivi au long terme afin de valider ces facteurs comme causes ultimes de la phénologie de l'hibernation. Pour cela, il faut déterminer quel(s) paramètre(s) influence(nt) la valeur sélective des individus au moment du début et de la fin de l'hibernation. Au contraire, une réponse à court terme pourrait suggérer que le risque de prédation soit une cause proximale de la phénologie d'hibernation. L'exclusion des prédateurs nécessite cependant des moyens importants ; une alternative serait de manipuler la perception de la prédation en modifiant par exemple le couvert végétal comme cela a été fait pour tester l'effet de la prédation sur les torpeurs journalières (Turbill and Stojanovski, 2018).

D'autres paramètres devraient être explorés pour mieux comprendre l'effet de la prédation sur la phénologie de l'hibernation. Pour commencer, le bénéfice pour la survie d'être en hibernation devrait augmenter avec le risque de prédation. Néanmoins, cette relation pourrait être plus complexe et dépendre de la stratégie d'histoire de vie de l'espèce. En effet, d'après la théorie du « rythme de vie » (Réale et al., 2009), les espèces avec une stratégie d'histoire de vie lente adoptent une stratégie averse au risque en privilégiant les bénéfices pour la survie aux dépens de la reproduction. De ce fait, les espèces à stratégie lente pourraient avoir tendance à rentrer en hibernation dès lors que les conditions ne sont plus optimales pour la reproduction, et ceci d'autant plus tôt que le risque de prédation est important. Par exemple, le loir, qui est une espèce située à l'extrême lent du continuum (longévité maximale jusqu'à 13 ans pour seulement 125g en moyenne), semble particulièrement enclin à éviter le risque de prédation en rentrant en hibernation prolongée alors qu'il n'y a pas de contrainte énergétique. Au contraire une espèce avec une stratégie rapide comme le hamster commun (une longévité maximale de 3,6 années en captivité pour une masse de 500g) devrait plutôt favoriser le fait de rester actif et d'augmenter le temps passé à se reproduire malgré les risques. Il serait donc intéressant de tester à l'échelle interspécifique (à l'aide de modèles phylogénétiques) l'effet du risque de prédation sur la durée de l'hibernation en prenant en compte la stratégie d'histoire de vie des espèces.

3. La compétition comme cause ultime

Jusqu'à présent, l'hypothèse du compromis s'est principalement focalisée sur la diminution du risque de prédation pendant l'hibernation. Néanmoins de rares études proposent que l'hibernation limiterait la compétition intraspécifique (Clark, 1977; Yeaton, 1972). Cette hypothèse provient du fait que chez un grand nombre d'espèces, les adultes rentrent en hibernation quelques semaines à plusieurs mois avant les juvéniles (Knopf and Balph, 1977; Michener, 1992; Millesi et al., 1999; Murie, 1973). Il a donc été proposé que l'immergence précoce des adultes permettrait d'augmenter directement la disponibilité alimentaire pour les jeunes ou indirectement en libérant des territoires défendus par des adultes. Néanmoins, deux arguments semblent réfuter cette hypothèse (Michener, 1984) : (1) La sélection naturelle opère à l'échelle individuelle. Ainsi, pour qu'un tel phénomène évolue, il faudrait que l'immergence précoce des adultes augmente la survie de leur propre descendance. Cependant, seuls les juvéniles des espèces d'hibernants sociaux comme les marmottes partagent le même territoire que leurs parents, et elles ne montrent que peu de différences de date d'immergence entre les adultes et les juvéniles (Armitage, 1991). (2) Chez certaines espèces, l'immergence précoce des mâles ne pourrait avoir qu'un effet très limité sur la baisse de la compétition. Un cas extrême est celui des spermophiles de Richardson (*Urocitellus richardsonii*) où les mâles immergent jusqu'à 2 mois avant les juvéniles. Au moment de l'immergence au début de l'été, la disponibilité en nourriture est considérée « non limitante » et les mâles ne représentent qu'une petite proportion de la population (parfois 7 mâles adultes pour 493 juvéniles ; Michener, 1984). Il est donc peu probable que la phénologie de l'hibernation soit expliquée par la réduction de la compétition intraspécifique du moins dans le cadre spécifique des différences entre adultes et juvéniles.

Cette hypothèse, souligne néanmoins la complexité de mesurer la disponibilité alimentaire pour un individu dans son environnement, une mesure pourtant importante pour l'hypothèse de la balance énergétique. En effet, la disponibilité alimentaire « réelle/effective » pour un individu doit tenir compte à la fois de la pression de compétition directe, *i.e.*, le nombre d'individus sur une surface donnée, et indirecte, *i.e.*, la nourriture défendue par un individu.

C. Ouverture à la dormance des ectothermes

La dormance saisonnière (terme générique pour qualifier tout type de stratégie de « vie ralentie ») permet à de nombreuses espèces à travers l'arbre du vivant de rester cachées pendant plusieurs mois dans des endroits protégés (Wilsterman et al., 2021). Cette similitude entre espèces parfois très éloignées phylogénétiquement pourrait suggérer l'existence de causes et conséquences évolutives communes à la dormance. Pourtant l'étude de la dormance saisonnière a longtemps été séparée entre groupes phylogénétique, limitant la possibilité de faire des généralités. Il y a notamment une séparation importante dans la littérature entre l'étude de la dormance des ectothermes et des endothermes du fait de différences physiologiques dans la capacité de thermorégulation. Une étude récente a néanmoins montré que des similitudes physiologiques et chronobiologiques permettaient de regrouper les différents types de dormance animale en plusieurs catégories, indépendamment de leur lien phylogénétique (Wilsterman et al., 2021). Le chapitre 2 de cette thèse s'intègre dans ce contexte en testant l'hypothèse de causes évolutives communes dans la phénologie de la dormance entre espèces endothermes et ectothermes. La dormance des ectothermes a pendant longtemps été vue comme une simple phase d'inactivité passive induite par le froid du fait de leur capacité limitée à thermoréguler physiologiquement par rapport aux endothermes (Gregory, 1982; Mayhew, 1965). Au contraire, cette revue de la littérature suggère que les ectothermes ont des capacités de thermorégulation comportementale et/ou des capacités physiologiques suffisantes pour entrer en dormance dans des situations thermiques très diverses en exploitant les opportunités que leur offre leur environnement. De plus, nous avons compilé des faisceaux d'indices chez des taxons très éloignés phylogénétiquement qui suggèrent que la dormance des ectothermes pourrait aussi être expliquée par une réduction du risque de mortalité extrinsèque. Ainsi le compromis entre survie et reproduction qui explique la phénologie de l'hibernation pourrait aussi s'appliquer à la dormance des ectothermes. De plus, certains facteurs responsables de la différence entre les sexes dans la phénologie de l'hibernation sont communs à la dormance des endothermes et ectothermes. L'hypothèse développée par Ruf *et al.* (2012) selon laquelle l'hibernation permettrait d'augmenter la survie lorsque les conditions sont peu favorables à la reproduction, pourrait donc aussi s'appliquer à la dormance de certains ectothermes.

Élargir l'étude des causes évolutives de la dormance aux espèces ectothermes permettrait de : (1) tester la robustesse des hypothèses présentées sur un panel plus diversifié de situations. Par exemple, contrairement aux espèces hibernantes, chez certains insectes ce sont les femelles qui émergent en premier. Il semblerait que ce phénomène puisse être expliqué par le fait que chez ces espèces, le dernier individu mâle à s'accoupler a plus de chances de féconder les œufs que les autres individus (Kawakami et al., 2017; Van Timmerman et al., 2001). Ainsi, les mâles retarderaient leur émergence après les femelles pour favoriser leur succès reproducteur, en accord avec l'hypothèse du compromis entre survie et reproduction proposée pour expliquer la phénologie de la dormance. (2) L'inclusion des espèces ectothermes permettrait également de profiter des avancées réalisées dans d'autres domaines qui pourraient inspirer l'étude de l'hibernation des mammifères et des oiseaux. Par exemple, chez les invertébrées, plusieurs approches théoriques basées sur les traits d'histoire de vie ou la stratégie de « bet-hedging » ont été largement développées pour comprendre la phénologie de la dormance (Cohen, 1970; Hairston Jr and Munns Jr, 1984; Hopper, 1999; Ji, 2011). (3) Enfin, les études expérimentales sur des espèces ectothermes sont moins contraignantes. Par exemple, certains taxons comme les invertébrés montrent un cycle de vie court ce qui devrait simplifier la mise en place d'études nécessitant un suivi à long terme comme l'étude des causes ultimes de la dormance. De plus, d'un point de vue technique, la petite taille des insectes pourrait faciliter la mise en place des études sur l'effet de la prédation et des contraintes énergétiques en menant un suivi sur de plus petites parcelles.

II. Conséquences évolutives de l'hibernation

A. Intégration des résultats dans le contexte actuel des connaissances

Depuis quelques décennies, il a été montré que les espèces hibernantes ont une longévité plus importante et des traits d'histoire de vie plus lents que les espèces non hibernantes de même taille (Turbill et al., 2013; Wilkinson and South, 2002). Plusieurs hypothèses ont été proposées pour expliquer cet effet. De la même manière que pour les causes évolutives de l'hibernation, l'attention a tout d'abord été portée sur les aspects physiologiques exceptionnels des hibernants pour expliquer leur longévité. Ainsi, la première hypothèse se base sur la théorie « des radicaux libres du vieillissement », et suppose que la réduction drastique du métabolisme pendant l'hibernation, diminue les dommages oxydatifs et augmenterait la longévité (Lyman et al., 1981). De plus, de nombreux mécanismes impliqués dans le processus de vieillissement comme les voies de signalisation de l'insuline sont inhibées pendant les torpeurs (Wu and Storey, 2016). Néanmoins, les torpeurs profondes (à basse température corporelle) seraient associées à d'autres couts physiologiques comme la réduction du système immunitaire ou l'accumulation de déchets métaboliques (compilé par in Humphries et al., 2003). Ainsi, il a été montré chez de nombreuses espèces que les individus ayant suffisamment de réserves énergétiques limitent les torpeurs profondes malgré un coût énergétique plus important (hypothèse de l'optimisation des torpeurs ; Humphries et al., 2003). En réponse à ce constat, il a été proposé que les hibernants investissent davantage dans la maintenance somatique que les espèces non hibernantes de même taille. Il a d'abord été proposé qu'un changement d'allocation d'énergie de la croissance et de la reproduction vers la maintenance somatique pendant l'hibernation pourrait être une réponse adaptative à la pénurie en ressources alimentaires pendant cette période (Humphries et al., 2003). En accord avec cette hypothèse, la croissance et la reproduction sont inhibées pendant les torpeurs. Cependant, quelques exceptions dérogent à cette règle puisque certaines chauves-souris, ainsi que les échidnés et les ours maintiennent une activité de reproduction au cours de l'hibernation (McAllan and Geiser, 2014; Wilsterman et al., 2021). Enfin, d'après la théorie des traits d'histoire de vie, une réduction du risque de mortalité extrinsèque pendant l'hibernation est susceptible de favoriser l'évolution d'un investissement dans la maintenance plus importante que chez les espèces non hibernantes de même taille (Ruf et al., 2012). D'après cette hypothèse, la longévité importante des hibernants serait indépendante des conditions physiologiques pendant l'hibernation contrairement aux deux autres hypothèses. A ce jour, aucune de ces hypothèses ne fait consensus.

L'une des prédictions communes à ces hypothèses, est que l'augmentation de la durée de l'hibernation devrait s'accompagner d'une augmentation de la longévité. Nous avons donc vérifié cette prédiction dans **le chapitre 1** à partir d'une analyse phylogénétique comparée prenant en compte 82 espèces hibernantes très diverses sur le plan géographique et phylogénétique. L'effet de la durée d'hibernation est inférieur à celui de la masse, du style de vie arboricole ou aérien (pour les chauves-souris). Mais de manière intéressante, cet effet est plus important chez les espèces de petite taille inférieure à 1,5 kg et en particulier chez les chauves-souris. En effet les espèces de petite taille sont davantage soumises à la prédation (Cohen et al., 1993) et à un stress oxydatif potentiellement plus important (métabolisme relatif à la taille plus important, Speakman, 2005). L'ensemble de ces résultats semble donc en accord avec les hypothèses présentées mais nécessite des investigations plus précises pour les conforter.

Nous avons donc réalisé, **dans le chapitre 3**, une étude expérimentale visant à tester les hypothèses sur la longévité des hibernants chez 50 jeunes femelles hamster commun, un hibernant « foodstoring ». Dans cette étude, la longueur relative des télomères (RTL) et sa variation ont été utilisées comme biomarqueur du vieillissement. En accord avec l'hypothèse de la réduction du métabolisme, les résultats montrent que l'augmentation du temps total passé en torpeur est le facteur le plus important pour expliquer l'élongation des télomères pendant la période d'hibernation, ce qui suggère que le faible taux métabolique pendant l'hibernation ralentit le vieillissement, en particulier avec une température corporelle élevée en torpeur. Par ailleurs, en accord avec l'hypothèse de la maintenance pendant l'hibernation, il semblerait que l'effet positif du temps passé en torpeur sur la RTL (avec une élongation chez certains individus) puisse être expliqué par un ralentissement de la croissance pendant cette période. Cela suggère une redirection de l'énergie allouée à la croissance et probablement à la reproduction vers la maintenance somatique. Néanmoins, nous n'avons pas observé de différence dans les changements de RTL entre la période active et l'hibernation. De plus, l'investissement dans la maintenance semble être limité et soumis à un compromis d'allocation dans le temps de tel sorte qu'une élongation de la RTL pendant l'hibernation conduit à une érosion de la RTL pendant la saison active (et inversement pour une érosion pendant l'hibernation). En accord avec la théorie des traits d'histoire de vie, ces résultats pourraient soutenir l'hypothèse d'un investissement important dans la maintenance au cours de l'année favorisé par une réduction des risques de mortalité extrinsèque. Ces résultats montrent **une possible influence des trois hypothèses pour expliquer la plus grande longévité des hibernants**.

Ensuite dans **le chapitre 4**, en vue d'un élargissement de notre compréhension des conséquences de l'hibernation sur la valeur sélective, nous avons étudié comment les bénéfices de survie associés à une longue hibernation s'intègrent dans l'histoire de vie des individus. La phénologie de l'hibernation étant soumise à un compromis entre survie et reproduction, elle est susceptible de covarier avec d'autres traits biologiques présentant le même compromis. Nous avons donc testé l'intégration de la phénologie de l'hibernation dans le contexte du « rythme de vie ». Nous avions prédit que les individus ayant une longue hibernation présenteraient une croissance lente, un faible investissement dans la reproduction, une faible érosion de la RTL et un comportement averse au risque. Cependant, les résultats obtenus ne soutiennent pas cette prédiction mais montrent plutôt une covariation de l'hibernation avec un POLS plus rapide. En effet, une hibernation longue et profonde est associée à une croissance rapide, une érosion plus importante de la RTL, davantage de comportement exploratoire, une descendance plus grande (bien que non significatif, mais inclus dans le meilleur modèle) avec une faible masse corporelle à la naissance. À l'échelle individuelle, une hibernation longue et profonde serait le résultat d'un manque de masse grasse avant l'hibernation conduisant à une diminution de la probabilité de survie future. Une faible probabilité de survie dans le futur est justement supposée favoriser le développement d'un POLS plus rapide. Nous proposons que l'hibernation chez le hamster commun **ne puisse pas être intégrée dans le POLS** car son expression ne s'explique pas par un compromis entre reproduction et survie. Néanmoins, elle peut être **un indicateur du POLS à l'échelle individuelle** en reflétant les chances de survie future.

Ces études montrent qu'il est important de ne pas tirer de conclusion à l'échelle individuelle à partir de résultats obtenus à d'autres échelles (populations, espèces). Cette erreur de raisonnement s'appelle « l'erreur écologique » (Robinson, 2009). En effet, j'ai montré dans cette thèse que l'augmentation de la durée de l'hibernation entre espèces était associée à une longévité plus importante. Mais contrairement à ces résultats, chez le hamster commun, l'augmentation de la durée de l'hibernation entre individus semble plutôt être associée à des traits d'histoire de vie rapides. De plus, le compromis entre survie et reproduction explicatif de la phénologie de l'hibernation mis en évidence à l'échelle des espèces, ne semble pas permettre d'expliquer la durée de l'hibernation à l'échelle individuelle chez le hamster commun.

Enfin, ces deux études des conséquences évolutives de l'hibernation à l'échelle individuelle se sont basées sur la longueur des télomères comme biomarqueur du vieillissement. Des précautions quant à cette utilisation des télomères ont déjà été évoquées dans une étude montrant des résultats contrastés de l'effet de l'hibernation sur la longueur des télomères mesurés dans différents tissus chez des spermophiles (Wilbur et al., 2019). Par ailleurs, il a été montré que certaines espèces saisonnières y compris des hibernants étaient capables d'allonger leurs télomères au cours de l'année (Criscuolo et al., 2020; Fairlie et al., 2016; Haussmann et al., 2003; Hoelzl et al., 2016a; Olsson et al., 2018) voire au cours de leur vie (Hoelzl et al., 2016b; Tissier et al., 2021). Pourtant, jusqu'à ce jour aucune étude n'a été menée pour vérifier la validation de la longueur des télomères comme biomarqueur du vieillissement. D'autant plus que les résultats de deux études montrent des effets potentiellement contradictoires de l'effet du temps passé en torpeur sur la RTL. Néanmoins, ces deux études sont difficilement comparables car elles ne présentent pas le même environnement photopériodique et de température (influençant les profils d'hibernation). Cela pourrait donc supposer une influence complexe de cet environnement pour expliquer l'effet de l'hibernation sur la RTL.

Dans une étude longitudinale à long terme, présentée dans le **chapitre 5**, nous avons souhaité vérifier la validité de l’utilisation des télomères comme biomarqueur du vieillissement chez le hamster commun. Nous avons constaté une érosion de la RTL des hamsters pendant l’hibernation qui s’accélère au cours de la vie des individus. Cet effet de l’âge dépend de la période de l'année et s'ajoute à une dynamique saisonnière de la RTL. Après avoir pris en compte l'effet de l'âge sur les télomères, il apparaît que la RTL et leur variation sont peu répétables et ne permettent pas de prédire la durée de vie restante. Il semblerait donc qu’en plus de l'effet saisonnier et de l'âge, il existe une variation importante et non expliquée de la RTL au cours du temps qui empêche l'établissement de l'âge biologique d'un individu. Cependant, lorsque les télomères atteignent une longueur critique, les chances de mourir l'année suivante augmentent considérablement. Les télomères chez le hamster réunissent donc certaines caractéristiques utiles pour un biomarqueur du vieillissement comme **leurs variations avec l’âge chronologique, une sensibilité aux évènements stressants** (variations saisonnières des télomères) et **une capacité à prédire la vie restante à très court terme** (en moyenne 6 mois avant la mort). Néanmoins, ils ne **permettent pas de caractériser l’âge biologique entre des individus de même âge** ce qui limite leur utilisation à des questions spécifiques. Par exemple, l’utilisation des télomères pourrait se révéler peu pertinente pour tester l'impact sur la survie de l'investissement reproducteur ou des profils d'hibernation. Les résultats de cette thèse, obtenus à partir de l’analyse des télomères, devront être pris avec précaution et comparés à d’autres études employant d’autres méthodes d’analyse du vieillissement comme la méthylation de l'ADN (Jylhävä et al., 2017).

B. Perspectives sur les conséquences évolutives de l'hibernation

Un élément à prendre en compte qui pourrait limiter la généralisation des résultats de cette thèse aux autres hibernants est la faible longévité du hamster commun. En effet, le hamster commun ne semble pas être une espèce particulièrement longévive par rapport aux espèces non hibernantes de même taille. Le hamster commun a une longévité maximale de 3,6 années en captivité pour une masse de 500 g comparé au surmulot (*Rattus norvegicus*) qui vit 3,8 années pour 300 g (Magalhães and Costa, 2009). Le hamster pourrait ne pas disposer des caractères explicatifs de la longévité des hibernants. Pour vérifier la généralisation des résultats aux espèces d'hibernants longévifs, il serait donc intéressant de tester si, dans des conditions de laboratoire identiques, les hibernants (*e.g.*, hamster commun, loir gris) présentent une capacité de maintenance plus importante que les espèces non hibernantes de même taille (*e.g.*, surmulot, Écureuil roux (*Sciurus vulgaris*)), et si la différence de capacité de maintenance explique les différences de longévité entre hibernants. De la même manière, il pourrait être intéressant de comparer cette capacité de maintenance avec la durée d'hibernation des espèces en milieu naturel pour vérifier l'hypothèse d'un lien évolutif entre la maintenance et la diminution de la mortalité extrinsèque au cours de l'hibernation.

Depuis plusieurs années, les avancées dans le domaine de la biologie moléculaire ont permis de proposer de nombreux biomarqueurs du vieillissement (Jylhävä et al., 2017). Parmi ces biomarqueurs, la méthylation de l'ADN (ADNm) est considérée par certaines études comme le meilleur prédicteur actuel de l'âge biologique (état physiologique de l'organisme ; Jylhävä et al., 2017). La méthylation de l'ADN est un mécanisme moléculaire lors duquel des groupes méthyles se fixe sur des gènes, en particulier les cytosines des sites cytosine-phosphate-guanine, empêchant leur expression (Xiao et al., 2019). Ce mécanisme se produit lors du fonctionnement normal de l'organisme en permettant une régulation de l'expression des gènes. Mais avec le vieillissement, une hyperméthylation ou une hypométhylation de certains gènes (*e.g.*, les répétitions dispersées, les gènes ribosomaux) est observée et permet de mesurer l'âge biologique (Xiao et al., 2019). Plusieurs éléments suggèrent que la méthylation de l'ADN est un bon biomarqueur comme le fait qu'elle : (1) soit corrélée à la longévité à l'échelle individuelle et entre espèces (2) s'accélère avec des facteurs de stress comme les maladies liées à l'âge et (3) est ralentie par les facteurs connus prolongeant la survie (Horvath, 2013; Pinho et al., 2021; Xiao et al., 2019). Plusieurs mesures dérivées de l'analyse de l'ADNm comme l'horloge épigénétique ou le « pacemaker » épigénétique peuvent être utilisés comme biomarqueurs (Pinho et al., 2021).

Des études récentes se sont penchées sur l'effet de l'hibernation sur l'ADNm de deux espèces hibernantes, la marmotte à ventre jaune (*Marmota flaviventris*) et la Sérotine brune (*Eptesicus fuscus*). Les résultats montrent un ralentissement de l'ADNm pendant la période d'hibernation par rapport à la période active (Pinho et al., 2021; Sullivan et al., 2022). Contrairement à cette thèse, ces études supposent un effet spécifique des conditions physiologiques au cours de l'hibernation sur le vieillissement sans pouvoir expliquer les détails de cette influence. Ces recherches récentes et prometteuses doivent donc se poursuivre pour discriminer les hypothèses sur les facteurs explicatifs de la longévité des hibernants. Comme nous l'avons fait pour les télomères, il est important de tester la validité de l'ADNm comme biomarqueur du vieillissement biologique des hibernants, par exemple, en évaluant si l'ADNm permet de prédire le temps de vie restant des individus et tester l'influence de l'hibernation sur ce paramètre. Les premiers résultats semblent tout de même encourageants puisque l'ADNm n'est pas constante au cours du temps et montre un changement plus rapide en début de vie, ce qui suggère une sensibilité à des facteurs responsables du vieillissement biologique (Pinho et al., 2021).

C. Ouverture aux conséquences évolutives de la dormance des ectothermes

Étonnamment, très peu d'études ont vérifié les conséquences évolutives de la dormance des ectothermes sur leur longévité (Axelsson et al., 2020; Burraco et al., 2020; Hoekstra et al., 2020). Bien que la dormance des ectothermes soit différente d'un point de vue physiologique, les 3 hypothèses formulées pour expliquer la longévité des hibernants sont susceptibles de s'appliquer aussi aux espèces ectothermes. 1) En effet, une réduction du métabolisme est aussi observée pendant l'hibernation des ectothermes parfois même de façon active (Wilsterman et al., 2021), pouvant ainsi réduire les dommages oxydatifs. Néanmoins, des phases de réchauffement ont été découvertes chez plusieurs ectothermes (poisson : Campbell et al., 2008; insecte : Crozier, 1979; reptile : Rismiller and McKelvey, 2000) pouvant limiter les bénéfices de l'hypométabolisme. (2) Tout comme les hibernants, les ectothermes montrent une réduction de la reproduction et de la croissance au cours de la dormance, ce qui pourrait laisser supposer une redirection de l'énergie vers la maintenance somatique (Garstka et al., 1982; Sinsch et al., 2007; Wilsterman et al., 2021), bien que des exceptions existent (Loumbourdis and Kyriakopoulou-Sklavounou, 1996). (3) Enfin, il a aussi été mis en évidence une réduction de la prédation au cours de la dormance de certains ectothermes (Blouin-Demers et al., 2000; Ji, 2011; Kroon et al., 2008; Slusarczyk, 1995) pouvant favoriser l'évolution d'une capacité de maintenance plus importante que pour d'autres espèces non dormantes de même taille. D'ailleurs, la capacité à allonger les télomères ou l'activité de la télomèrase a déjà été mise en évidence chez plusieurs espèces ectothermes (Axelsson et al., 2020; Burraco et al., 2020; Fitzpatrick et al., 2021; McLennan et al., 2018).

Ces exemples montrent le potentiel important des études rassemblant ectothermes et endothermes pour améliorer notre compréhension des causes et conséquences de la phénologie de la dormance.

D. Ouverture aux sciences de l’espace

L’hibernation a pendant longtemps été dans l’imaginaire de la science-fiction comme un moyen de suspendre le vieillissement notamment pour les vols spatiaux. En réalité, des recherches scientifiques se sont penchées sur la faisabilité d’appliquer ce phénomène chez les hommes depuis longtemps (Cockett and Beehler, 1962; Hock, 1960). Mais c’est seulement récemment qu’elles sont devenues plus réalistes grâce à des méthodes qui ont permis d’induire un état de torpeur (appelé « torpeur synthétique ») chez des espèces non hibernantes comme le rat et la souris (Cerri et al., 2013; Shi et al., 2021; Tupone et al., 2013). L’hibernation est supposée être intéressante pour le voyage à long terme parce qu’elle permettrait de diminuer la quantité de nourriture et d’eau à emporter dans les vaisseaux et prolonger l’espérance de vie. Ainsi, les sciences spatiales s’intéressent particulièrement aux études sur le vieillissement des hibernants (Cerri et al., 2021). En effet, selon les hypothèses explicatives de la longévité des hibernants, les applications techniques pour les voyages spatiaux ne seront pas les mêmes. Par exemple, si la longévité des hibernants est expliquée par l’hypothèse d’un investissement plus important dans la maintenance associé à une réduction de la mortalité extrinsèque ou la pénurie de ressource pendant l’hibernation, alors ce n’est pas une mise en « torpeur synthétique » des hommes qui permettra de prolonger la survie contrairement à l'hypothèse de la réduction du métabolisme. Mieux comprendre le rôle des phases de réchauffement pendant l'hibernation est aussi primordial pour une application à l'être humain étant donné leur coût physiologique et énergétique (Cerri et al., 2021). Il est donc probable que la recherche spatiale et médicale s'intéresse de plus en plus au cas des hibernants et des espèces dormantes de manière générale.

III. Application aux changements globaux

A. Contribution aux approches évolutives des changements de phénologie

L'une des réponses de la biodiversité aux changements globaux est le changement de phénologie avec des conséquences potentielles pour la valeur sélective des individus, la dynamique des populations et les écosystèmes. Un changement de phénologie ne permet pas de savoir si une population s'adapte, ni de prédire les conséquences de ce changement. Pour répondre à ces questions, il est nécessaire de développer des approches évolutives. Dans l'introduction de cette thèse, trois approches ont été présentées pour mieux comprendre les causes et conséquences évolutives de la phénologie. Ces approches ont été une base sur laquelle la thèse s'est construite. Cette partie de la discussion présente les contributions des différents chapitres de cette thèse aux approches évolutives présentées dans l'introduction.

Au cours de l'année, certains organismes partagent leur temps entre des activités qui impactent fortement la survie, comme la reproduction (forte mortalité) et des activités qui l'impactent moins, comme la dormance et la migration (faible mortalité). Des changements de phénologie entre ces activités pourraient donc affecter la survie annuelle et l'histoire de vie de ces espèces (approche de survie annuelle). Jusqu'à présent, aucune étude sur un large échantillon d’espèces n’avait permis de tester si la phénologie de la dormance ou de la migration jouait un rôle clé sur la survie ou la longévité de ces organismes. Récemment, il a été montré chez 45 espèces migratrices, que les espèces qui migraient sur une longue distance avaient une survie annuelle plus importante (Winger and Pegan, 2021). Un départ précoce pour la halte migratoire et un retour tardif sur le lieu de reproduction augmenteraient donc la survie. En comparant 82 espèces hibernantes, nous avons montré que l’augmentation de la durée de l’hibernation était associée à une longévité plus importante. De plus, des indices exposés dans le **chapitre 2** supposent un effet similaire pour la dormance des espèces ectothermes. Ainsi, ces résultats montrent que **les changements de phénologie d’autres activités que la reproduction (majoritairement étudiée) peut avoir des conséquences importantes sur l’histoire de vie chez de nombreux organismes**.

Une autre approche importante à considérer est la diversité des causes ultimes qui peuvent expliquer la phénologie d’une activité (approche des communautés). La disponibilité alimentaire est probablement un des facteurs majeurs explicatifs de la phénologie de nombreuses activités mais d’autres interactions interspécifiques existent et doivent être prises en compte (Lindén, 2018; Nakazawa and Doi, 2012). Dans les **chapitres 1 et 2**, nous avons mis en évidence des faisceaux d’indices qui suggèrent que le risque de mortalité extrinsèque tel que la prédation ou la compétition pourrait influencer la phénologie de la dormance des espèces endothermes et ectothermes. Ces résultats confirment **l’importance des relations interspécifiques agonistiques pour expliquer la phénologie des activités**. Des effets similaires devraient être observés entre espèces ayant des relations bénéfiques (*e.g.*, mutualisme, coopération, et symbiose). D’un point de vue plus global, l’étude de la phénologie nécessite son intégration dans le fonctionnement des écosystèmes.

La dernière approche présentée, suppose que de la même manière qu'il existe un compromis dans l'allocation d'énergie entre les traits d'histoire de vie, la phénologie pourrait être soumise à un compromis d'allocation du temps entre différentes activités (approche compromis). Ainsi, il a été montré que les espèces migratrices longue distance passaient moins de temps sur le site de reproduction et réduisaient leur investissement annuel dans la reproduction (Winger and Pegan, 2021). Dans le **chapitre 2**, nous avons montré chez plus d'une vingtaine d'espèces hibernantes, que le sexe qui investit le plus de temps dans la reproduction passait moins de temps en hibernation. Ce compromis semble aussi expliquer la variation de la phénologie à d'autres échelles ainsi que la phénologie de la dormance des ectothermes. **La phénologie d'activités associées à des composantes concurrentielles de la valeur sélective semble donc être expliquée par un compromis d'allocation du temps**.

A une autre échelle, le compromis dans l'allocation du temps entre différentes activités pourrait expliquer le maintien de différences interindividuelles dans la phénologie. La phénologie d'une activité soumise à un tel compromis est supposée s'intégrer dans le concept du POLS. Il a été montré chez une espèce d'oiseaux et de poissons que la phénologie de la reproduction et de la migration covariait avec le caractère plus ou moins exploratoire et audacieux des individus (Abbey-Lee and Dingemanse, 2019; Chapman et al., 2011). Dans **le chapitre 4**, nous avons donc testé l'intégration de l'hibernation dans le POLS chez une espèce hibernante. Les résultats montrent que **la phénologie de l'hibernation ne semble pas pouvoir s'intégrer dans le POLS** du hamster commun car son expression ne s'explique pas par un compromis entre survie et reproduction mais serait plutôt **un bon indicateur de la place de l'individu sur le continuum lent-rapide**. Malgré le rejet de l'hypothèse, l'approche utilisée doit encourager à développer d'autres études sur le lien entre phénologie et POLS.

B. Changement climatique et phénologie de l'hibernation

1. Préambule

L'un des effets principaux du changement climatique est la hausse rapide et globale des températures environnementales. Une récente étude a réalisé un état des lieux des effets du réchauffement climatique sur les traits d'histoire de vie et la phénologie des hibernants (Wells et al., 2022). Une réduction de la durée de l'hibernation est globalement observée bien qu'il y ait des exceptions. De plus, le réchauffement de la température associé à une augmentation de la durée de la saison active a souvent un effet positif sur la reproduction. Au contraire, la hausse des températures influence la survie de manière plus complexe, avec à la fois des effets positifs, négatifs ou neutre. Dans la suite de cette partie, les causes de ces changements et de leurs conséquences sur la valeur sélective sont discutés au regard des résultats obtenus dans cette thèse

2. Causes évolutives et changement de phénologie

Sur la base des résultats de cette thèse, il est possible de faire des prédictions sur l'évolution de la phénologie de l'hibernation à long terme. Nous avons vu précédemment que l'expression de l'hibernation pouvait être expliquée par deux compromis principaux. Le premier entre la survie et la reproduction est supposé expliquer la phénologie de l'hibernation. Le second entre les coûts et bénéfices des torpeurs est supposé expliquer les profils d'hibernation. La sélection naturelle devrait favoriser une expression de l'hibernation qui optimise ces deux compromis. Si la hausse des températures s'accompagne d'un allongement de la saison favorable à la reproduction alors la durée de l'hibernation pourrait être diminuée pour favoriser la reproduction. Cependant, la stratégie d'histoire de vie des espèces pourrait jouer un rôle dans la réponse observée de telle façon que les espèces à stratégie d'histoire de vie rapide (plus opportunistes) seraient favorisées par les nouvelles opportunités de reproduction comparativement aux espèces à stratégie d'histoire de vie lente. La hausse de la température ambiante est susceptible d'augmenter la consommation énergétique au cours de l'hibernation, ce qui pourrait potentiellement affecter la survie des individus au cours de l'hiver (si pas suffisamment de nourriture et/ou de nutriments essentiels). Dans ce cas de figure, la sélection naturelle pourrait favoriser une réduction de la durée de l'hibernation. Néanmoins, des adaptations comportementales pourraient aussi atténuer ces effets comme le fait de creuser un terrier offrant un microclimat optimal (Goldberg and Conway, 2021).

Cette thèse permet aussi de mieux comprendre les réponses à court terme des hibernants. Par exemple, **le chapitre 2** suggère que la phénologie de l'hibernation est liée à la variation de la masse corporelle au cours de la saison active, en particulier pour les mâles. Bien que ces cycles aient une composante endogène chez les espèces saisonnières (John, 2005), les conditions environnementales peuvent jouer un rôle important dans l'ampleur des changements saisonniers de la masse corporelle. Les variations interannuelles de la disponibilité de la nourriture et des sécheresses, qui devraient être exacerbées par le changement climatique (Trenberth et al., 2014), montrent des effets variés sur la phénologie qui peuvent être expliqués par le compromis entre reproduction et survie. Pour certaines espèces, les années où la disponibilité alimentaire est réduite sont associées à une immergence précoce (Kawamichi, 1996) qui peut être encore plus précoce lorsque la reproduction est avortée (Hoelzl et al., 2015; Munro et al., 2008). Mais une faible disponibilité alimentaire peut également conduire à une immergence plus tardive (Alcorn, 1940; Harris and

Leitner, 2004; O’Farrell et al., 1975) en retardant probablement l'accumulation des réserves. Ceci contredit l'idée que la durée d'hibernation devrait nécessairement augmenter avec les contraintes énergétiques. Chez *Urocitellus mollis* (le spermophile de Piute), les années pauvres en nourriture peuvent entraîner soit un retard (Alcorn, 1940), soit une immergence précoce lorsque la reproduction est avortée (Smith and Johnson, 1985). D’une part, ces observations suggèrent l’existence d’un lien complexe entre les conditions environnementales, la reproduction et la variation de la masse corporelle, qui permettrait d’expliquer l’immergence. D'autre part, elles indiquent une plasticité dans la phénologie de certains hibernants obligatoires en réponse aux variations environnementales. Cette réponse plastique laisserait envisager une vulnérabilité moins importante de certains hibernants obligatoires aux changements globaux que précédemment proposée (Geiser and Turbill, 2009).

Si la diminution de la durée d’hibernation avec la hausse des températures se poursuit, il est légitime de se demander si elle pourrait conduire à un arrêt total de l’expression de l’hibernation. En se basant sur la méthode de « substitution du temps par l’espace » alors les prédictons supposent que l’hibernation pourrait disparaitre. En effet, certaines espèces avec une large répartition géographique montrent à la fois des populations hibernantes (aux latitudes les plus hautes) et des populations non hibernantes (aux latitudes les plus basses, données compilées par (Nevo and Amir, 1964). Il est aussi possible d’observer, au sein d’une même population, un seul groupe d’individus qui hibernent comme par exemple uniquement les adultes (Dobson and Davis, 1986) ou uniquement les femelles (Dobson and Davis, 1986; Dunford, 1974; Holekamp and Nunes, 1989; Karanewsky et al., 2015). Cependant, certaines espèces non holarctiques comme les échidnés ou les chirogales entrent en hibernation pendant plusieurs mois malgré un climat plutôt doux toute l’année (Grigg and Beard, 2000). Enfin, l’évolution vers une étape intermédiaire entre le maintien et l’arrêt de l’hibernation a aussi été proposée en prenant comme exemple des espèces qui, comme le hérisson du désert (*Paraechinus aethiopicus*), pratiquent des torpeurs de plusieurs jours interrompues par des périodes d'activité (Boyles et al., 2017). L'évolution vers des torpeurs journalières est moins probable car les hibernants et les hétérothermes quotidiens sont des groupes fonctionnellement distincts notamment au niveau des mécanismes de la rythmicité des torpeurs (Ruf and Geiser, 2015). L'étude des causes ultimes de la phénologie de l'hibernation chez les espèces mentionnées ci-dessus pourrait permettre de mieux comprendre l'évolution future de l'hibernation. Par ailleurs, le **chapitre 1** a montré une forte influence de la phylogénie pour expliquer la variation de la durée de l'hibernation entre espèces. Ainsi des contraintes évolutives pourraient aussi influencer l'évolution future de l'hibernation.

3. Conséquences évolutives et changement de phénologie

L'augmentation de la survie avec le réchauffement climatique mise en évidence chez certaines espèces dans la revue citée en préambule (Wells et al., 2022), est en contradiction avec les résultats du **chapitre 1 et 2** mais pourrait être plus cohérente avec les résultats obtenus dans le **chapitre 4**. Dans ce chapitre, nous avons mis en évidence que les individus avec une longue hibernation développaient un POLS rapide. Ces individus sont supposés avoir moins de réserves énergétiques avant l'hibernation et donc moins de chances de survie, ce qui les pousse à économiser davantage d'énergie malgré les coûts physiologiques des torpeurs profondes. Si la hausse de la température en hiver conduit à une réduction de la durée de l'hibernation alors les individus ayant habituellement trop peu de réserves pour survivre devraient profiter de cette réduction des contraintes énergétiques. Ainsi à court terme, une survie plus importante chez ces individus pourrait expliquer l'augmentation globale de la survie au sein de la population. Cependant, une diminution de la survie avec la diminution de la durée de l'hibernation pourrait s'avérer exacte sur le long terme si l'augmentation de la période d'activité s'accompagne d'une augmentation du taux de prédation et/ou d'une redirection de l'allocation d'énergie vers la reproduction.

Comme le démontre **le chapitre 3**, il n'existe encore aucun consensus sur les mécanismes expliquant la longévité plus importante des hibernants. Mais quelles que soit les hypothèses proposées, elles supposent toutes globalement une réduction de la longévité avec la hausse des températures et la diminution de la durée de l'hibernation. (1) L'hypothèse de la réduction des dommages oxydatifs : si l'augmentation de la température ambiante conduit à une augmentation de la consommation énergétique au cours de l'hibernation, alors une augmentation des dommages oxydatifs devrait être observée et impacter la survie. Cependant, l'augmentation de la température ambiante pourrait diminuer le delta de température (entre la température corporelle en torpeur et l'euthermie) au moment des phases de réchauffement et donc diminuer le coût des torpeurs (comme démontré dans Nowack et al., 2019). (2) L'hypothèse de l'investissement dans la maintenance pendant l'hibernation : la réduction de la durée d'hibernation devrait réduire la période favorable à un investissement dans la maintenance. De plus, comme nous avons pu le montrer dans le **chapitre 3**, une température corporelle plus élevée en torpeur est associée à un développement de la reproduction plus important, ce qui limite donc la possibilité d'investir dans la maintenance. (3) L'hypothèse de la maintenance au cours de l'année : la diminution de la durée de l'hibernation devrait augmenter le risque de mortalité extrinsèque et diminuer la survie annuelle. À long terme, la sélection naturelle devrait favoriser un investissement plus important dans la reproduction et la croissance que dans la maintenance (Healy et al., 2019).

Short summary

Causes évolutives de la phénologie de l'hibernation (chapitres 1 et 2, figure 8) :

L'hypothèse des contraintes énergétiques suppose un début d'hibernation lorsque la balance énergétique des individus devient négative avec la diminution de la disponibilité alimentaire (figure 8a). La fin de l'hibernation est attendue lorsque la disponibilité alimentaire est suffisante pour maintenir une balance énergétique positive. L'hypothèse du compromis suppose au contraire que les individus débutent l'hibernation pour échapper aux prédateurs lorsque les conditions sont sous-optimales à la reproduction même si la disponibilité alimentaire est suffisante pour maintenir une activité (figure 8a). La fin de l'hibernation est supposée arriver lorsque les conditions sont favorables à la reproduction.

Le compromis entre survie et reproduction mesuré au même moment de l'année est supposé prédire le début de l'hibernation de telle manière que l'espèce ayant un compromis plus équilibré devrait débuter l'hibernation plus tôt (figure 8b). Le début de l'hibernation est supposé arriver lorsque le compromis est plus important pour la survie, et la fin de l'hibernation lorsque le compromis est plus important pour la reproduction.

Le sexe qui passe le plus de temps dans une activité post reproduction est celui qui entre le dernier en hibernation (figure 8c). La reproduction se déroule quelques jours seulement après l'émergence des femelles. Ainsi, les mâles anticipent la sortie des femelles, d'autant plus que leur temps de préparation à la reproduction est long. Pour simplifier la compréhension des schémas, nous n'avons pas intégré la période d'accumulation des réserves avant hibernation. C'est précisément l'accumulation des réserves énergétiques qui est supposée démarrer lorsque les bénéfices pour la reproduction sont moins importants que ceux de la survie. Cette activité est donc incluse dans la période « hibernation » sur les schémas même si elle est encore soumise à un risque de prédation.

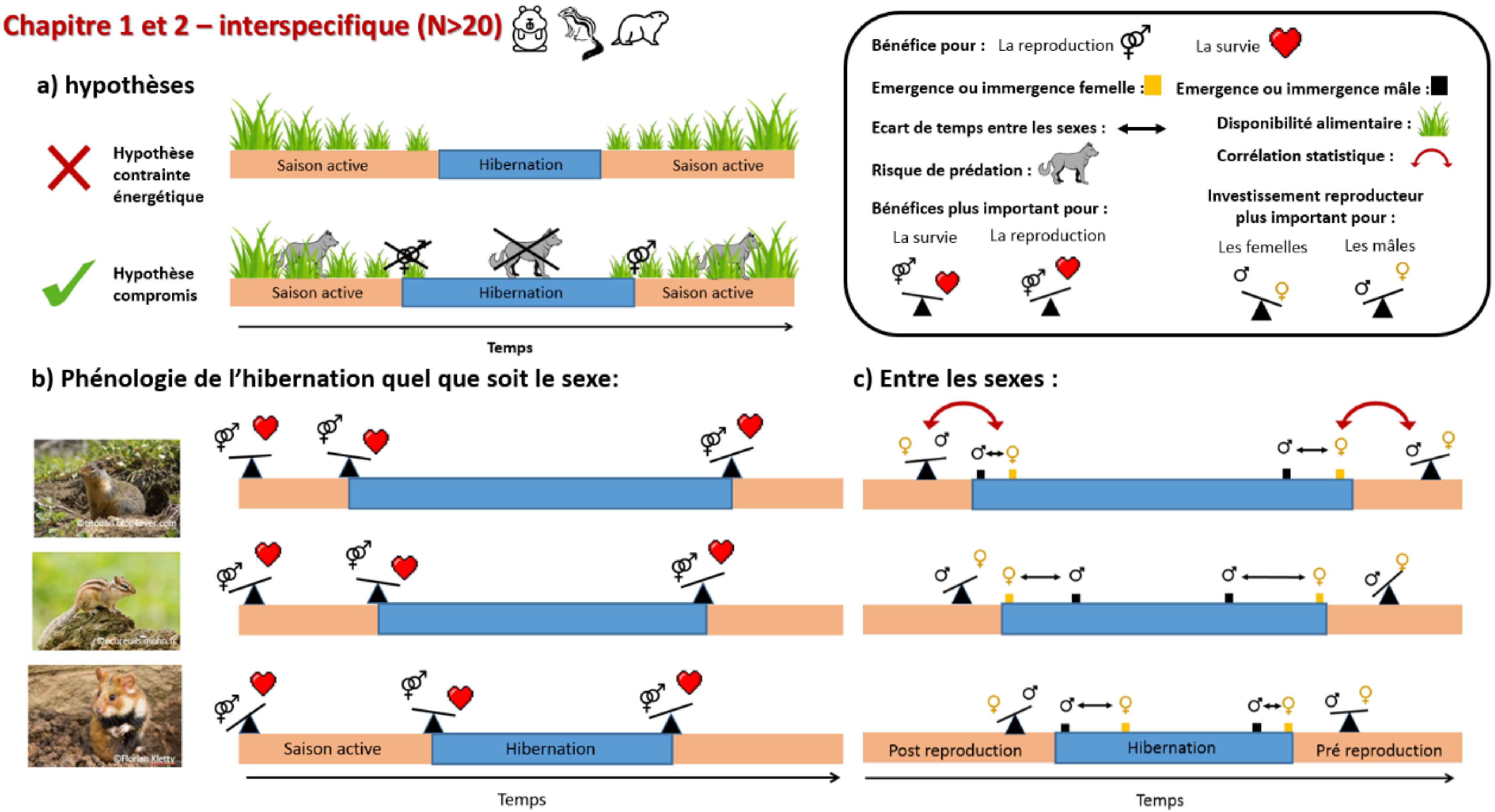


Figure 8 : schémas représentant les causes évolutives de la phénologie de l'hibernation proposées dans les chapitres 1 et 2. a) les deux hypothèses susceptibles d'expliquer la phénologie de l'hibernation ; b) variation au cours de l'année et entre espèces du compromis entre les bénéfices d'être en hibernation pour la survie et les bénéfices d'être actif pour la reproduction ; c) compromis entre la survie et reproduction expliquant la différence de phénologie de l'hibernation entre les sexes.

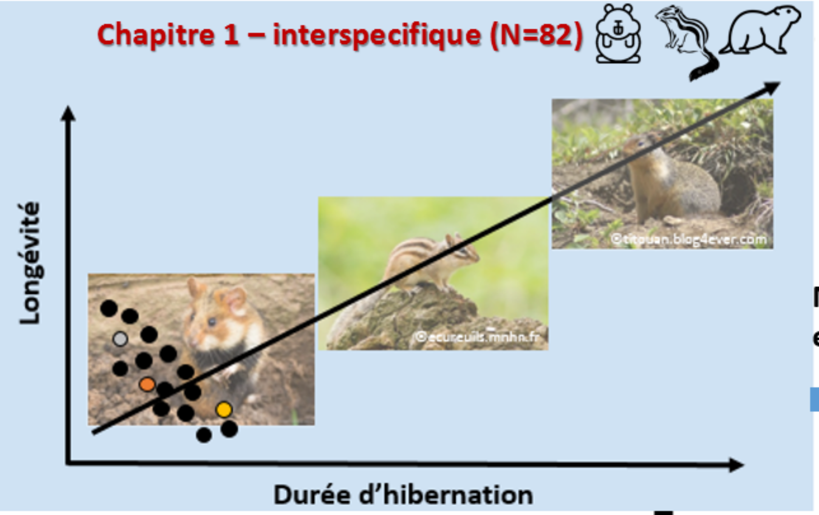
Conséquences évolutives de la phénologie de l'hibernation (chapitres 1, 3 à 5, figure 9) :

Mes études montrent un lien positif entre la longévité et la durée d'hibernation chez 82 espèces hibernantes (chapitre 1).

Les résultats d'une expérience réalisée sur le hamster commun (*Cricetus cricetus*) supposent que la réduction du métabolisme et/ou le ralentissement de la croissance et du développement du système reproducteur avec le temps total passé en torpeur augmentent la taille des télomères au cours de la période d'hibernation (chapitre 3). Ces conditions physiologiques pendant une hibernation longue et profonde permettraient d'allonger les télomères au cours de cette période. Néanmoins, les hamsters semblent avoir un investissement dans la maintenance limité au cours de l'année puisqu'une élongation lors de l'une de ces périodes (active ou hibernation) est associée à une érosion pendant l'autre partie de l'année. Ces résultats montrent une possible influence des trois hypothèses pour expliquer la plus grande longévité des hibernants.

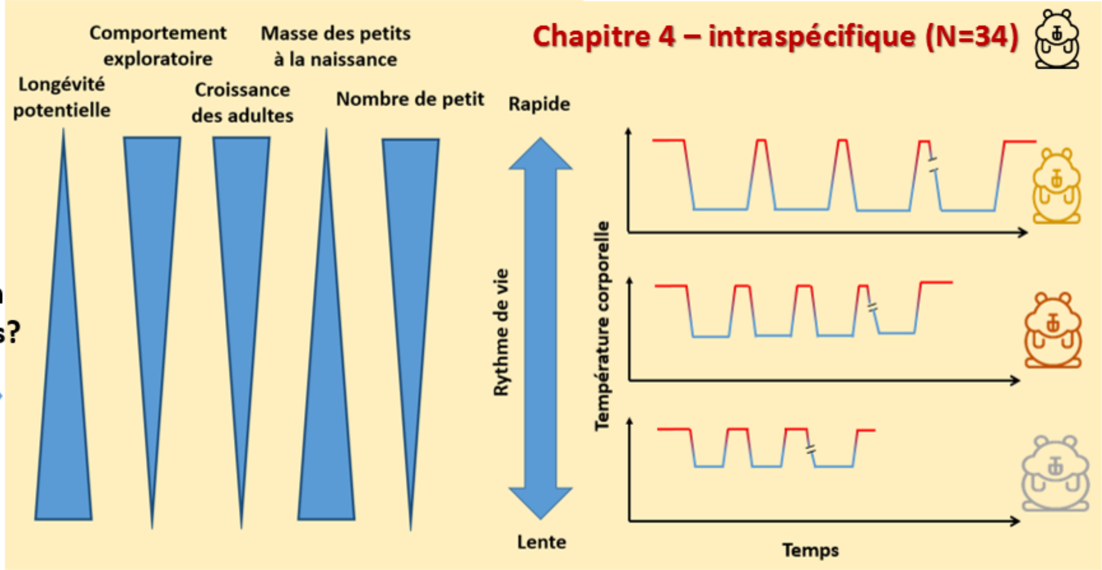
Une autre de mes études chez le hamster commun montre qu'une longue hibernation à l'échelle interindividuelle n'est pas associée à un « *pace of life lent »* chez cette espèce (chapitre 4), contrairement à mon étude interspécifique (chapitre 1). En accord avec l'hypothèse de l'optimisation des torpeurs, les hamsters qui passent le plus de temps en torpeur profonde semblent être ceux ayant le moins de réserves énergétiques. Ces individus auraient moins de chances de survie dans le futur et développeraient un pace of life rapide en accord avec la théorie des traits d'histoire de vie.

Néanmoins, les résultats obtenus à partir de l'analyse des télomères doivent être interprétés avec précaution car mes résultats montrent que la taille des télomères mesurée chez le hamster commun ne permet pas de prédire le temps de vie restant si l'on compare des individus du même âge (chapitre 5). Par contre, ils montrent une érosion des télomères à la sortie de l'hibernation qui s'accentue avec l'âge, associé à une dynamique saisonnière des télomères.



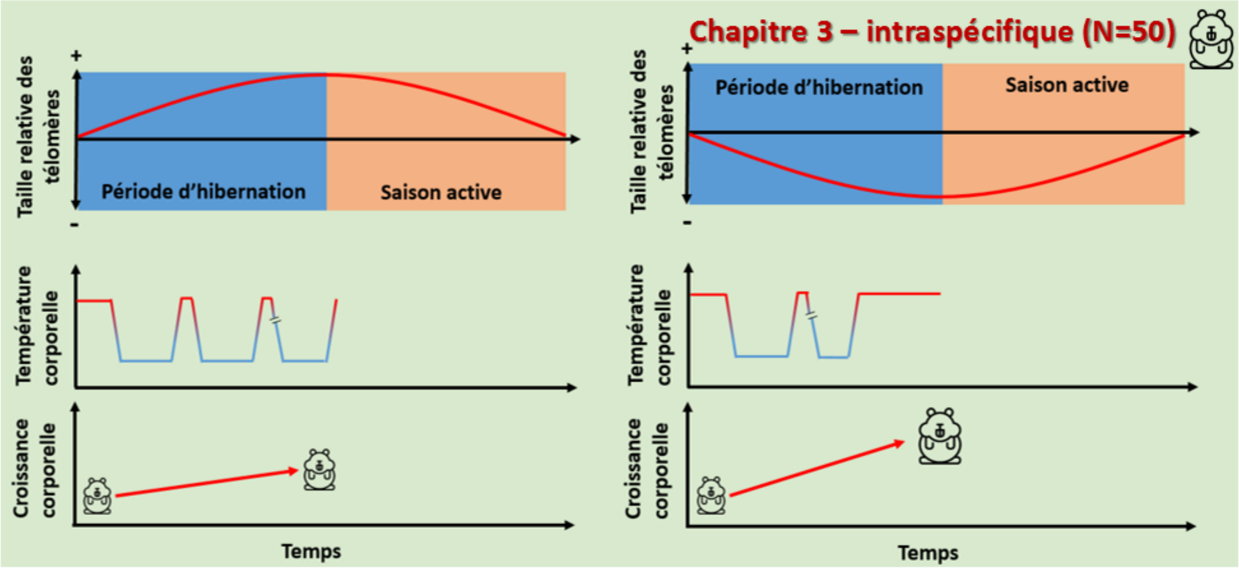
Chapitre 1 – interspecifique (N=82)

Même relation entre individus?

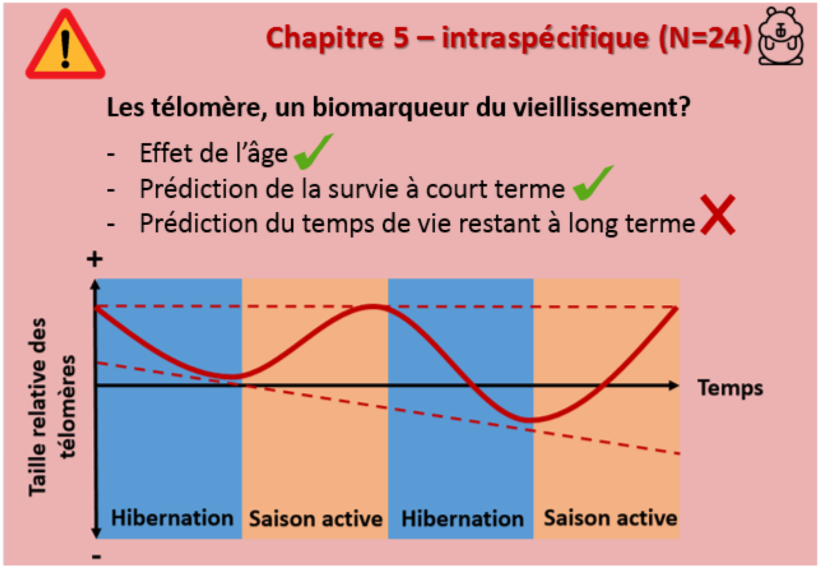


Chapitre 4 – intraspécifique (N=34)

Quels mécanismes?



Chapitre 3 – intraspécifique (N=50)



Chapitre 5 – intraspécifique (N=24)

Les télomère, un biomarqueur du vieillissement?

- Effet de l'âge ✓
- Prédiction de la survie à court terme ✓
- Prédiction du temps de vie restant à long terme ✗

Figure 9 : schémas représentant les conséquences évolutives de la phénologie de l’hibernation présentées dans la thèse. Chapitre 1 : lien positif entre la longévité et la durée d’hibernation chez 82 espèces hibernantes ; chapitre 3 : mécanismes explicatifs de la longévité des hibernants ; chapitre 4 : lien entre durée d’hibernation et pace of life chez le hamster commun ; chapitre 5 : variation de longueur des télomères chez le hamster commun au cours de la vie.

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Supplementary materials

Running head: Yardsticks for phenological shifts

Title: Towards evolutionary ecology approaches to phenological shifts

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Abstract

A phenological shift is a major response to global change, with perhaps varying magnitudes among species. One way of understanding these changes is to study whether reproductive phenology continues to match the annual food resource peak, following a strong phenological shift. We term this the “reproductive success approach”. Here, we provide an overview of understudied alternative approaches that might reveal how phenology responds to the diversity of global climatic changes. Herein, we examine (1) whether a large part of the year is devoted to activities with high survival rates (*e.g.*, dormancy and stay on migration areas) relative to periods devoted to reproduction. Changes in the time allocated between seasonal activities may significantly modify annual survival (termed “the annual approach”). In addition, a shift in phenology could be viewed as a means of defense against predators, to limit competition, or to confer a competitive advantage. Thus, we also examined (2) whether inter or intraspecific interactions within the ecosystem influence phenology (viz., “the community approach”). Finally, we investigated (3) the mechanisms underlying interindividual differences in phenology, the basis of the organisms' adaptation. Trade-offs between reproduction and survival in the phenology of some activities may be associated with life history tactics, which suggest their integration in evolutionary theory (*i.e.*, “the trade-off approach”). These multiple and non-exclusive approaches complement the reproductive success approach, and should encourage the development of an evolutionary framework for understanding phenological shifts.

Key words : evolutionary cause ; evolutionary consequence ; ultimate cause ; proximate cause, pace of life syndrome ; life history theory ; landscape of fear ; annual cycle ; wintering strategy ; food chains ; climate change yardstick ; mismatch.

1) Introduction

Biodiversity is facing increasing anthropic pressures (*i.e.*, global change) such as habitat destruction, pollution and climate change, threatening the persistence of many species (Tilman et al. 2017). Among the observed responses is a shift in their annual timing of life history events (*i.e.*, phenology) such as dormancy, migration arrival or breeding (Cohen et al. 2018). These are common and important adjustments for many species, especially those living in seasonal environments, where the impacts of changing climates are greatest (Pörtner et al. 2022). Seasonal species are supposed to have a relatively similar phenology each year due to fluctuating but somewhat predictable changes in their environment. Phenological shift as such is not a phenomenon specific to global change. It is also an adaptation that allows species to adapt to "natural" interannual changes in living conditions. What is unusual is the magnitude and in some case the one-way direction of these changes (Pörtner et al. 2022).

Although a variety of anthropic pressures may be responsible for phenological changes (Zeng et al. 2013, Zohner 2019, Senzaki et al. 2020, Lian et al. 2021), a major focus has been climate change (Donnelly and Yu 2017). Taking the example of the influence of climate change, an advance in spring phenology and a delay in fall phenology can be broadly observed (Walther et al. 2002, Parmesan and Yohe 2003, Ge et al. 2015, Vitasse et al. 2021). These responses are not universal, and much variation occurs in their direction and degree (Forrest 2016, Thackeray et al. 2016). A shift in phenology may allow adaptation to environmental changes or, on the contrary, may create a mismatch between activities and favorable conditions, or between activities and adjacent trophic levels, perhaps threatening the equilibrium of entire ecosystems (Solga et al. 2014). Therefore, consequences of global change cannot be estimated simply on the basis of a shift or the absence of a shift (Visser and Both 2005). Rather, the primary objective is to find clear measures (or yardsticks) to better interpret currently observed phenological shifts and predict their future evolution (Hodgson et al. 2011, Pau et al. 2011, Kharouba and Wolkovich 2020).

Phenology is an adaptation of organisms to conditions that vary in a quasi-predictable manner (*e.g.*, seasonal changes). Throughout the year, individuals have only a limited period of time when conditions are most favorable (*i.e.*, the "optimal period") for performance of activities important to their survival and reproduction. In particular, energy expensive activities such as reproduction require high food availability (Visser and Both 2005), and thus are generally performed when annual production of vegetation or prey are at their greatest abundance. Individuals whose phenology of reproductive activity matches the highest resource periods are expected to benefit from superior fitness. In this way, different physiological and molecular mechanisms (*i.e.*, timekeeping mechanisms) may be selected to track, anticipate, and prepare for these optimal periods (Paul et al. 2008). Most timekeeping mechanisms rely to a greater (*e.g.*, interval timer) or lesser extent (*e.g.*, endogenous circannual clocks) on the seasonal variation of one or more environmental cues (*e.g.*, temperature, photoperiod). Environmental cues are accurate when strongly correlated with the optimal period from year to year. The modification of these cues via global anthropotenic changes may explain, at least in part, the observed phenological shift (McNamara et al. 2011).

Timekeeper mechanisms induce a direct physiological response of phenology (*i.e.*, proximate or mechanistic causes). Study of proximate causes promotes an understanding of "how" an organism matches its activity to seasonal changes in the environment. These mechanisms, and more particularly the environmental cues, should not be confused with the biotic and/or abiotic factors that characterize the favorable conditions of the optimal period (*i.e.*, ultimate evolutionary causes), although some environmental cues may be present in both categories. Ultimate causes are often termed “selective agents” or “agents of selection” in evolutionary biology (Endler 1986, Wade and Kalisz 1990). These ultimate causes correspond to selection pressures that explain “why” organisms match an activity such as reproduction to a specific time period: the optimal period. Thus, knowledge of the ultimate causes and consequences of phenology are necessary to understand phenological shifts. However, evolutionary approach to phenology is relatively less studied in comparison to mechanistic approach, and is primarily focused on reproduction (table 1).

Herein, we present under-studied approaches that can be used to improve our knowledge of the evolutionary causes and consequences of phenology. More specifically, these approaches aim to show (1) the interest of studying the phenological shift of other activities than reproduction (*e.g.*, annual survival approach), (2) the diversity of ultimate causes (viz., community approach,) and (3) the importance of trade-offs between fitness components to understand the evolution of phenology and their consequences (viz., trade-offs approach). Before presenting the approaches, we clarify some notions about evolutionary studies (ultimate causes and consequences) in contrast to mechanistic studies (proximate causes), providing useful notions to implement these approaches.

Table 1 number of publications on the ultimate and proximate causes of phenology according to the activities studied. The results are from a specific search conducted in Web of science on 12/14/2021. Searches include the following terms: (a) TS=(((phenolog*) OR (phenophase*)) AND ("evolutionar*" OR "ultimate$" OR "distal$" OR "fundamental$") NEAR ("cause*" or "factor$" or "mechanism$" or "influence$")) (b) TS=(("phenolog*" OR "phenophase*") AND ((("functional*" OR "proximate$" OR "mechanistic$") NEAR ("cause*" or "factor$" or "mechanism$" or "cue$" or "influence$")) OR "cue$")). The other searches included in addition to the terms used for (a) and (b) the terms: (c) “AND (reproduction OR breeding OR flowering OR masting OR fruiting))”, (d) “AND (growth))”, (e) “AND ("dormancy*" or "hibernation$" or "diapause$" or "quiescence$" or "overwintering"))”, (f) “AND (migration*))”.

	Ultimate (percentage of total)	**Proximate (percentage of total)**
Total (a,b)	305	1066
Breeding (c)	180 (59%)	602 (56%)
Growth (d)	73 (24%)	303 (28%)
Migration (e)	36 (12%)	165 (15%)
Dormancy (f)	15 (5%)	143 (13%)

2) Ultimate causes and consequences

a) Proximate vs ultimate causes

There is a scientific debate about the use of the terms ‘ultimate’ and ‘proximate’, especially because some proximate factors could also play a role in the evolution of traits and thus also be considered as ‘ultimate’, making the dichotomy between the terms permeable (Laland et al. 2011). Nevertheless, it remains useful to distinguish why (evolutionary approach) and how (mechanistic approach) organisms match their activity with a specific time of the year. These two types of approach are based on different time frames and scale (*e.g.*, individuals or population) to study the same trait (Haig 2013). Mechanistic studies try to understand how, at a given time (synchronic), one or more individuals (representative of a particular class) synchronize their activity within a specific period. Thus, mechanistic studies are conducive to short-term correlative studies and laboratory experiments. To the contrary, evolutionary studies try to understand why, within a population, selection has favored over time (diachronic) a specific period for a given activity. Thus, evolutionary studies are more conducive to longer-term studies in natural environments with causal links that are more difficult to establish. The complementary study of ultimate and proximate factors promotes a better understanding of current responses, and improve prediction of phenological evolution in the face of global change. However, the study of ultimate causes of phenology is relatively low in comparison to proximate mechanisms (table 1). Differences in methodology and in particular the long-term monitoring required for evolutionary studies may explain their lower number. There is need to develop evolutionary studies/approach of phenology.

b) Ultimate causes

Ultimate causes (or selective agents) are factors in the social or ecological environment that interact with phenotypic traits by affecting fitness and thus the trait distribution in the population (Wade and Kalisz 1990). An ultimate cause can be identified by measuring the correlation between its variation in time or space and the variation of the distribution of phenotypic traits in the population. However, natural selection or phenotypic plasticity (see definition below) may not track the ultimate cause perfectly and decrease the detection of the correlation. But this does not mean that the selective agent has a weak influence (Merilä and Hendry 2014). It is then possible to use complementary approaches to find this relationship, such as by the "space for time substitution" method (Pickett 1989). This method posits that if the variation of the ultimate cause in time (*e.g.*, global warming) is supposed to influence the distribution of phenotypes, it is also possible that the same influence is found in space (*e.g.*, temperature gradient with altitude or latitude). Nevertheless, without demonstrating a causal link, the relationship between the phenotypic and environmental changes often remains presumed, especially with the concomitant change of many other environmental factors, as it is the case with global warming (Merilä and Hendry 2014).

For a direct test of a causal link, it is necessary to modify the ultimate cause in nature, and then measure the effect on the trait distribution (Wade and Kalisz 1990). Because of the difficulty of setting up this type of study, most of the research of this type is carried out in controlled laboratory conditions or in micro/mesocosms (Van Doorslaer et al. 2007, Merilä and Hendry 2014). At the interspecific scale, the phylogenetic comparative method can be used to identify an ultimate cause by comparing its variation with the distribution of the phenotypic trait among species, which also allows testing for past selection (termed macroevolution; Paradis, 2014).

Nevertheless, precautions must be taken when studying macroevolution because traits may have evolved in the past, but no longer be under current natural selection. Thus, evolutionary studies are more conducive to longer-term studies in natural environments with causal links that are more difficult to establish compared to mechanistic studies.

c) Ultimate consequences

The ultimate consequences are all the phenotypic traits that have evolved in response to an ultimate cause. First, ultimate causes affect the fitness of an organism. Fitness is a complex metric supposed to reflect the average contribution of an individual to the gene pool of the next generation, for which a large number of measures have been proposed ranging from more “theoretical” to more “practical” ones. In the wild or laboratory, population monitoring may provide practical fitness estimates such as annual adult survival and reproductive success (see Dobson et al., 2020; Viblanc et al., 2022). Then, current selection (also termed “microevolution”) and response to selection can be observed within and between generations of a population by a change in the distribution (*e.g.*, mean value) of a phenotypic trait (here phenology) and allele frequencies of the associated genes (Wade and Kalisz 1990). A part of the trait variation within and between generations may be explained by phenotypic plasticity. Phenotypic plasticity is a trait itself, and thus subject to selection, to produce different phenotypes in response to different environmental conditions (Nussey et al. 2007, Lane et al. 2019). In addition, another part of phenotypic variation between generation is attributed to genetic variation (*i.e.*, heritability) and studied by quantitative genetic methods (Lane 2012). Several methods allow evaluation of whether the phenotypic change is related to a genetic or plastic change, such as "animal model analyses" or "common-garden studies” (see review by Merilä and Hendry, 2014). To summarize, there are

3 sources of phenotypic variation: microevolution of traits, plasticity of traits, and microevolution of plasticity.

Finally, phenotypic variation can be considered adaptive if fitness in the population is maintained following environmental change, otherwise the change is considered non-adaptive. A distinction can be made between whether it is the direction or pace of phenotypic change that is adaptive, with complete adaptation requiring both direction and pace (Boutin and Lane 2014). Some methods are used to determine whether a phenotypic change is adaptive, such as « reciprocal transplants » or « phenotypic selection estimates » (review in Merilä and Hendry, 2014). Measuring the current level of phenotypic plasticity, genetic variability and heritability allows estimation of the adaptability of a species or population to environmental change. Adaptability is the "ability to become adapted to live and reproduce under a particular range of environmental conditions" (Angeler et al. 2019). Furthermore, in the same way as for ultimate causes, the consequences of past selection can be studied at the interspecific scale by comparative phylogenetic methods. With proper precautions, the consequences of a past selection may also provide insight on future selections.

d) Application in the context of phenological shift

The ultimate causes allow identification of the optimal period of activity under study. Then, to measure to what extent the phenological shift alters or not the match with the optimal conditions, it is necessary to measure the gap, in time units (*e.g.*, day or month), between the optimal period of the activity and its phenology (Fig. 1; Visser and Both 2005). There may be no gap or mismatch if the timekeeper mechanisms still tracks the optimal period, with or without adaptation due to environmental changes (via microevolution or phenotypic plasticity). On the contrary, in this changing environment, previously reliable timekeepers may no longer be adaptive resulting in an increasing gap. In this case, organisms may be "trapped" by their evolutionary responses to cues and suffer survival or reproductive costs. This phenomenon is called evolutionary trap (Schlaepfer et al. 2002).

In the context of global change, ultimate consequences allow an understanding of current trait changes and predict future phenological shifts, given the specific population dynamics. For this purpose, it is necessary to measure the effect of the gap (between the optimal period of activity and the current phenology) on fitness (ultimate consequence), with negative consequence which is supposed to increase with the gap's length. Furthermore, predictions of population dynamics can also be improved by studying such trait phenomena as phenotypic plasticity or microevolution (see section X for method). Phenotypic plasticity is assumed to be an important mechanism for short-term response and may be limited in responding to long-term directional change (Bernstein et al. 2008). "Natural" year-to-year shifts that occurred in the past were the basis of the evolution of plasticity in phenological events. It is on this plasticity that current shifts are initially based, and it is when anthropogenic shifts exceed the scope of adaptive plastic responses that species will fail to adjust. Microevolutionary change is therefore assumed to be necessary for population survival in the long term (Phillimore et al. 2010).

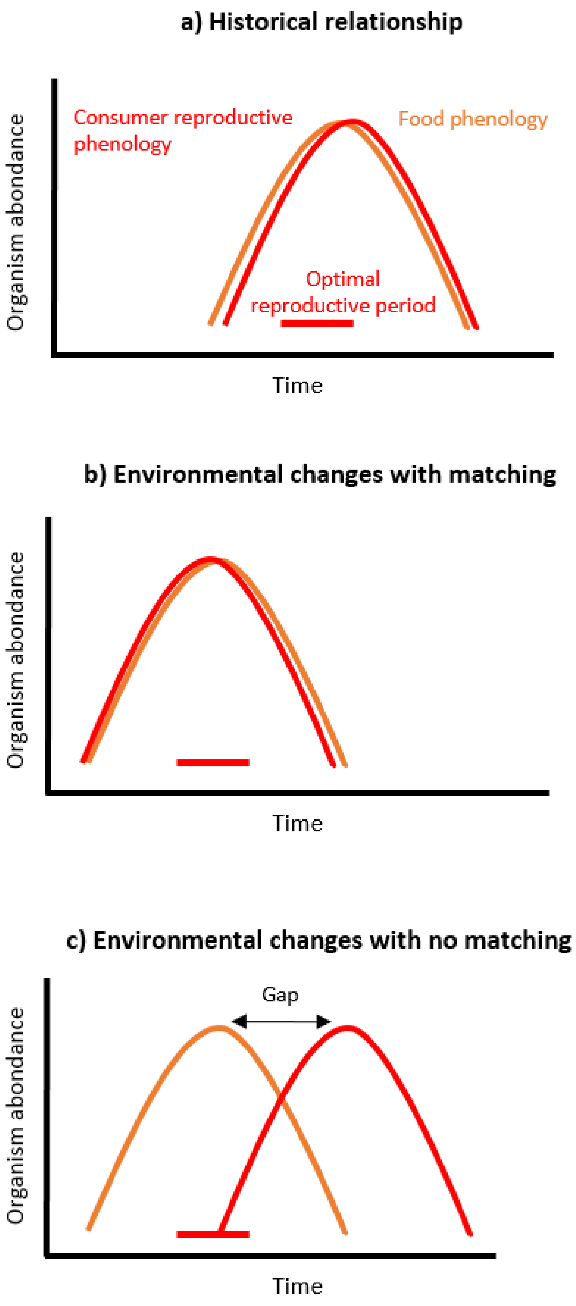


Figure 1. Schematic representation of environmental changes effect on phenology with matching or non-matching between phenology and the optimal period. In this example, the optimal period for the phenology of reproduction corresponds to the peak of food availability. The advance of food availability, compared to a) the historical relationship, leads to b) an advance of the phenology

of reproduction or c) a gap between the optimal period and the phenology of reproduction (c). The length of black double arrow indicates the extent to which a species should shift to adapt to its changing environment. This figure was inspired by Iler et al. (2021).

3) Annual approach

The annual approach is based on the simple premise that during the year several seasonal activities exist, and their phenology may influence survival and reproduction. Focusing on the impact of environmental changes on the phenology of only one of these activities may produce inaccurate predictions about future population dynamics. As studies have so far focused on reproduction (Table 1), we propose an approach to investigate the link between phenology and survival that could be applied to virtually all species. We introduce this approach using hibernation and migration, as it is particularly relevant for these species with strong seasonal patterns of survival.

The focus of the research on breeding phenology (*i.e.*, reproductive success approach) can be explained by its major influence on the life histories of species. Plant breeding phenology (flowering, fruiting, and masting) influences the duration of primary production and thus the phenology of higher trophic levels (Morellato et al. 2016). This focus may also be explained by the fact that plant and animal breeding phenology has economic relevance for humans (Chmielewski 2003). Such knowledge enables estimates of future yields (Diao et al. 2021) or increased productivity (Chemineau et al. 1992). In many animals, the timing of reproduction can have a considerable influence on reproductive success and thus population dynamics. For some species, reproductive success depends on whether the key events of reproduction (hatching, lactation, weaning) matches the peak of food availability (Both 2010), or births occur early enough in the year so that the newborns have time to grow, develop, and accumulate energy reserves before the onset of adverse environmental conditions and subsequent hibernation (Franceschini-Zink, 2008; Murie and Harris, 1982; and see Bieber et al., 2012). Nevertheless, these researches focus only on one part of the year (the reproduction part) while the survival strategies employed during the rest of the year when conditions deteriorate are understudied. In the context of global change, some studies have focused on the phenological shift of these survival strategies to deteriorating conditions (*e.g.*, dormancy and spring migration), especially because these are key periods for reproductive success (Gordo 2007, Lane et al. 2012, Charmantier and Gienapp 2014, Gallinat et al. 2015). However, a seldom estimated parameter, but potentially sensitive to phenological shift, is the relatively high survival rate during such activities compared to the breeding period.

Spending a lot of time in reproduction is supposed to increase mortality risks because of oxidative stress related to high energy expenditure (Alonso-Alvarez et al., 2004) and an increase in predator detection (increased activity to find partners and visual, olfactory, and vocal signals; Magnhagen 1991). Among traits that favor survival during adverse conditions, some animals remain on the breeding grounds and drastically modify their behavior, morphology and physiology. Other adaptations are characterized by prolonged inactivity of several months, associated with hypometabolism and hypothermia such as hibernation, dormancy and diapause. This type of life history is found across the animal kingdom, and even occurs in *Echinoderms* (Bao et al. 2010, Klanian 2013), despite earlier evidence to the contrary (Hand 1991, Guppy et al. 1994). There are important differences between some groups of species, with respect to physiological aspects of “dormancy” (used as an overarching term as in (Wilsterman et al., 2021)). For example, ectotherms have little or no physiological control over the induction of hypometabolism and hypothermia compared to endotherms, so ectotherm dormancy is assumed to be more temperature-dependent (Staples, 2016 but see Constant et al., in prep). However, strong similarities have allowed the recent creation of a universal framework that classifies these strategies along just 3 axes (induction, recalcitrance and magnitude) irrespective of their phylogeny (Wilsterman et al. 2021).

Dormancy is associated with a high survival rate when compared to the active season (Tanner and Jorgensen 1963, Bauwens 1981, Ruby and Dunham 1984, Litzgus et al. 1999, Wilson and Cooke 2004, Sperry et al. 2010, Turbill et al. 2011) and increased longevity at both intra- and interspecific levels, compared to similar size non-dormant species (Lyman et al. 1981, Wiklund et al. 2003, Wilson and Cooke 2004, Collatz 2006, Turbill et al. 2011, Magombedze et al. 2018). A recent study showed an increase in longevity related to increased hibernation duration when comparing 82 geographically and taxonomically diverse hibernating species (Constant et al. 2020).

In contrast, other animals escape from deteriorating living conditions by changing their physical location. This type of seasonal migration, called "refuge" migration, consists of an annual two-way movement between at least one place, often favorable for reproduction, and another place that improves the survival of adults or newborns for the rest of the year (Shaw 2016). This pattern is common throughout the tree of life in taxa with a high capacity for mobility (Alerstam et al. 2003). According to several studies, migratory individuals or species show either higher (Moenkkoenen 1992, Møller 2007, Zúñiga et al. 2017, Winger and Pegan 2021) or lower (Buchan et al. 2020, Soriano-Redondo et al. 2020) annual survival or longevity compared to residents. Similarly, additional studies, mainly on birds, show a lower, similar or higher survival during the non-reproductive period than during the breeding season (lower: Leyrer et al., 2013; Robinson et al., 2020; similar: Robinson et al., 2020; Rockwell et al., 2017; Sillett and Holmes, 2002; higher:

Blackburn and Cresswell, 2016; Buechley et al., 2021; Dokter et al., 2018; Lok et al., 2015; Swift et al., 2020). Mortality during migratory movement appears to vary among species ranging from low (Leyrer et al. 2013, Conklin et al. 2017, Senner et al. 2019) to high mortality risk (Rockwell et al. 2017, Rushing et al. 2017). Such variation could be explained by different strategies and context of seasonal migration among species (Winger and Pegan 2021), but also perhaps by a greater sensitivity of migratory species to current anthropogenic changes (Both et al. 2010, Buchan et al. 2020). Across taxa, it is assumed that migration is adaptively favored if the costs incurred during the migration movement (*e.g.*, high risk of predation) are less important than the benefits of changing habitat (Fryxell and Sinclair 1988, Alerstam et al. 2003).

Phenological shifts may modify the time allocated between seasonal activities with different survival values, such as reproduction compared to dormancy or migration. These changes alter survival over time and thus annual survival with potential consequences on population dynamics. Space for time substitution studies may help to investigate the relevance of this annual approach using the example of climate change (Blois et al. 2013). This method is based on the use of contemporary spatial phenomena to understand and model temporal processes that are not observable (future or past). For example, some ectotherms and endotherms show decreasing time allocate to dormancy and decreased survival, with decreasing altitude and latitude, and thus warmer climate (Nevo and Amir 1964, Pianka 1970, Bronson 1979, Murie and Harris 1982, Adolph and Porter 1993, Turbill and Prior 2016). Thus, differences in annual activity patterns at the spatial scale is associated with annual survival variation, which presumes an application of this annual survival approach to climate change in time (Turbill and Prior 2016). Based on this approach, phenological shift, even if it leads to a perfect match with the environmentally influenced change in optimal period, may induce changes in annual survival. In addition, this effect may influence the entire life history of organisms if phenological shifts affect the allocation of time between different activities associated with competing fitness components (see trade off approach).

On the contrary, an imperfect match with the optimal period may also lead to a discrepancy between preparation (*e.g.*, quantity of energy reserves stored) and the needs covered during these periods which may decrease the usually high survival rate during dormancy (Chinellato et al., 2014; Cordes et al., 2020; Reading, 2007; but see Ozgul et al., 2010) and non-breeding periods of migrants (Belpaire et al. 2009, Klaassen et al. 2012). In addition, changes in environmental conditions are also likely to promote other mortality risks associated with disease or parasite transmission (migration : Crossin et al., 2008; hibernation : Maher et al., 2012). The adaptability of species (microevolution and phenotypic plasticity) should therefore be a determinant factor for maintaining a high survival rate during these activities.

The example presented of some migrant and dormant species is perhaps one of the most striking in terms of survival differences between seasonal activities, but an annual survival approach as stated above could be extended to other species that show significant variation in mortality between their seasonal activities. The annual approach highlights the need for knowledge about the ultimate causes of seasonal activity phenology to determine their current and future optimal periods. Ideally, the annual approach should be coupled with the study of other life history traits because a changes in a single life history traits may influence trade-offs between energy allocation and thus overall life history (Healy et al. 2019).

4) Community approach

The community approach is based on the principle that the optimal period of an activity may be explained by several ultimate causes. By focusing on a single pairwise interaction (phenology-environmental factor), the determination and impact of the optimal period may be misidentified. In this section, we focused primarily on biotic factors that can influence the optimal period of an activity, to develop the concept of phenology as a means of defense against extrinsic mortality risks (*e.g.*, competition, predation) or on the contrary as a competitive advantage. Nevertheless, the inclusion of abiotic factors should constitute an even broader approach (ecosystem approach).

Among seasonal activities, the optimal period for reproduction is the most studied. It is assumed that the main ultimate cause is the peak of food availability and its influence on reproduction (Visser and Both 2005, Bronson 2009). The temporal match-mismatch hypothesis suggests that the consumer species (*i.e.*, predators, herbivores) match their period of peak energy demand with that of peak resource (*i.e.*, prey, plants) availability (Visser and Gienapp 2019). This hypothesis has been widely demonstrated from the relationship between the peak of food availability and egg laying or hatchling in birds (Both 2010, Tomás 2015), but is also verified in other taxa such as primates (Meyers and Wright 1993), bats (Cumming and Bernard 1997), rodents (Kenagy et al. 1989), and fish larvae (Durant et al. 2007). It has recently been generalized to interactions between plants and pollinators (Hegland et al. 2009), and parasites and their hosts (Paull and Johnson 2014). Because of its major influence, the timing of the resource peak may be used as a yardstick to determine whether breeding phenology has been sufficiently adapted to climate change (Visser and Both 2005). Additional metrics have been suggested, including the height and width of the resource peak (Visser and Gienapp 2019). Indeed, the impact of a lag in the breeding period, in relation to the food peak, on reproductive success could be reduced in years of high food abundance.

However, this pairwise concept between food peak and reproduction phenology may not be sufficient to determine the optimal period of breeding, questioning its efficacy as a yardstick (Nakazawa and Doi 2012). It has recently been suggested that the study of a species phenology should be integrated into the functioning of its ecosystem, and should thus take into account interspecific interactions (Nakazawa and Doi 2012, Lindén 2018). Indeed, antagonistic (*e.g.*, predation, competition) and beneficial (*e.g.*, mutualism, cooperation, and symbiosis) interactions should favor respectively, a mismatch and a match between species (Lindén 2018). For example, high nesting predation during the breeding season can lead to delays (Hušek et al. 2012, Reneerkens et al. 2016) or advances (Götmark 2002) in laying dates in relation to food peaks. In this case, the optimal period for reproduction is the result of a trade-off between high food availability and predation risk (Fig. 2a). There are examples in other taxa of the influence of interspecific relationships (other than a consumer towards his resource) on reproductive phenology. In plants for example, flowering phenology might be determined by competition for pollinators (de Jong and Ahlén 1991). Or even in the beetle *Ellychnia corrusca* (Winter Firefly), where reproduction takes place in the spring to escape its specialist predators that are active in the summer (Deyrup et al. 2017).

The influence of these other interspecific relationships does not seem to be limited to the reproductive period, but would concern the whole annual cycle including survival strategies (*e.g.*, dormancy, migration) supposed to be employed only during adverse season. Dormancy is still widely seen as an adaptation only used for energetic reasons in unfavorable conditions (too high or too low temperature, lack of food, water stress). And indeed, in various taxa, increased energy constraints along latitudinal and altitudinal gradients (associated with a decrease in primary productivity and temperature, etc.) is accompanied by an increase in dormancy duration (Pianka 1970, Turbill and Prior 2016, Wilsterman et al. 2021). Energy constraints are assumed to influence at least part of the optimal dormancy period. However, in heterothermic endotherms, which are capable of producing metabolic heat when sufficient food is available, there is little or no evidence that entry into dormancy (*i.e.*, immergence) occurs when individuals can no longer maintain a positive energy balance (Constant et al., 2020 ; Constant et al., in prep). Other abiotic factors have been proposed to favor dormancy, such as water stress especially in summer (*i.e.*, estivation) and in non-Holarctic regions (Abe 1995, Nowack et al. 2020). Nevertheless, other evidence suggests that hibernation is not initiated solely in response to deficiencies in energy, water, or poor food quality.

Several observations in both heterothermic endotherms and ectotherms seem to suggest that dormancy may occurs while energetic conditions may enable activity (review in Constant et al, 2020 and Constant et al., in prep). Edible dormouse (*Glis glis*) is a rodent that expressed a prolonged hibernation of 8 to 11.7 months while there is no apparent energetic constraints in environment but supposedly to escape predators (Hoelzl et al., 2015). Indeed, the plant growing season exceeds the dormouse active season by 2 months (in the case of an 8-month hibernation; Bieber et al., 2014). A similar example is observed in insects where the female common brimstone butterfly (*Gonepteryx rhamni*) delays emergence compared to males (3 weeks), despite favorable energetic conditions, presumably to avoid extrinsic mortality prior to breeding (Fig. 2b) (Wiklund et al. 1996). In some species, early emergence or entry into dormancy may limit competition with other species. For example, in the Eastern Montpellier snake (*Malpolon insignitus*), early emergence would provide a competitive advantage at basking sites over another species using the same hibernaculum (Dyugmedzhiev et al. 2019). In mammals, competition between black bears (*Ursus americanus)* and mesocarnivorous species (*e.g.*, coyote) decreases when bears hibernate (Moll et al. 2021). This may be a consequence of bear hibernation due to low food availability in winter, but it also raises the question of whether reduced competition might be a cause of bear hibernation. Although to date there are no experiments that demonstrate that these factors are ultimate causes of seasonal dormancy, some experiments have been able to demonstrate the influence of predation (Turbill and Stojanovski 2018, Turbill et al. 2019) and competition (Levy et al. 2011) on the induction of daily torpor in several species.

Causes of migration vary across species and ecosystems. Refuge migration is evolutionarily favored in response to seasonal changes in food availability, weather conditions, or predation risk (Shaw 2016). In both terrestrial and marine mammals, predation risk for adults or newborns (migratory movement to specific calving areas) is believed to be an important factor promoting migration to a safer location (Fryxell and Sinclair 1988, Avgar et al. 2014, Shaw 2016). Several experiments with partial migration of fish populations elegantly demonstrate that the influence of risk or perceived risk of predation are important factors promoting individual migration (Brodersen et al. 2008, Skov et al. 2011, Hulthén et al. 2015). In both mammals and fish, migration can even be towards a less favorable place from an energetic point of view, but with a less intense risk of predation (Fig. 2c) (Brodersen et al. 2008, Hebblewhite and Merrill 2011). Finally, other types of antagonistic interaction could be important causes of migration, such as parasite avoidance (Poulin and de Angeli Dutra 2021).

There are still too few studies regarding the importance of interspecific interactions as ultimate causes of phenology, compared to food availability. Present evidence suggests that such factors may have a significant influence, and be spread across taxa and activities. Thus the way organisms organize their activities (*e.g.*, daily, annual) can be seen as a means of defense against predators and/or a way to limit competition, allowing the coexistence of species within an ecosystem, or on the contrary to confer a competitive advantage (see coexistence theory ; Blackford et al., 2020). A prominent example on a daily time scale is the hypothesis that in the past, mammals were nocturnal to avoid predation and competition with dinosaurs during daytime (Gerkema et al. 2013). An interesting perspective is the recent addition of a temporal dimension to the “landscape of fear” theory. This theory proposes that the perception of predation risk by a prey species influences its organization in space and time (Kohl et al. 2018). This adaptive role of phenology has long been underestimated and could have consequences for the life histories of species.

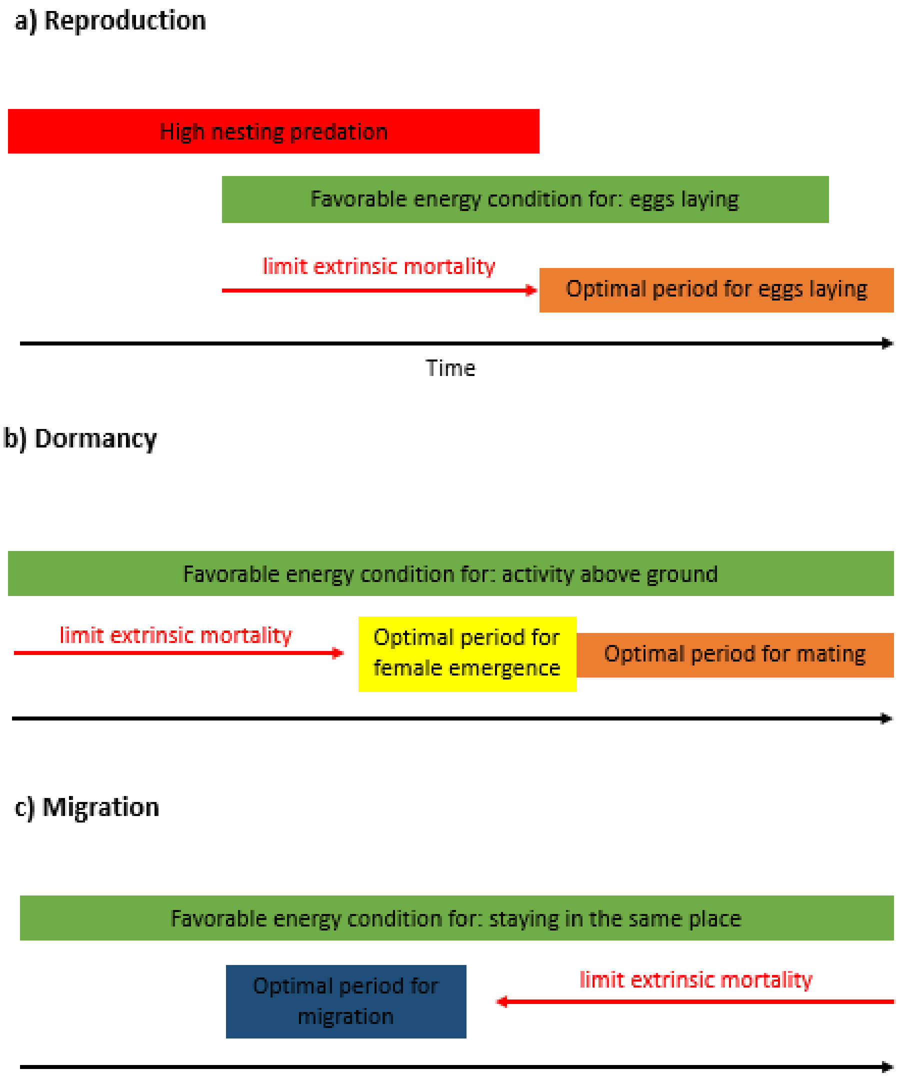


Figure 2. Schematic representation of interspecific relationship (*e.g.*, predation) influence on optimal period of phenology for several seasonal activities. In these examples, food availability (supposed to be the major cause of optimal period in the reproductive success approach), does not explain the optimal period of these activities alone. The red arrow represents the survival benefits of a phenological shift compared to what might be expected from an energetic point of view. These example represent a) a high early clutch predation favor a later reproductive timing compared to food peak (Reneerkens et al. 2016), b) females of dormant species emerge late compared to males whereas the energetic conditions are favorable, perhaps to limit the risks of dying before mating

(Wiklund et al. 1996), c) partial migratory fish population where part of the individuals seem to migrate to limit predation risks while energetic conditions are less favorable on the migration site (Brodersen et al. 2008, Hebblewhite and Merrill 2011).

5) Trade-off approach

The trade-off approach is complementary to the ideas developed in the reproductive, annual, and community approaches. It is based on the principle that, like energy, time is a finite resource that must be shared between different activities. Time allocation can create trade-offs between activities that influence different components of fitness (*e.g.*, growth, reproduction, survival). In evolutionary ecology, trade-offs help explain the maintenance of different life history patterns at different scales of life (*e.g.*, inter-specific, inter-individual). The trade-off approach is intended to better understand phenology evolution and its integration in evolutionary theories.

The time allocation trade-off should provide an understanding of the evolution of seasonal activities which influence competing fitness components. For example, dormancy phenology may have evolved based on a trade-off between the survival benefits of being in dormancy and the reproductive benefits of being active (Constant et al., in prep). On the one hand, the reduction of extrinsic (including predation and competition) mortality risks may explain longer dormancy than expected from energy constraint. On the other hand, reproductive benefits seem to promote early emergence, at a time where it would be more favorable from an energetic point of view to be dormant (Constant et al., in prep). This trade-off between the benefits of survival and reproductive appear to explain the sex difference in dormancy phenology in endotherms and ectotherms (Constant et al., in prep).

Phenological shifts in activities subject to a time allocation trade-off may have consequences for overall life history traits. In the annual approach discussed above, we suggested that annual survival of dormant species decreases with decreasing time allocated to dormancy and increasing ambient temperature in space. However, increasing temperature in space may also be associated with increased time allocated to reproduction and faster life history traits (Nevo and Amir 1964, Pianka 1970, Bronson 1979, Murie and Harris 1982, Adolph and Porter 1993, Turbill and Prior 2016). According to the method of space for time substitution, the effects of increasing temperature in space should be expected with global warming in time in the case of a perfect matching (between activity phenology and their optimal period; Fig. 3a). However, in the case of imperfect matching, reproductive success may not increase and annual survival may even decrease due to an imbalance between energy reserves and expenditure during dormancy (Fig. 3b).

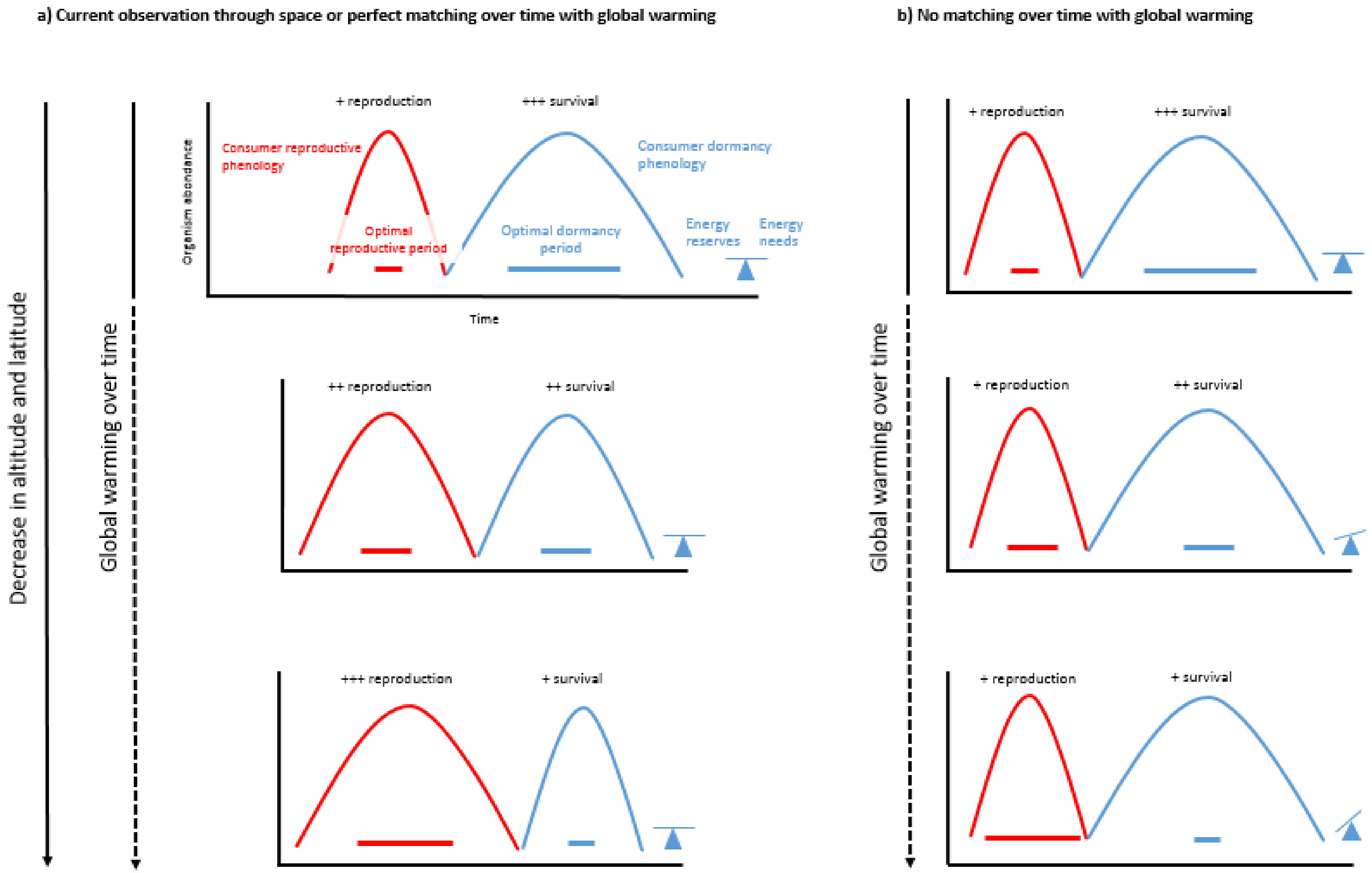
Variation in phenology may therefore be associated with variation in life history traits. We can therefore speculate if the theories that explain variation in life history traits may be applied to explain variation in phenology at different scales (*e.g.*, inter-specific, inter-individual). Life history theory proposes that life histories first vary with the body size of species such that large animal species usually have a late maturing age, lower annual reproductive rates, and live longer compared to small species (Dobson 2007). But at a given body size, species, populations or individuals can be distributed along a slow-fast continuum. At the slow end, there are species that invest more energy in survival with smaller litter sizes, slower growth, or later sexual maturity than at the fast end (Stearns 1989). The pace of life syndrome is an extension of this theory that proposes to add physiological, hormonal and behavioral parameters with a similar trade-off along this axis (Réale et al. 2010). For example, individuals with slow life history would tend to have a risk-averse behaviors, low sensitivity to oxidative stress and high immune response. The distribution of time allocated to activities with a strong trade-off between survival and reproduction may therefore be distributed along these axes.

A few studies have attempted to develop this concept across different taxa. In plants, for example, species with a rapid life history strategy have a more opportunistic phenology in spring (*e.g.*, development with increasing temperature) allowing them to have a longer growing season, but at the same time are more likely to be impacted by frost (Tang et al. 2016). In boreal birds, long-distance migration would result in higher annual survival than short-distance migration. However, the time spent on the breeding grounds is shorter and these birds have lower clutch sizes and annual fecundity (Winger and Pegan 2021). The authors therefore propose that migration distance, which is linked to species phenology (MacMynowski and Root 2007), should be included as an axis of pace of life in these bird species. The pace of life syndrome is also interesting for explaining the maintenance of inter-individual differences within the same population (Réale et al. 2010). Phenology of certain activities could therefore be associated with some behavioral, physiological or hormonal parameters. In Eurasian blackbird (*Turdus merula*), there seems to be a link between the exploratory character of individuals (fast-slow) and their breeding phenology that depends on perceived predation levels (Abbey-Lee and Dingemanse 2019). Another example is that in a migratory fish population with migratory and resident individuals, bold individuals are more likely to migrate than shy ones (Chapman et al. 2011).

A last intriguing example is that of the edible dormouse (*Glis glis*), a hibernating mammal. With increasing age, edible dormouse spent more time breeding and less time hibernating. Old individuals are less likely to encounter good conditions (masting year) to reproduce in the future

(Bieber et al. 2018). It was suggested that they take more risk to reproduce (especially in terms of predation) and thus spend a longer period while breeding. The authors proposed that in this species, hibernation should be seen as “an age-affected life-history trait that is flexibly used to maximize fitness”.

If the phenology of an activity involves trade-offs between survival and reproduction, then the optimal period within a population may be viewed as a continuum with each end being associated with an energy and time allocation strategy. Attention should be drawn to identify this type of trade-off that might maintain inter-individual differences in phenology. Furthermore, inter-individual differences are a prerequisite for natural selection, and as phenology has a strong genetic component (Forrest and Miller-Rushing 2010), these studies could provide a better understanding of the adaptability under climate change.



a) Current observation through space or perfect matching over time with global warming

b) No matching over time with global warming

Figure 3. Schematization of the space for time substitution method applied to phenological shift with global warming. a) Represents the change in time allowed between reproduction and dormancy as well as life history changes observed with decreasing altitude and latitude. Thus, the optimal period for reproduction is expected to increase and the optimal period for hibernation is expected to decrease with decreasing latitude and altitude. Based on this method, the same pattern is assumed with global warming over time in the case of a perfect match between the phenology and their optimal period. Survival decreases as dormancy duration decreases due to the increased risk of mortality associated with aboveground activity. In this case, we assume a maintenance of the balance between energy reserves and expenditure during dormancy with phenological shift over time, having no additional impact on survival. b) Represents the case of no phenological shift and a mismatch between phenology and optimal period following global warming. In this case, we assume an imbalance between energy reserve and expenditure during dormancy, decreasing survival. For example, increasing ambient temperature during dormancy with climate change is thought to increase energy expenditure. The dotted part of the arrows represents the prediction in the future. Note: the scheme is intended to illustrate life history changes in time and space and the magnitude of these changes (especially between (a) and (b)) is not to scale.

6) Conclusion

Ideally, studies aimed at better understanding and predicting the phenological shifts exhibited by a species should be conducted from a holistic approach that takes into account the full range of activities and the variety of trophic interactions of species, paying attention to inter-individual differences. But this type of study is complex to design and execute. Therefore, the first key message of the present study is to urge researchers to investigate the different approaches presented here, when: (1) the phenological shift does not reflect the general trend observed (advanced spring phenology and delayed autumn phenology; see section "Community approach") (2) the ultimate cause of phenology does not correspond to a common pairwise interaction with food availability (see section "Community approach") (3) population dynamics are not consistent with the change in reproductive success with phenological shift suggesting an impact of phenological shift on other fitness component (see section "annual approach") (4) there is a large interindividual difference in the phenology of an activity (see section "Trade-off approach"). The second key message is to encourage research on ultimate causes of phenology, which is essential to identify optimal period of activity and thus interpret phenological responses (Fig. 4). Finally, the integration of the phenology of certain activities into the pace of life syndrome and the landscape of fear seems to be an interesting prospect. It could provide a better understanding of the causes underlying the maintenance of interindividual differences in phenology and therefore of the adaptive potential of species in the face of anthropic pressure. It now appears necessary to set up a universal framework for the adaptive role of time organization at different scales (*e.g.*, daily, annual) to better understand the responses to anthropic pressure.

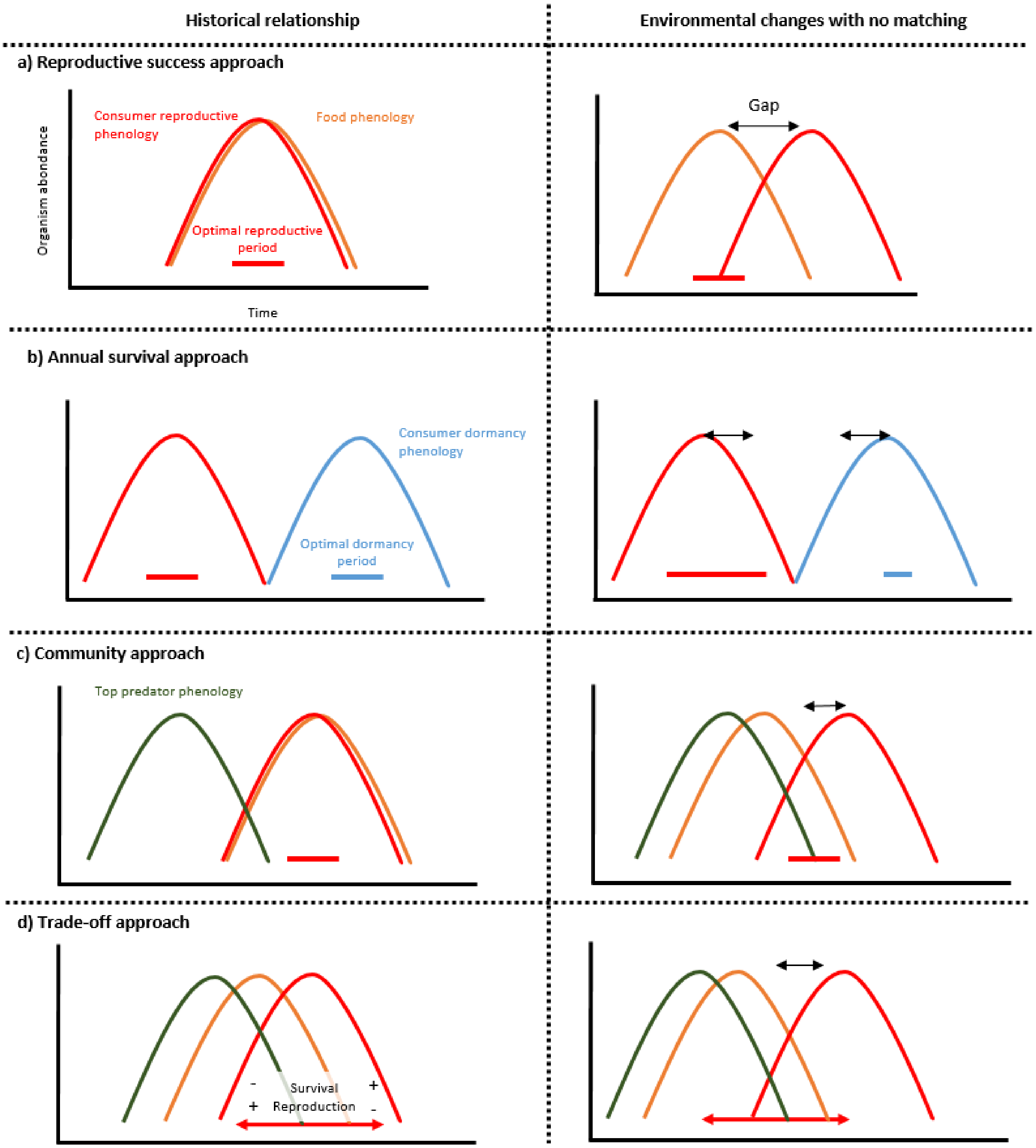

Historical relationship
Environmental changes with no matching
a) Reproductive success approach
Consumer reproductive phenology
Food phenology
Organism abondance
Optimal reproductive period
Time
Gap
b) Annual survival approach
Consumer dormancy phenology
Optimal dormancy period
c) Community approach
Top predator phenology
d) Trade-off approach
-
Survival
+
+
Reproduction
-

Figure 4. Schematic representation of the optimal period of activity and its gap with phenology following environmental change according to the different approaches presented. The length of black double arrow indicates the extent to which a species should shift to adapt to its changing environment. a) The reproductive success approach is based on the measurement of the gap between the peak of food abundance and reproductive phenology. b) The annual survival approach takes into account the gap of different seasonal activities to measure the effect on annual survival. c) The community approach takes into account the different interspecific interactions that may influence optimal period. Note that the gap between the reproductive phenology and its optimal period is less important in this case compared to reproductive success approach due to predation pressure (see Reneerkens et al. 2016). d) In the case where phenology would represent a trade-off between survival and reproduction benefits, this approach shows that optimal period can be considered as a continuum depending on the life history strategies of individuals. Note the increase of the optimal period compared to other approaches because the trade-off approach takes into account the optimal conditions according to the different life history strategies. This figure was inspired by Iler et al. (2021).

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8) Statement of authorship

TC conceived the study and drafted the manuscript under the supervision of SG and CH. SG, CH and FD contributed to the development of the concept and writing of the manuscript. FD contributed to the English editing. All authors agreed with the content of the study and contributed to the revisions.

9) Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

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Chapitre 1

Table S1: Summary of the hibernators selected in this study among the 152 listed hibernators. Species (1) in black are listed in Turbill et al (2011), (2) in dark blue represent the other species listed by Ruf and Geiser (2015) and (3) in light blue represent other known hibernators. AnAge refers to AnAge data base (The Animal Aging and Longevity Database; https://genomics.senescence.info/species/search_list.php; Human Ageing and Genomic Resources; Magalhães and Costa, 2009), and PanTHERIA refers to the PanTHERIA data base (https://ecologicaldata.org/wiki/PanTHERIA; Ecological Archives, Ecological Society of America; Jones et al., 2009). We mention the new nomenclature for ground squirrel species, which may not correspond to the nomenclature of the lists presented. Some species were first excluded according to the exclusion criteria listed in the publication. We then investigate the longevity of hibernators according to the methods described in the publication. Only species for which we have found both the hibernation season duration and longevity were included in the study. All references for longevity and hibernation duration data are presented in Table S2.

*Note that longevity (12.5 years) and hibernation season duration (90 day) of *Zaedyus pichiy* are known (Magalhaes and Costa, 2009; Superina and Abba, 2014) but by including this species the binary condition of the phylogenetic tree was not satisfied. A rooted tree is considered binary if all nodes (including the root node) have exactly two descendant nodes. This condition was tested using the ‘ape 5.0’ packages in R v. 3.6.2.

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Species	*Familly*	*Exclusion criteria*	*Longevity data*	*Hibernation data*	*Species included in study*
Echinops telfairi	Afrosoricida	No	AnAge	No data	No
Ursus americanus	Carnivora	No	AnAge	Yes	Yes
Ursus arctos	Carnivora	No	AnAge	Yes	Yes
Ursus maritimus	Carnivora	Criteria 1			No
Ursus thibetanus	Carnivora	No	AnAge	Yes	Yes
Antrozous pallidus	Chiroptera	No	AnAge	No data	No
Barbastella barbastellus	Chiroptera	No	AnAge	Yes	Yes
Corynorhinus rafinesquii	Chiroptera	No	PanTHERIA	Yes	Yes
Corynorhinus townsendii	Chiroptera	No	PanTHERIA	No data	No
Eptesicus fuscus	Chiroptera	No	AnAge	Yes	Yes
Eptesicus nilssonii	Chiroptera	No	AnAge	Yes	Yes
Eptesicus serotinus	Chiroptera	No	AnAge	Yes	Yes
Lasionycteris noctivagans	Chiroptera	No	AnAge	No data	No
Lasiurus cinereus	Chiroptera	No	AnAge	Yes	Yes
Miniopterus schreibersii	Chiroptera	No	AnAge	Yes	Yes
Myotis austroriparius	Chiroptera	No	PanTHERIA	Yes	Yes
Myotis bechsteinii	Chiroptera	No	AnAge	No data	No
Myotis blythii	Chiroptera	No	AnAge	No data	No
Myotis brandtii	Chiroptera	No	AnAge	Yes	Yes
Myotis californicus	Chiroptera	No	PanTHERIA	No data	No
Myotis dasycneme	Chiroptera	No	PanTHERIA	Yes	Yes
Myotis daubentonii	Chiroptera	No	AnAge	Yes	Yes
Myotis emarginatus	Chiroptera	No	AnAge	No data	No
Myotis evotis	Chiroptera	No	AnAge	No data	No
Myotis grisescens	Chiroptera	No	AnAge	Yes	Yes
Myotis keenii	Chiroptera	No	AnAge	Yes	Yes
Myotis leibii	Chiroptera	No	AnAge	No data	No
Myotis lucifugus	Chiroptera	No	AnAge	Yes	Yes
Myotis myotis	Chiroptera	No	AnAge	Yes	Yes
Myotis mystacinus	Chiroptera	No	AnAge	No data	No
Myotis nattereri	Chiroptera	No	AnAge	No data	No
Myotis sodalis	Chiroptera	No	AnAge	Yes	Yes
Myotis thysanodes	Chiroptera	No	AnAge	No data	No
Myotis velifer	Chiroptera	No	AnAge	Yes	Yes
Myotis volans	Chiroptera	No	AnAge	No data	No
Myotis yumanensis	Chiroptera	No	AnAge	No data	No
Nyctalus leisleri	Chiroptera	No	No data		No
Nyctalus noctula	Chiroptera	No	AnAge	Yes	Yes
Pipistrellus hesperus	Chiroptera	No	PanTHERIA	No data	No
Pipistrellus nathusii	Chiroptera	No	AnAge	No data	No
Pipistrellus pipistrellus	Chiroptera	No	AnAge	Yes	Yes
Pipistrellus subflavus	Chiroptera	No	AnAge	Yes	Yes
Plecotus auritus	Chiroptera	No	AnAge	Yes	Yes
Plecotus austriacus	Chiroptera	No	AnAge	Yes	Yes
Rhinolophus ferrumequinum	Chiroptera	No	AnAge	Yes	Yes
Rhinolophus hipposideros	Chiroptera	No	AnAge	Yes	Yes

Rhinolophus megaphyllus	Chiroptera	No	No data		No
Vespertilio murinus	Chiroptera	No	AnAge	No data	No
Zaedyus pichiy	Cingulata	No	AnAge	yes	No*
Acrobates pygmaeus	Diprotodontia	Criteria 3			No
Burramys parvus	Diprotodontia	No	AnAge	Yes	Yes
Cercartetus nanus	Diprotodontia	Criteria 3			No
Erinaceus concolor	Erinaceomorpha	No	AnAge	Yes	Yes
Erinaceus europaeus	Erinaceomorpha	No	AnAge	Yes	Yes
Hemiechinus auritus	Erinaceomorpha	No	AnAge	Yes	Yes
Paraechinus hypomelas	Erinaceomorpha	No	AnAge	No data	No
Dromiciops gliroides	Microbiotheria	No	No data		No
Tachyglossus aculeatus	Monotremata	No	AnAge	Yes	Yes
Cheirogaleus major	Primates	No	AnAge	Yes	Yes
Cheirogaleus medius	Primates	No	AnAge	Yes	Yes
Microcebus murinus	Primates	No	AnAge	Yes	Yes
Microcebus rufus	Primates	No			No
Allactaga euphratica	Rodentia	No	AnAge	No data	No
Callospermophilus lateralis	Rodentia	No	AnAge	Yes	Yes
Callospermophilus saturatus	Rodentia	No	No data		No
Chaetodipus formosus	Rodentia	No	AnAge	Yes	Yes
Cricetus cricetus	Rodentia	No	AnAge	Yes	Yes
Cynomys gunnisoni	Rodentia	No	No data		No
Cynomys ludovicianus	Rodentia	Criteria 1			No
Eliomys quercinus	Rodentia	No	AnAge	Yes	Yes
Glis glis	Rodentia	No	Other source	Yes	Yes
Graphiurus murinus	Rodentia	No	AnAge	No data	No
Jaculus jaculus	Rodentia	No	AnAge	No data	No
Marmota bobak	Rodentia	No	PanTHERIA	Yes	Yes
Marmota flaviventris	Rodentia	No	AnAge	Yes	Yes
Marmota marmota	Rodentia	No	AnAge	Yes	Yes
Marmota monax	Rodentia	No	AnAge	Yes	Yes
Marmota vancouverensis	Rodentia	No	AnAge	Yes	Yes
Mesocricetus auratus	Rodentia	No	AnAge	No data	No
Microdipodops megacephalus	Rodentia	No	Other source	Yes	Yes
Muscardinus avellanarius	Rodentia	No	Other source	Yes	Yes
Napaeozapus insignis	Rodentia	No	PanTHERIA	Yes	Yes
Otospermophilus beecheyi	Rodentia	No	Other source	Yes	Yes
Perognathus flavescens	Rodentia	No	No data		No
Perognathus flavus	Rodentia	No	PanTHERIA	No data	No
Perognathus longimembris	Rodentia	No	AnAge	Yes	Yes
Perognathus parvus	Rodentia	No	AnAge	Yes	Yes
Sicista betulina	Rodentia	No	Other source	Yes	Yes
Spermophilus citellus	Rodentia	No	AnAge	Yes	Yes
Spermophilus dauricus	Rodentia	No	Other source	Yes	Yes
Tamias amoenus	Rodentia	No	Other source	Yes	Yes

Tamias minimus	Rodentia	No	AnAge	No data	No
Tamias sibiricus	Rodentia	No	AnAge	Yes	Yes
Tamias striatus	Rodentia	No	AnAge	Yes	Yes
Tamias townsendii	Rodentia	No	AnAge	Yes	Yes
Urocitellus armatus	Rodentia	No	Other source	Yes	Yes
Urocitellus beldingi	Rodentia	No	Other source	Yes	Yes
Urocitellus columbianus	Rodentia	No	Other source	Yes	Yes
Urocitellus parryii	Rodentia	No	Other source	Yes	Yes
Urocitellus richardsonii	Rodentia	No	Other source	Yes	Yes
Urocitellus townsendii	Rodentia	No	No data		No
Zapus hudsonius	Rodentia	No	AnAge	Yes	Yes
Zapus princeps	Rodentia	No	Other source	Yes	Yes
Amblysomus hottentotus	Afrosoricida	No	No data		No
Setifer setosus	Afrosoricida	No	AnAge	Yes	Yes
Tenrec ecaudatus	Afrosoricida	No	AnAge	Yes	Yes
Meles meles	Carnivora	No	AnAge	Yes	Yes
Chalinolobus gouldii	Chiroptera	No	No data		No
Hipposideros terasensis	Chiroptera	No	No data		No
Lasiurus borealis	Chiroptera	No	No data		No
Mops condylurus	Chiroptera	No	No data		No
Myotis adversus	Chiroptera	No	No data		No
Nyctophilus bifax	Chiroptera	No	No data		No
Nyctophilus geoffroyi	Chiroptera	No	No data		No
Nyctophilus gouldi	Chiroptera	No	No data		No
Rhinopoma microphyllum	Chiroptera	No	No data		No
Tadarida aegyptiaca	Chiroptera	No	No data		No
Tadarida brasiliensis	Chiroptera	No	AnAge	No data	No
Tadarida teniotis	Chiroptera	No	AnAge	No data	No
Vespadelus vulturnus	Chiroptera	No	No data		No
Cercartetus concinnus	Diprotodontia	Criteria 3			No
Cercartetus lepidus	Diprotodontia	Criteria 3			No
Atelerix algirus	Eulipotyphla	No	PanTHERIA	Yes	Yes
Atelerix frontalis	Eulipotyphla	No	No data		No
Elephantulus edwardii	Macroscelidea	Criteria 3			No
Elephantulus myurus	Macroscelidea	Criteria 3			No
Cheirogaleus crossleyi	Primates	No	No data		No
Microcebus griseorufus	Primates	No	No data		No
Allactaga williamsi	Rodentia	No	No data		No
Cynomys parvidens	Rodentia	No	No data		No
Cynomys leucurus	Rodentia	No	No data		No
Glirulus japonicus	Rodentia	No	AnAge	Yes	Yes
Graphiurus ocularis	Rodentia	No	No data		No
Ictidomys tridecemlineatus	Rodentia	No	AnAge	Yes	Yes
Ictidomys mexicanus	Rodentia	No	No data		No
Jaculus orientalis	Rodentia	No	AnAge	No data	No

Marmota broweri	Rodentia	No	No data		No
Mesocricetus brandti	Rodentia	No	AnAge	No data	No
Microdipodops pallidus	Rodentia	No	No data		No
Otospermophilus variegatus	Rodentia	No	AnAge	Yes	Yes
Spermophilus xanthoprymnus	Rodentia	No	No data		No
Urocitellus elegans	Rodentia	No	No data		No
Xerospermophilus tereticaudus	Rodentia	No	AnAge	Yes	Yes
Myotis septentrionalis	Chiroptera	No	Other source	Yes	Yes
Myotis kuhlii	Chiroptera	No	AnAge	Yes	Yes
Rhinolophus euryale	Chiroptera	No	Other source	Yes	Yes
Dryomys nitedula	Rodentia	No	Other source	Yes	Yes
Marmota caligata	Rodentia	No	AnAge	Yes	Yes
Poliocitellus franklinii	Rodentia	No	AnAge	Yes	Yes
Spermophilus pygmaeus	Rodentia	No	AnAge	Yes	Yes
Urocitellus brunneus	Rodentia	No	Other source	Yes	Yes
Xerospermophilus mohavensis	Rodentia	No	AnAge	Yes	Yes

Species	*Family*	*Hibernation season duration (day)*	*Body mass (g)*	*Longevity (year)*	**Arboreality**	*Wild or Captivity*
Burramys parvus	Burramyidae	210 [1,2]	45 [3]	12 [3]	Yes [4]	Wild
Cheirogaleus major	Cheirogaleidae	150 [5–7]	395 [3]	13.4 [3]	Yes [8,9]	Captivity
Cheirogaleus medius	Cheirogaleidae	210 [10]	380 [3]	29 [3]	Yes [4,8,11]	Captivity
Microcebus murinus	Cheirogaleidae	186 [12]	64.8 [3]	18.2 [3]	Yes [4,13]	Captivity
Cricetus cricetus	Cricetidae	180 [14]	506.7 [3]	3.6 [3]	No [15]	Captivity
Napaeozapus insignis	Dipodidae	210 [16] *	22.25 [17]	4 [17]	No [18]	Wild
Sicista betulina	Dipodidae	210 [19] *	8.92 [17]	3.5 [20]	No [9]	Wild
Zapus hudsonius	Dipodidae	265 [21]	18 [3]	5.6 [3]	No [22]	Captivity
Zapus princeps	Dipodidae	296 [23]	27.2 [17]	6 [24]	No [25]	Wild
Atelerix algirus	Erinaceidae	120 [26]	958 [17]	7 [17]	No [27]	Captivity
Erinaceus concolor	Erinaceidae	210 [28]	719 [3]	7 [3]	No [9]	Captivity
Erinaceus europaeus	Erinaceidae	225 [29]	750 [3]	11.7 [3]	No [4]	Captivity
Hemiechinus auritus	Erinaceidae	150 [30]	342 [3]	7.6 [3]	No [9]	Captivity
Dryomys nitedula	Gliridae	240 [31]	26 [3]	8 [31]	Yes [9,32]	Wild
Eliomys quercinus	Gliridae	210 [33]	82.5 [3]	5.5 [3]	Yes [9,34]	Captivity
Glirulus japonicus	Gliridae	195 [35]	27 [3]	7 [3]	Yes [9,36]	Captivity
Glis glis	Gliridae	282 [37]	125 [3]	13 [38]	Yes [9,39]	Wild
Muscardinus avellanarius	Gliridae	210 [40]	27.3 [3]	6 [40,41]	Yes [9,42]	Wild
Chaetodipus formosus	Heteromyidae	105 [43]	19 [3]	7.1 [3]	No [9]	Captivity
Microdipodops megacephalus	Heteromyidae	150 [44]	12.3 [17]	5.42 [17]	No [45]	Captivity
Perognathus longimembris	Heteromyidae	195 [43]	8 [3]	8.3 [3]	No [9]	Captivity
Perognathus parvus	Heteromyidae	120 [46]	20.1 [3]	5.8 [3]	No [47]	Captivity
Miniopterus schreibersii	Miniopteridae	150 [48] *	13 [3]	22 [3]	No [4]	Wild
Meles meles	Mustelidae	180 [49] *	13000 [3]	18.6 [3]	No [4]	Captivity
Rhinolophus euryale	Rhinolophidae	150 [50–52]	8.2 [3]	21 [53]	No [9]	Wild

Rhinolophus ferrumequinum	Rhinolophidae	225 [54]	22.875 [3]	30.5 [3]	No [4]	Wild
Rhinolophus hipposideros	Rhinolophidae	210 [55]	4.6 [3]	29.4 [3]	No [4]	Wild
Callospermophilus lateralis	Sciuridae	274 [56]	157.6 [3]	10.4 [3]	No [57]	Captivity
Ictidomys tridecemlineatus	Sciuridae	225 [58]	172.7 [3]	7.9 [3]	No [59]	Captivity
Marmota bobak	Sciuridae	240 [60] *	7300 [17]	15 [17]	No [9]	Wild
Marmota caligata	Sciuridae	240 [61] *	4300 [3]	12.1 [3]	No [61]	Captivity
Marmota flaviventris	Sciuridae	240 [62]	3500 [3]	21.2 [3]	No [63]	Captivity
Marmota marmota	Sciuridae	195 [64]	3500 [3]	17.4 [3]	No [4]	Captivity
Marmota monax	Sciuridae	166.9 [65]	4000 [3]	14 [3]	No [4]	Captivity
Marmota vancouverensis	Sciuridae	210 [66]	4750 [3]	12.1 [3]	No [4]	Captivity
Otospermophilus beecheyi	Sciuridae	210 [67]	508.5 [68]	5 [53]	No [69]	Wild
Otospermophilus variegatus	Sciuridae	210 [70] *	663 [3]	9.8 [3]	Yes [71–74]	Captivity
Poliocitellus franklinii	Sciuridae	255 [75]	459 [3]	7.2 [3]	No [76]	Captivity
Spermophilus citellus	Sciuridae	225 [77]	217 [3]	6.7 [3]	No [4]	Captivity
Spermophius dauricus	Sciuridae	210 [78] *	223.8 [68]	7 [78]	No [9]	Wild
Spermophilus pygmaeus	Sciuridae	240 [79]	136 [3]	7.1 [3]	No [9]	Captivity
Tamias amoenus	Sciuridae	150 [80]	50.63 [17]	5.17 [81]	Yes [9,82–84]	Wild
Tamias sibiricus	Sciuridae	210 [85]	85 [3]	9.6 [3]	Yes [9,84–86]	Captivity
Tamias striatus	Sciuridae	210 [87]	96 [3]	9.5 [3]	Yes [9,84,88–90]	Captivity
Tamias townsendii	Sciuridae	135 [91]	75 [3]	9.3 [3]	Yes [9,84,92–94]	Captivity
Urocitellus armatus	Sciuridae	289 [95]	306.48 [17]	7 [96]	No [97]	Wild
Urocitellus beldingi	Sciuridae	270 [98]	265.2 [68]	12 [99]	No [100]	Wild
Urocitellus brunneus	Sciuridae	240 [101]	300 [17]	8 [101]	No [102]	Wild
Urocitellus columbianus	Sciuridae	285 [103]	470.94 [17]	11 [104]	No [105]	Wild
Urocitellus parryii	Sciuridae	240 [106]	524.3 [68]	10 [107]	No [108]	Wild
Urocitellus richardsonii	Sciuridae	258 [109]	325.1 [17]	6 [110]	No [111]	Wild
Xerospermophilus mohavensis	Sciuridae	210 [112] *	150 [3]	7.8 [3]	No [113]	Captivity

Xerospermophilus tereticaudus	Sciuridae	240[114]	163.3[3]	8.9[3]	No[112]	Captivity
Tachyglossus aculeatus	Tachyglossidae	180[115]	3500[3]	49.5[3]	No[4]	Captivity
Setifer setosus	Tenrecidae	210[116]	225[3]	14.1[3]	Yes[4,117,118]	Captivity
Tenrec ecaudatus	Tenrecidae	270[119]	900[3]	8.7[3]	No[120]	Captivity
Ursus americanus	Ursidae	210[121] *	154250[3]	34[3]	No[4]	Captivity
Ursus arctos	Ursidae	215[122]	277500[3]	40[3]	No[4]	Captivity
Ursus thibetanus	Ursidae	150[123]	103750[3]	39.2[3]	Yes[4,124,125]	Captivity
Barbastella barbastellus	Vespertilionidae	225[126]	10.25[3]	23[3]	No[4]	Wild
Corynorhinus rafinesquii	Vespertilionidae	135[127]	9.15[17]	10.1[17]	No[128]	Wild
Eptesicus fuscus	Vespertilionidae	180[129]	23[3]	19[3]	No[4]	Wild
Eptesicus nilssonii	Vespertilionidae	180[130] *	13[3]	20[3]	No[4]	Wild
Eptesicus serotinus	Vespertilionidae	210[131]	18.2[3]	21[3]	No[4]	Wild
Lasiurus cinereus	Vespertilionidae	180[132]	24[3]	14[3]	No[4]	Wild
Myotis austroriparius	Vespertilionidae	210[133,134] *	7.35[17]	6[17]	No[133]	Wild
Myotis brandtii	Vespertilionidae	255[135] *	7[3]	41[3]	No[4]	Wild
Myotis dasycneme	Vespertilionidae	195[136] *	15.16[17]	19.5[17]	No[4]	Wild
Myotis daubentonii	Vespertilionidae	240[137]	8.5[3]	28[3]	No[4]	Wild
Myotis grisescens	Vespertilionidae	120[138] *	9.25[3]	16.5[3]	No[4]	Wild
Myotis keenii	Vespertilionidae	180[139]	7.4[3]	19[3]	No[4]	Wild
Myotis lucifugus	Vespertilionidae	241[140]	10[3]	34[3]	No[4]	Wild
Myotis myotis	Vespertilionidae	150[141]	28.55[3]	37.1[3]	No[4]	Wild
Myotis septentrionalis	Vespertilionidae	180[142]	7[143]	19[144]	No[145]	Wild
Myotis sodalis	Vespertilionidae	210[146]	7.7[3]	20[3]	No[4]	Wild
Myotis velifer	Vespertilionidae	180[147]	10.1[3]	11.3[3]	No[4]	Wild
Nyctalus noctula	Vespertilionidae	150[52,148]	27.75[3]	12[3]	No[4]	Wild
Pipistrellus kuhlii	Vespertilionidae	150[149]*	6[3]	8[3]	No[4]	Wild
Pipistrellus pipistrellus	Vespertilionidae	150[52,150]	5[3]	16.6[3]	No[4]	Wild

Pipistrellus subflavus	Vespertilionidae	180 [151]	7.5 [3]	14.8 [3]	No [4]	Wild
Plecotus auritus	Vespertilionidae	150 [152]	7.8 [3]	30 [3]	No [4]	Wild
Plecotus austriacus	Vespertilionidae	180 [152]	12 [3]	25.5 [3]	No [4]	Wild

Table S2: Data on hibernation season duration, body mass, longevity and arboreality lifestyle of all mammals studied in the different models. Hibernation season duration with (*) corresponds to publications for which the methodology used to determine this duration could not be verified. The “Wild or Captivity” parameter refers to the source of longevity data. The “arboreality” parameter distinguishes between species considered arboreal and semi-arboreal (Yes) and non-arboreal (No). Brown bear (*Ursus arctos*) and American black bear (*Ursus americanus*) have been defined as non-arboreal, as in Healy et al, 2014, as the majority of adults are losing this lifestyle [153] contrary to Asian black bear (*Ursus thibetanus*) [124]. Bats were considered to be non-arboreal even though it nests in trees as nesting in a protected area is a common characteristic of all bats and therefore already taken into account in the “bat (yes/no)” factor.

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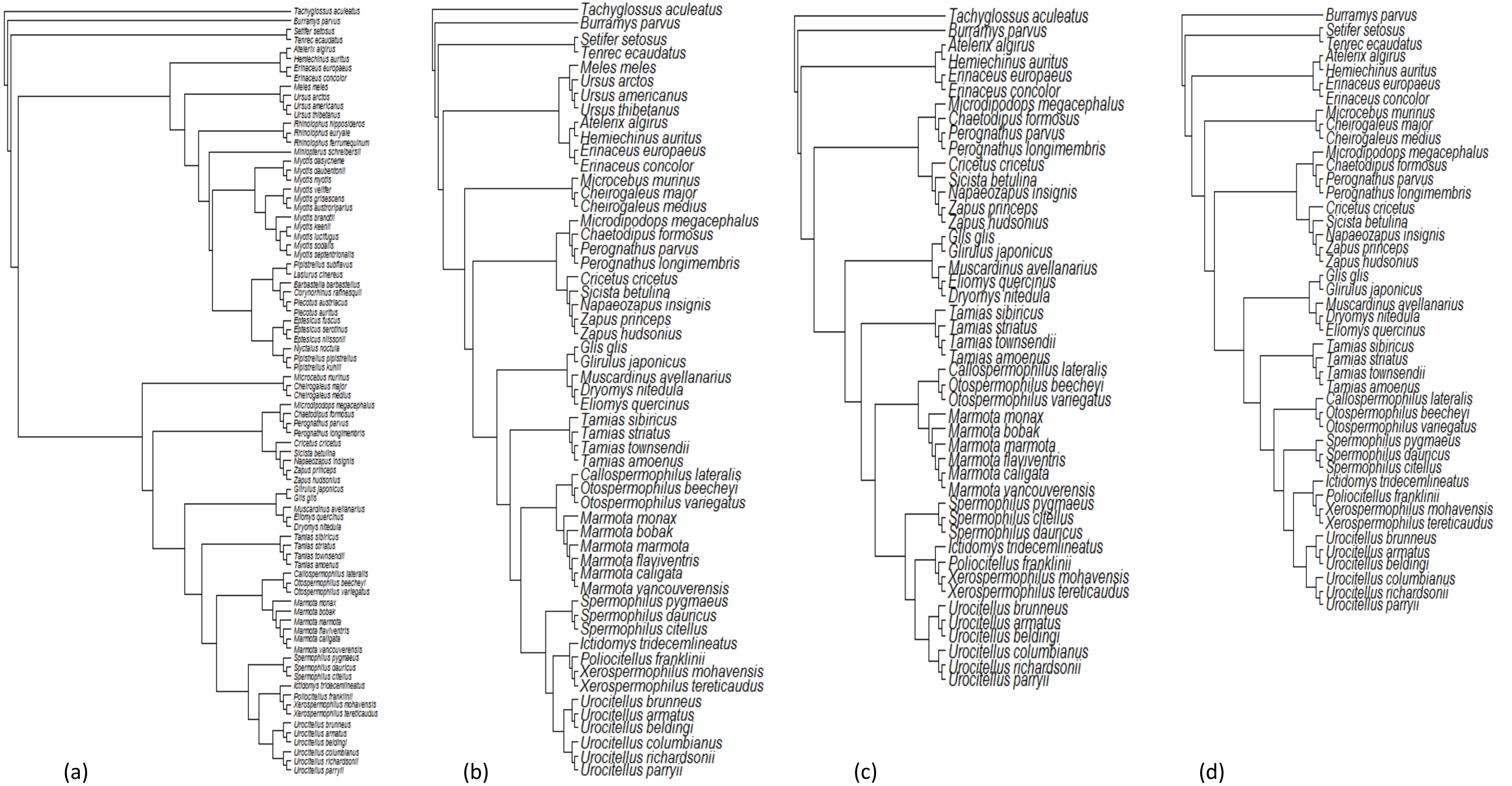

Figure S1. Consensus phylogenetic trees for the species under study: (a) all hibernators data set (N = 82), (b) the data set without bats (N =55), (c) the data set of deep hibernators without bats (N = 46) and (d) the data set of small hibernators (<1.5 kg) without bats (N = 44). Each consensus tree was built from 100 trees obtained from http://vertlife.org/phylosubsets/. Branch lengths were calculated using Grafen's computations with the 'ape' package in R (see Methods).

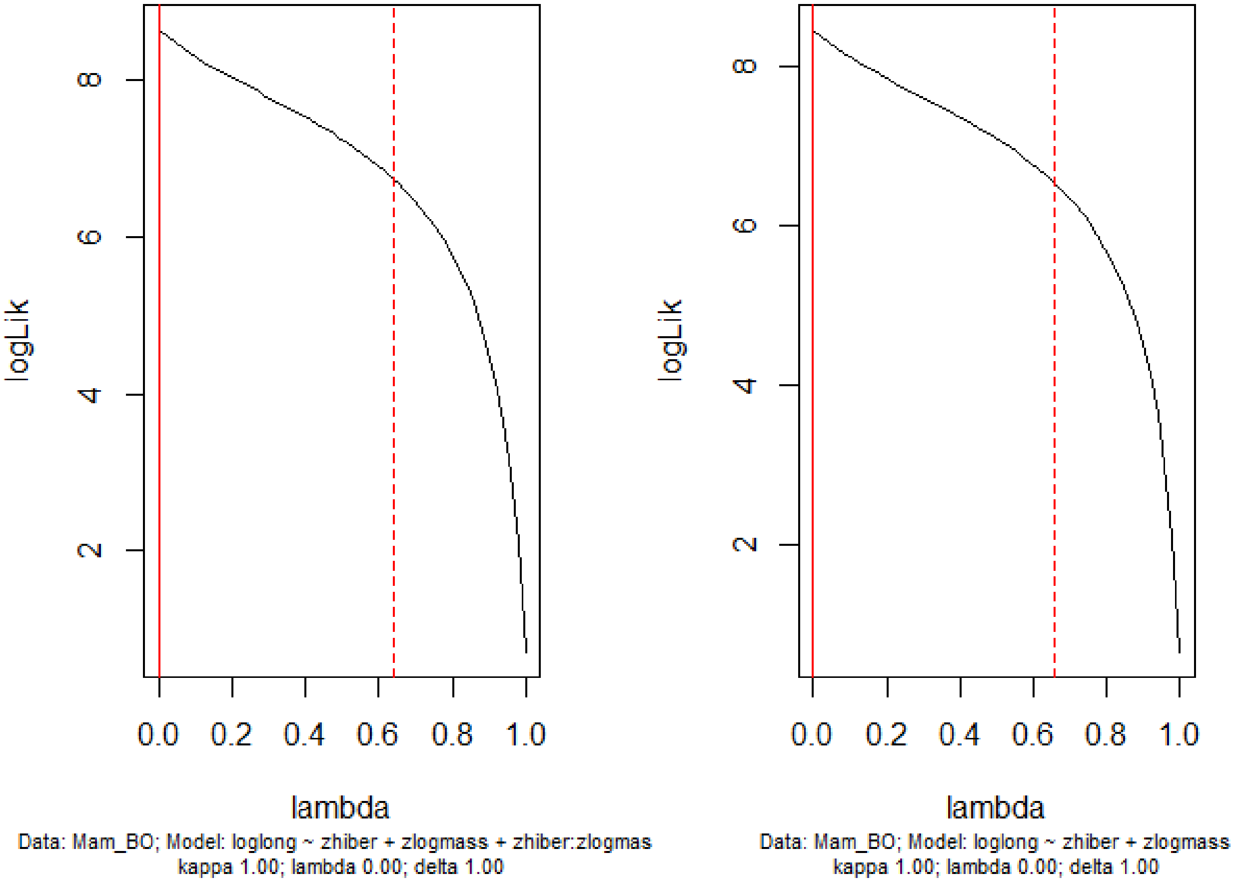

Figure S2: Likelihood profile of λs for bat models only (N = 27): (a) including the effects of hibernation season duration (standardized), body mass (standardized and log transformed) and interaction hibernation duration x body mass, (b) without interaction. logLik represent the likelihood value log-transformed. Lambda (λ) correspond to the relative effect of the phylogenetic tree on the linear model, ranging between 0 (covariation among species measurements is independent of co-ancestry) and 1 (covariance entirely explained by co-ancestry). Location of the maximum likelihood estimate of λ is symbolised by a red line, upper 95% CI is symbolized by a dashed red line. Note that the lower 95% CI can not be estimated.

			λ_{ML}	
		Model terms	AIC	R^2 / R^2_{adj}
Phylogenetic correction (PGLS)	Model 1: All hibernators (82 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+bats+arboreality	-50.51046	0.2653/ 0.2065
		zhiber+zlogmass+C_W+bats+arboreality	-52.49145	0.2637/**0.2152**
		zhiber+zlogmass+bats+arboreality	-52.01818	0.2242/0.1839
	Model 2: Hibernators without bats (55 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-42.84827	0.4048/0.3441
		zhiber+zlogmass+C_W+arboreality	-44.84158	0.4038/0.3561
		zhiber+zlogmass+arboreality	-44.92069	0.3744/0.3376
	Model 3: Deep hibernators without bats (46 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-37.18019	0.2105/0.1118
		zhiber+zlogmass+C_W+arboreality	-39.17963	0.2104/0.1334
		zhiber+zlogmass+arboreality	-38.92486	0.1718/0.1126
		zhiber+zlogmass+	-40.34324	0.1592/0.1201
	Model 4: Small hibernators (<1,5 kg) without bats (44 species)	zhiber+zlogmass+zhiber:zlogmass+C_W+arboreality	-48.57117	0.3206/0.2312
		zhiber+zlogmass+C_W+arboreality	-49.04655	0.3038/0.2324
		zhiber+zlogmass+arboreality	-48.3023	0.2662/0.2112
No phylogenetic correction (linear model)	Model 5: Bats only (27 species)	zhiber+zlogmass+zhiber:zlogmass	-7.308115	0.193/0.0877
		zhiber+zlogmass	-8.912492	0.1811/0.1128

Table S3: Model selection for the effects of hibernation season duration (zhiber), body mass (zlogmass), the interaction zhiber x zlogmass, bats and arboreality lifestyle and the effect of captivity (C_W; captive vs. wild) on longevity in hibernating mammals.

Chapitre 2

Appendix S1

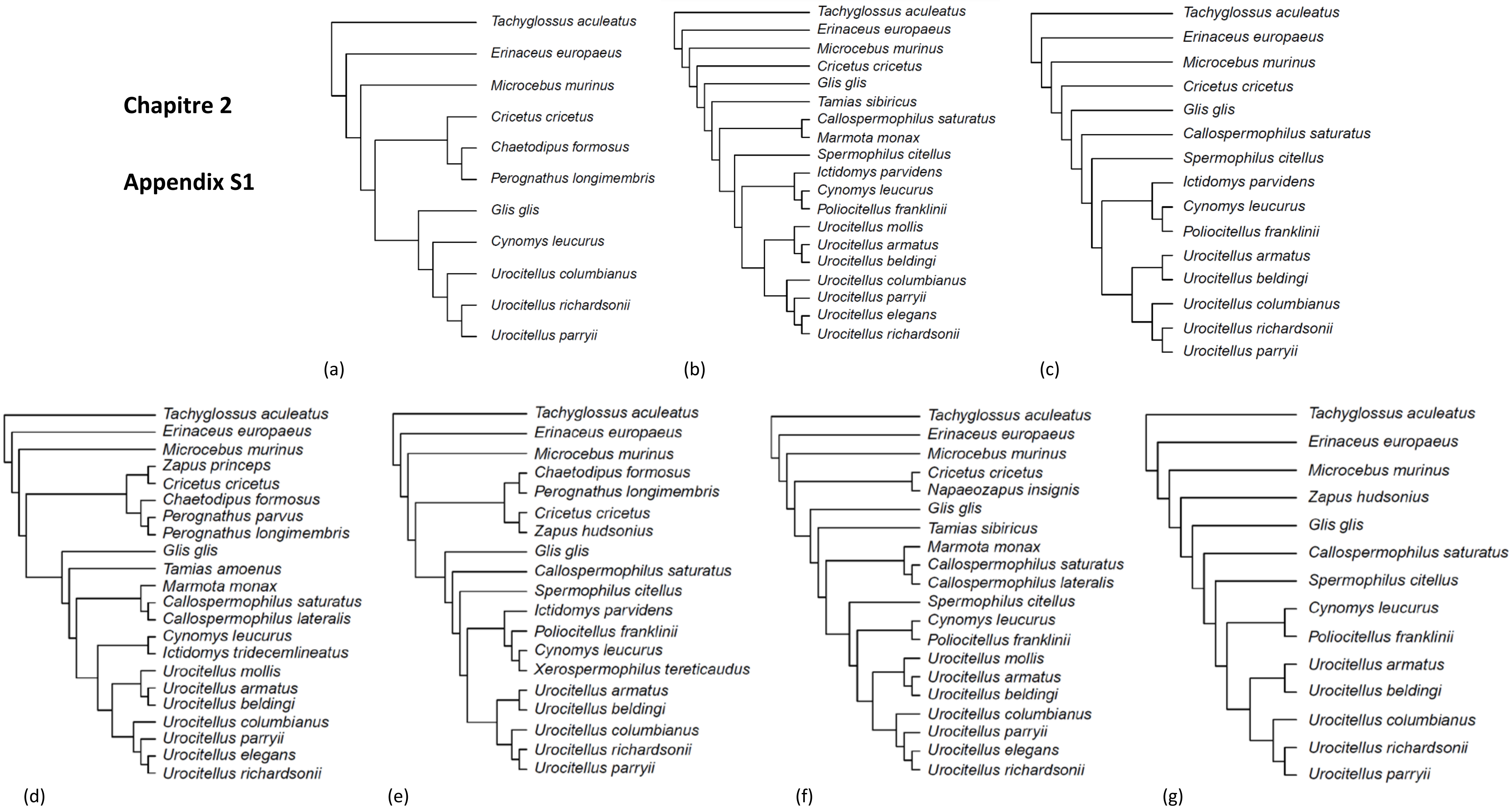

Figure S1. Consensus phylogenetic trees for the species under study: (a) model 1 and 2 (b) model 3 (c) model 4 (d) model 5 (e) model 6 (f) model 7 (g) model 8. Each consensus tree was built from 100 trees obtained from http://vertlife.org/phylosubsets/. Branch lengths were calculated using Grafen's computations with the 'ape' package in R (see Materials and Methods

Appendix S2

Table S1 Data on dependent and independent factors used in models 1 and 2. The body mass gain before mating was used as the dependent factor in model 1 and 2. The body mass change during mating and the relative testes mass (log-transformed) were considered as independent factors in models 1 and 2 respectively. The body mass and testes mass data were used to calculate relative testes mass. Stars indicate body mass extracted from graphs with the software Plot Digitizer at the time of the seasonal maximum in testes mass. For *Cricetus cricetus* and *Tachyglossus aculeatus,* the relative testes mass are directly available in the cited references.

Species	**Body mass gain before mating**	**Body mass change during mating**	**Log (relative testes mass)**	**Body mass (g)**	**Testes mass (g)**
Chaetodipus formosus	7,10[1]	0,83[1]	0,03	19,7[2]	0,21[2]
Cricetus cricetus	9,35 [3]	-5,61[3]	0,16[4]	NA	NA
Cynomys leucurus	4,90[5]	-21,61[5]	-0,25	870[5]	4,88[5]
Erinaceus europaeus	2,74[6,7]	-12,52[6,7]	-0,46	665[2]	2,31[2]
Glis glis	6,63[8]	-8,65[8]	0,16	113,98[9]*	1,632[9]
Microcebus murinus	9,01[10]	-20,71[10]	0,48	70,83[11,12]	2,16[11,12]
Perognathus longimembris	7,85[1]	3,25[1]	-0,05	7,8[2]	0,07[2]
Tachyglossus aculeatus	6,96[13]	-12,73[13]	-0,08[14]	NA	NA
Urocitellus columbianus	8,88[15]	-0,35[15]	-0,02	518[15]*	4,95[16]
Urocitellus parryii	0,49[17]	-21,62[17]	-0,32	936,12[17]*	4,5[16]
Urocitellus richardsonii	6,09[18,19]	-9,96[18,19]	-0,25	371[20]	2,11[20]

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Table S2 Data on dependent and independent factors used in models 3 and 4. Active time after mating was used as the dependent factor in model 3 and 4. The body mass change during mating and the body mass change before and during mating were considered as independent factors in models 3 and 4 respectively. Immergence date for males *Cricetus cricetus,* used to calculate active time after mating*,* have been confirmed by the authors.

Species	**Active time after mating (day)**	**Body mass change during mating (%)**	**Body mass change before and during mating (%)**
Callospermophilus saturatus	129,00[1]	-6,38[1]	-13,13[1]
Cricetus cricetus	50,00[2,3]	-5,61[3]	3,21[3]
Cynomys leucurus	115,00[4,5]	-21,61[5]	-17,77[5]
Erinaceus europaeus	80,75[6–9]	-12,52[6,7]	-10,12[6,7]
Glis glis	62,00[10]	-8,65[10]	-2,59[10]
Marmota monax	174,00[11]	-6,25[11]	NA
Microcebus murinus	162,00[2,3]	-20,71[12]	-13,57[12]
Poliocitellus franklinii	96,00[13,14]	-2,02[13,14]	-4,59[13,14]
Spermophilus citellus	139,00[15]	-9,83[15]	-13,39[15]
Tachyglossus aculeatus	165,00[16]	-12,73[17]	-6,66[17]
Tamias sibiricus	147,00[18]	1,55[18]	NA
Urocitellus beldingi	78,00[19,20]	-1,01[20,21]	-5,47[21]
Urocitellus columbianus	90,00[22,23]	-0,35[24]	8,49[24]
Urocitellus elegans	96,00[25]	-3,82[25]	NA
Urocitellus mollis	69,00[26]	9,47[26]	NA
Urocitellus parryii	141,00[27]	-21,62[28]	-21,24[28]
Urocitellus richardsonii	65,50[29]	-9,96[29,30]	-4,48[29,30]
Ictidomys parvidens	69,00[31]	-10,49[31]	24,48[31]
Urocitellus armatus	58,67[32]	6,82[32]	2,28[32]

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Table S3 Data on dependent and independent factors used in models 5. Protandry was used as the dependent factor and relative testes mass (log-transformed), late mating, strategy fatstoring or foodstoring and minimum temperature were considered as independent factors. Protandry was calculated as follows: male Julian date – female Julian date. The body mass and testes mass data were used to calculate relative testes mass. Stars indicate body mass extracted from graphs with the software Plot Digitizer at the time of the seasonal maximum in testes mass. For *Cricetus cricetus* and *Tachyglossus aculeatus,* the relative testes mass are directly available in the cited references. The exact hibernation phenology data for *Cricetus cricetus* have been confirmed by the authors. See materials and methods for the acquisition of minimum temperature data.

Species	**Protandry (day)**	**Late mating (week)**	**Fatstoring/ Foodstoring**	**Log (relative testes mass)**	**Body mass (g)**	**Testes mass (g)**	**Mininum temperature (°C)**
Callospermophilus lateralis	-9,15[1,2]	2[2,3]	Food[4]	0,24	187,5[5]	3,25[5]	-10,54
Callospermophilus saturatus	-1,00[6,7]	1[7]	Food[7,8]	0,01	227[5]	2,3[5]	-7,50
Chaetodipus formosus	-14,00[9]	4[9]	Food[4]	0,03	19,7[5]	0,21[5]	-7,30
Cricetus cricetus	-20,00[10]	2,5[11,12]	Food[4]	0,16[13]	NA	NA	-2,70
Cynomys leucurus	-21,00[14,15]	1[14]	Fat	-0,25	870[14]	4,88[14]	-11,80
Erinaceus europaeus	-17,58[16,17]	1[17,18]	Fat	-0,46	665[5]	2,31[5]	-5,30
Glis glis	-30,00[19]	1[20]	Fat[19]	0,16	113,98[21]*	1,632[21]	-2,50
Ictidomys tridecemlineatus	-7,00[22]	1[22]	Fat	-0,12	228[23]	1,7308[23]	-11,60
Marmota monax	-22,00[24]	1[25]	Fat	-0,75	4165[5]	7,4[5]	-11,50
Perognathus longimembris	-14,00[26]	4[9]	Food[4]	-0,05	7,8[5]	0,07[5]	-7,30
Perognathus parvus	-23,23[27]	4[27]	Food[4]	-0,02	18,8[5]	0,18[5]	-4,20
Tachyglossus aculeatus	-45,00[28]	1[28]	Fat	-0,08[29]	NA	NA	3,60
Tamias amoenus	-10,50[26]	1[26]	Food[4]	0,29	46,8[5,30]	0,92[5,30]	-7,30
Urocitellus armatus	-4,05[31–33]	1[34]	Fat	-0,19	314,5[35]	2,0155[35]	-14,29
Urocitellus beldingi	-9,00[36]	1[34]	Fat	-0,03	231,65[37]	2,144[37]	-12,40
Urocitellus columbianus	-13,28[38,39]	1[34]	Fat	-0,02	518[39]*	4,95[40]	-16,80
Urocitellus mollis	-15,00[41]	1[42]	Fat	-0,27	115,19[42]*	0,62 [43]	-5,40
Urocitellus parryii	-12,5[44]	1[34]	Food[8]	-0,32	936,12[45]*	4,5[40]	-29,85
Urocitellus richardsonii	-12,87[8,46–51]	1[34]	Food[8]	-0,25	371[52]	2,11[52]	-16,60
Zapus princeps	-10,33[53]	1[53]	Fat	-0,40	27,2[53]	0,109[53]	-14,10

Urocitellus elegans	-17,33[54]	1[34]	Fat	-0,19	279[55]	1,8[55]	-16,60
Microcebus murinus	-48,00[56]	1[56]	Fat	0,48	70,83[30,57]	2,16[30,57]	14,60

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Table S4 Data on dependent and independent factors used in models 6 and 8. For the model 6, protandry was used as the dependent factor and body mass change before mating, late mating, strategy fatstoring or foodstoring and minimum temperature were considered as independent factors. Model 8 included the same dependent and independent factors with the exception of the late mating factor and species with late mating (indicated by a star) excluded from the model. The exact hibernation phenology data for *Cricetus cricetus* have been confirmed by the authors. Protandry was calculated as follows: male Julian date – female Julian date. See materials and methods for the acquisition of minimum temperature data.

Species	**Protandry (day)**	**Fatstoring/Foodstoring**	**Late mating (week)**	**Body mass change before mating (%)**	**Mininum temperature (°C)**
Callospermophilus saturatus	-4,00[1]	Food	1[1]	-7,21[1]	-7,30
*Cricetus cricetus***	-20,00[2]	Food	2,5[3,4]	9,35[5]	-2,70
Cynomys leucurus	-21,00[6,7]	Fat	1[6]	4,90[6]	-11,80
Erinaceus europaeus	-17,58[8,9]	Fat	1[9,10]	2,74[8,9]	-5,30
Glis glis	-30,00[11]	Fat	1[12]	6,63[11]	-2,50
Microcebus murinus	-48,00[13]	Fat	1[13]	9,01[14]	14,60
Poliocitellus franklinii	-11,00[15,16]	Fat	1[15,16]	-1,72[15,16]	-21,10
Spermophilus citellus	-23,00[17]	Fat	1[18]	-3,95[17]	-2,50
Tachyglossus aculeatus	-45,00[19]	Fat	1[19]	6,96[20]	3,60
Urocitellus beldingi	-9,00[21]	Fat	1[18]	-6,27[21]	-12,40
Urocitellus columbianus	-7,00[22]	Fat	1[18]	8,88[22]	-17,50
Urocitellus parryii	-14,00[23]	Food	1[18]	0,49[24]	-30,20
Urocitellus richardsonii	-16,02[25–28]	Food	1[18]	6,09[26,28]	-14,42
Zapus hudsonius	-14,00[23]	Fat	1[29]	-8,88[29]	-8,50
Urocitellus armatus	-5,00[30]	Fat	1[18]	-13,55[30]	-13,00
*Chaetodipus formosus***	-14,00[31]	Food	4[31]	7,10[31]	-7,30
*Ictidomys parvidens()***	-7,50[32]	Fat	6[32]	39,06[32]	-2,40
*Perognathus longimembris***	-14,00[33]	Food	4[31]	7,85[33]	-7,30
*Xerospermophilus tereticaudus***	-5,25[34]	Fat	4[34]	5,10[34]	2,40

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Table S5 Data on dependent and independent factors used in models 7. Sex difference in immergence was used as the dependent factor whereas active time after mating and maternal effort were considered as independent factors. The exact hibernation phenology data for *Cricetus cricetus* have been confirmed by the authors. Sex difference in immergence was calculated as follows: male Julian date – female Julian date.

Species	**Active time after mating (day)**	**Sex difference in immergence (day)**	**Maternal effort (day)**
Callospermophilus saturatus	129,00[1]	-3,00[1]	70,00[2,3]
Cricetus cricetus	50,00[4,5]	-27,00[4]	43,00[3]
Cynomys leucurus	115,00[6,7]	-11,00[6]	67,00[2]
Erinaceus europaeus	80,75[8–11]	-15,71[8,9]	72,00[3]
Glis glis	62,00[12]	-14,00[12]	58,00[3]
Marmota monax	174,00[13]	2,00[13]	76,05[2]
Microcebus murinus	162,00[4,5]	0,00[14]	98,00[3]
Poliocitellus franklinii	96,00[15,16]	-15,75[15,16]	58,00[2]
Spermophilus citellus	139,00[17]	21,25[17]	64,50[2]
Tachyglossus aculeatus	165,00[18]	-24,00[18]	167,5[3]
Tamias sibiricus	147,00[19]	9,80[19]	65,06[2]
Urocitellus beldingi	78,00[20,21]	-20,00[21,22]	51,53[2]
Urocitellus columbianus	90,00[23,24]	-11,77[24]	53,20[2]
Urocitellus elegans	96,00[25]	9,00[25]	55,58[2]
Urocitellus mollis	69,00[26]	-14,50[26]	58,00[2]
Urocitellus parryii	141,00[27]	28,00[27]	53,00[2]
Urocitellus richardsonii	65,50[28]	-12,16[28–31]	51,79[2]
Napaeozapus insignis	83,67[32]	-5,75[32]	65,00[3]
Callospermophilus lateralis	107,50[33]	8,25[33]	71,44[2]
Urocitellus armatus	58,67[34]	8,66[34,35]	45,00[2]

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Chapitre 4

Supplementary Materials S1

The different steps of development and validation of the PCA

To avoid over-fitting (Budaev, 2010), we limited the number of variables included to those most representative of hibernation patterns, namely: date of the first and last torpor bout, the average duration and number of torpor and finally the corrected minimum temperature in torpor. We used the function get_eigenvalue() from the package factoextra (version 1.0.7) to determine the number of principal component that can be extracted with eigenvalue >1 indicating that the principal component concerned explained more variance than a single original variable. We also used two more functions to measure the sampling adequacy of PCA (Budaev, 2010): the cortest.bartlett() from package psych (version 2.2.5) and KMO() from the package EFAtools (version 0.4.1). After this investigation, the date of the first torpor bout, was removed from the PCA because it does not seem adequate with a KMO of 0.23 (KMO < 0.5 are entirely inappropriate, Budaev, 2010). The first component of the PCA including the 4 remaining factors explained 67% of the total variance with an eigenvalue of 2.68. The other components had an eigenvalue <1 and were not retained for further analysis.

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Chapitre 5

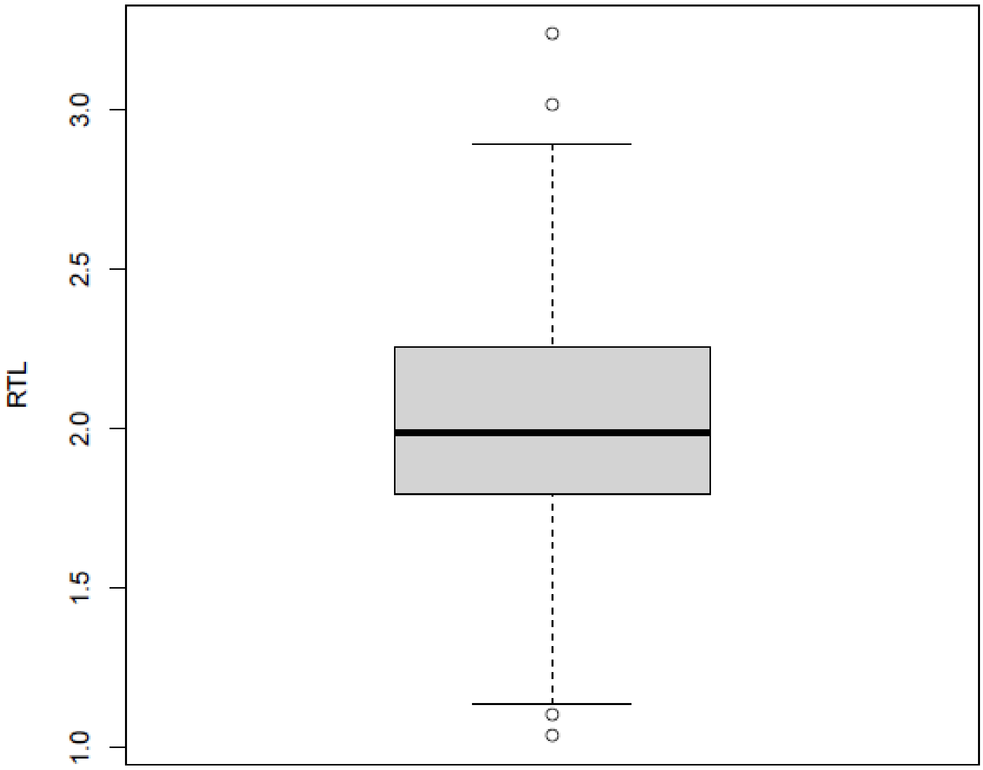

Figure S1. Boxplot of RTL with outliers

Table S1 Regression results for the best models explaining variation RTL and RTL change with mean age and exact age. The model estimates are presented by β. The abbreviation "sr" stands for "square root".

	R^2	**Dependent variable**	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 2	0.31	RTL pre hibernation	Intercept	2.42 ± 0.49	4.85	< 0.001***
			Mean age(sr transformed)	0.002 ± 0.005	0.46	0.64
			Exact age (sr transformed)	-0.02 ± 0.02	-0.88	0.38
Model 4	0.59	RTL change over hibernation	Intercept	1.40 ±0.48	2.87	< 0.001***
			RTL pre hibernation	-0.86 ± 0.12	-6.96	< 0.001***
			Mean age (sr transformed)	0.02 ± 0.01	1.32	0.20
			Exact age (sr transformed)	-0.01 ± 0.006	-2.20	0.03*
Model 6	0.34	RTL post hibernation	Intercept	1.84 ± 0.44	4.12	< 0.001***
			Mean age (sr transformed)	0.02 ± 0.02	1.08	0.29
			Exact age (sr transformed)	-0.01 ± 0.007	-1.96	0.05.
Model 8	0.65	RTL change over active period	Intercept	2.13 ± 0.65	3.26	< 0.001***
			RTL post hibernation	-0.69 ± 0.15	-4.59	< 0.001***
			Mean age (sr transformed)	-0.04 ± 0.02	-1.59	0.12
			Exact age (sr transformed)	0.01 ±0.01	1.58	0.12

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Théo CONSTANT

Causes et conséquences évolutives de la phénologie de l'hibernation

Résumé

Cette thèse vise à comprendre les causes et conséquences évolutives de la phénologie de l'hibernation. Mes résultats montrent que la phénologie de l'hibernation résulterait d'un compromis entre les bénéfices pour la survie d'hiberner et ceux d'être actif pour la reproduction. Par une approche interspécifique, j'ai aussi montré que la longévité augmentait avec la durée de l'hibernation chez 82 espèces. Par contre, j'ai observé par une approche intraspécifique chez le hamster commun, que l'augmentation de la durée de l'hibernation chez cette espèce serait associée à des traits d'histoire de vie rapide (longévité courte, descendance nombreuse). Mes résultats suggèrent enfin que la longévité des hibernants pourrait être expliqué par la réduction du métabolisme pendant l'hibernation et leur capacité d'élongation des télomères quelle que soit la période de l'année. Cette thèse ouvre donc de nouvelles voies dans la compréhension des réponses des espèces hibernantes au changement global.

Mots clés : Hibernation, phénologie, prédation, télomère, vieillissement, traits d'histoire de vie

Résumé en anglais

This thesis aims to better understand the evolutionary causes and consequences of hibernation phenology. My results show that hibernation phenology would be explained by a trade-off between survival benefits of hibernating and benefits of remaining active for reproduction. Using an interspecific approach, I also showed that longer hibernation duration was associated with increased longevity across 82 hibernating species. In contrast to these results, I observed by an intraspecific approach in the common hamster, that the increase in hibernation duration would instead be associated with fast life history traits (short longevity, numerous offspring). My results on the same species also suggest that longevity of hibernators could be explained by the metabolic reduction during hibernation and their ability to elongate telomeres regardless of the time of the year. This thesis therefore opens new avenues in understanding the responses of hibernating species in the context of global change.

Keywords: Hibernation, phenology, predation, telomere, aging, life history traits