

Trade-offs in dormancy phenology in endotherms and ectotherms

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Abstract

Seasonal dormancy (e.g. diapause, hibernation) is widely considered an adaptation for surviving life-threatening conditions during part of the year. However, the selective pressures acting on dormancy are poorly studied. An underestimated common aspect is the high survival rate during dormancy compared to the active period, perhaps due to the reduced risk of predation and competition. We hypothesize that dormancy phenology is influenced by a trade-off between the reproductive benefits of being active and the survival benefits of being dormant. Using a phylogenetic comparative method and more than 20 hibernating mammals, we find that the sex difference in hibernation phenology is explained by sex differences in physiological constraints that may influence this trade-off. Consistent with the trade-off hypothesis, 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). We then gathered evidence that dormancy in non-life-threatening periods that are unfavorable for reproduction may be more widespread than previously thought.

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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 considered an adaptation for surviving life-threatening conditions during part of the year. However, the selective pressures acting on dormancy are poorly studied. An underestimated common aspect is the high survival rate during dormancy compared to the active period, perhaps due to the reduced risk of predation and competition. We hypothesize that dormancy phenology is influenced by a trade-off between the reproductive benefits of being active and the survival benefits of being dormant. Using a phylogenetic comparative method and more than 20 hibernating mammals, we find that the sex difference in hibernation phenology is explained by sex differences in physiological constraints that may influence this trade-off. Consistent with the trade-off hypothesis, 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). We then gathered evidence that dormancy in non-life-threatening periods that are unfavorable for reproduction may be more widespread than previously thought.

1) Introduction

A large number of species across the tree of life enter dormancy each year, presumably to survive predictable harsh living conditions (Cáceres, 1997; Gregory, 1982; Hand, 1991; Ruf and Geiser, 2015; Wilsterman et al., 2021). Seasonal dormancy is an inactive phase, often of several months, which results in a drastic decrease in energy expenditure (Milsom and Jackson, 2011; Staples, 2016). The timing of initiation and termination (viz., the phenology) of dormancy is generally similar from year to year. However, phenological shifts are the most studied responses to climate change (Cohen et al., 2018) with substantial variations in the direction, magnitude, and timing of the phenological response among species (Forrest, 2016; Thackeray et al., 2016). Phenological shifts may have important consequences for population dynamics (Lane et al., 2012; Ozgul et al., 2010), given that dormancy plays a key role in life histories (Constant et al., 2020; Cushman et al., 1994; Franceschini-Zink and Millesi, 2008; Schmidt et al., 2005; Veiga and Salvador, 2001; Wapstra et al., 2001).

In keystone species, such as pollinating, parasitoid insects or zooplankton, variations in dormancy phenology may alter the ecosystem services that these species provide and thus modify entire ecosystems (Doi et al., 2008; 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). From a more anthropocentric point of view, changes in dormancy phenology may have consequences for 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). Understanding the selection pressures that act to shape the phenology of dormancy is therefore important for understanding the diversity of animal responses to climate change and predicting global impacts.

The study of dormancy has been studied independently in different phylogenetic groups (Wilsterman et al., 2021), which limits our understanding of the adaptiveness and generality of dormancy phenology. One major difference that separates the study of dormancy into two main taxa is probably metabolic activity during dormancy. Heterothermic endotherms (mammals and birds) are capable of generating metabolic heat and actively controlling metabolic variations (e.g. hibernation and estivation). Further, for endotherms food availability may be the most limiting factor on activity (Humphries et al., 2003; Lyman et al., 1982; Vuarin and Henry, 2014). In contrast, ectothermic species (invertebrates, fish, amphibians, and reptiles) have metabolic rates that are more subject to microclimatic fluctuations (Milsom and Jackson, 2011; Staples, 2016). As a consequence, seasonal inactivity of ectotherms may be more temperature dependent than in endotherms (Buckley and Jetz, 2010; Gao et al., 2015; Sexton and Hunt, 1980). This ectotherm-endotherm distinction helps to explain species distributions (Buckley et al., 2012).

In either case, however, when environmental conditions generally worsen with increasing latitude and altitude (e.g., increased annual fluctuation in temperature or the timing of food availability), a longer dormancy period is expected (Bronson, 1979; Pianka, 1970; Wilsterman et al., 2021). These variations in phenological timing led to the idea that dormancy was only a means of escaping seasonal life-threatening conditions. However, very few studies have investigated the adaptive role of dormancy phenology. Furthermore, at least a part of the dormancy of some insects (Košťál, 2006; Tauber and Tauber, 1976; Tougeron et al., 2020), reptiles (Etheridge et al., 1983; Jameson Jr, 1974), and mammals (Bieber and Ruf, 2009; Grigg et al., 1989; Humphries et al., 2002) seems to occur without immediate risk of mortality from cold temperature or food deprivation (Constant et al., 2020; Gregory, 1982; Ji, 2011). Despite the ecological and physiological differences in dormancy between phylogenetic

groups (Wilsterman et al., 2021), at least some benefits of being in dormancy may imply similar selection pressures on its phenology.

In some ectotherms and endotherms, longer dormancy is associated with increased longevity (Collatz, 2006; Constant et al., 2020; Lyman et al., 1981; Magombedze et al., 2018; Wiklund et al., 2003; Wilson and Cooke, 2004), higher survival rates compared to the active season (Ruby and Dunham, 1984; Sperry et al., 2010; Turbill et al., 2011; Wilson and Cooke, 2004) sometimes close to 100% (Bauwens, 1981; Litzgus et al., 1999; Tanner and Jorgensen, 1963; Turbill et al., 2011). These survival benefits may produce a trade-off between being active while investing in reproduction and being dormant to increase survival. A widespread example of this trade-off may be the sex difference 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 (Morbey and Ydenberg, 2001; Nicol and Morrow, 2012; Wang et al., 1990; Winck and Cechin, 2008). For females, emergence phenology may promote breeding and/or care of newborn during the most favorable annual period (e.g. at the peak of food availability).

Although males are active above ground, females may not emerge until later to limit mortality risks (see “Waiting cost hypothesis” in 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” in 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, higher 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 mammals, females might be constrained by the duration of maternal effort (e.g. gestation, lactation) from entering hibernation (Levesque et al., 2013), while males (with no paternal care) might rather be influenced by the time needed to recover from the intense stress of mating (Millesi et al., 1998).

In the present study, we tested if sex difference in hibernation phenology among mammal species was influenced by a sex difference in the trade-off between survival and reproduction (vi.z. the trade-off hypothesis). The two hypotheses examined types of sex specific physiological constraints supposed to influence the sex difference in the trade-off. At emergence from hibernation, we expected that at interspecific scale (1) males of species with longer mating preparation would have greater protandry. Mating preparation might increase with the maturation of higher testes mass or higher body mass gain. We tested whether, these parameters increase protandry. We also expected that (2) the species with higher sex difference in the time spent in activity post mating (maternal effort for female and recovery from mating stress for male) would have higher sex difference in emergence, with the sex that spend more time in their post-mating reproductive activity would be the one that emerges the latest. Using phylogenetic models, we tested these two hypotheses in more than 20 promiscuous and polygynous hibernating species. We discussed these results with regard to the numerous studies already conducted on ectotherms. In particular, we present evidence that dormancy may play a role in limiting intra- and interspecific antagonistic relationship. This led us to broaden our vision of the adaptive role of seasonal dormancy and the similar selection pressures on the phenology of ectotherms and endotherms.

2) Materials and methods

a) Review Criteria

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 hibernation phenology (elephant shrew and marsupial's 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). Furthermore, little information is available to analyze the particular phenology 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; Mouhoub sayah

et al., 2009; Randrianambinina et al., 2003). 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: male Julian date – female Julian date.

c) Sex differences in reproductive investment

i. Emergence

For relative testes mass, the 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 privileged data for which body mass of the studied individuals was indicated and 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: $\text{testes mass/body mass} \times 100$.

Relative body mass change between emergence and before mating hereafter referred to as “body mass change before mating” was calculated as follows: $((\text{Body mass before mating} - \text{Body mass at emergence}) / \text{Body mass before mating}) \times 100$.

- Body mass at emergence) / Body mass at emergence)*100. Relative “body mass change 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)*100.

ii. Immergence

In *Spermophilus citellus* (the European ground squirrel), the most actively mating males delay the onset of reserve accumulation of body mass and 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 “active time after mating” (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 female emergence, 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 “body mass change before and during mating” as follows: ((Body mass at the end of mating - Body mass at emergence) / Body mass at emergence)*100.

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 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, the studies were not considered.

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). For females having several litters per season, we were interested in the duration of maternal effort provided to the last litter and not the total time spent over the entire mating season, as the males prepare for hibernation only after the last mating.

d) Climate data

Species living in harsh conditions may be more time constrained by a short active season that might limit 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 km² 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, active time after mating data and minimum temperature, we first averaged by study when data were available over several years and then we averaged all the data for the species. This produces equal weighting between studies on the same species.

Then, while male body mass gain before female emergence is thought to be the cause of early emergence, it may also be the consequence. To answer this question, it is necessary to verify whether body mass gain before mating is related to a mating strategy. Thus, we tested whether the males of species that gain body mass (as dependent variable) are associated with greater competition between males (relative testicle mass) or body mass loss

during mating (as independent variables) as might be expected from capital breeders which use energy store to finance the mating.

To validate the active time after mating 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 active time after mating (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 the two hypotheses, protandry and sex difference in immergence was the dependent variable 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 or the influence of reproduction on hibernation phenology. We tested for lower protandry with decreasing temperature as species living in harsh condition may be more time constrained (Blouin-Demers et al., 2000). We also tested for lower protandry with a later mating period during the active season, as it has been shown for reptiles (Olsson et al., 1999). 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). These food-storing species have been identified according to the list in Vander Wall (1990) and other publications (Bieber and Ruf, 2004; Kenagy et al., 1989; Michener, 1992). In addition, we tested independently the temperature, late mating period and food-storing in interactions with the body mass change before mating and relative testes mass as we

expected their effect to decrease with decreasing temperature, the delay in the mating season, and for food-storing species.

All full models tested are described in Table 1 with their respective sample size (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 multicollinearity using the variance inflation factor ($VIF < 3$) on linear models including the factors of the best models given that PGLS models do not include calculations of VIFs (Ancona et al., 2020; Wartel et al., 2019). 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).

3) Results

a) Preliminary assumption

There is no significant relationship between body mass gain before mating and body mass change during mating as 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, the influence of phylogeny is absent.

Body mass change during mating does not have a significant influence (but almost significant, model 3 in table 2) on the time spent active after mating. However, the body mass lost from emergence until the end of reproduction by males increased significantly with the

time spent active after mating (model 4 in table 2). This result validate the active time after mating as a proxy of the recovery period from reproductive stress for males. In these models, the influence of phylogeny is strong. Nevertheless, by excluding the effect of phylogeny ($\lambda = 0$), we obtain a relatively similar explanatory power and effect size.

b) Emergence

Surprisingly, protandry decreases with the increase in the relative testes mass of the males. By contrast, the relationship is reversed with increasing minimum temperature, so that protandry increases with relative testes mass (model 5 in Table 2 and Fig. 1).

The increase in body mass before mating significantly increase protandry (model 6 in Table 2 and Fig. 2). In addition, a later mating period during the active season appears to reduce protandry in this model.

The two explanatory models for protandry show different influences of covariates. The significant effect of late mating period is not present in the model 5 unlike 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). Similarly, model 6 (Table 2) does not show a significant effect of minimum temperature unlike model 5. However, if we exclude species with late mating period from this model, then the best model includes an interaction between body mass change before mating and annual minimum temperature, but this effect is almost significant (model 8, Table 2). The effect of body mass gain before mating seems to 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 important with phylogeny as without. In addition, the influence of body mass change before mating and late mating are weaker in the model with phylogeny taken into account, which may imply that part of these influences is explained by phylogeny.

c) Immergence

The model 7 (Table 2) highlights the significant influence of the maternal effort and the active time after mating on the sex difference in immergence (Fig. 3). Thus, for the same active time after mating for males, the increase in maternal effort delays the female immergence compared to males. Conversely, for the same maternal effort, the increase in the active time after mating delays the male immergence compared to females. Finally, phylogeny has no influence on this model.

4) Discussion

- a) Sex difference in dormancy phenology
 - i. Endotherms dormancy

As predicted by the trade-off hypothesis, we showed that the sex differences in hibernation phenology are explained by sex differences in energy and time investments in reproduction (Fig. 4). Thus, the sex that spends the least amount of time in an activity directly (e.g. testicular maturation, gestation) or indirectly (e.g. recovery from reproductive stress)

associated with reproduction spends more time hibernating and gives priority to somatic maintenance and survival, hence longevity (Constant et al., 2020; Lyman et al., 1981; Turbill et al., 2011).

Protandry seems to increase in males for which the preparation for reproduction takes longer. To begin with, the more males accumulate energy reserves before mating, the earlier they emerge. This body mass gain does not seem to be the consequence but the cause of an early emergence. Contrary to our expectations, it 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 the female. Further, those males that lose mass before mating might have important costs if they emerge long before females, probably due to harsh conditions.

The difference in emergence date with females increases with the relative testes mass of males in species living in warm environment. Indeed, gonadal maturation requires euthermic conditions and can start during 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 and it seems that gonadal maturation can take several weeks for both sexes (Barnes et al., 1986, 1987; Millesi et al., 2008; Morrow et al.,

2009). Since relative testicular mass is also a proxy for sperm competition (Harcourt et al., 1995), it is possible that the physiological and behavioral preparation associated with this mating strategy influences protandry, but this requires further study. 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 to invest in testes maturation or maintenance in a harsh environment. To avoid this, males of some fat-storing species hoard small amounts of food in their burrows. This energetic supply would support a return to euthermy of up to a few weeks prior to emergence and allow for testes maturation and fat accumulation (Michener, 1992; Williams et al., 2014), while remaining sheltered in the burrow.

As for lizards and snakes (Graves and Duvall, 1990; Olsson et al., 1999), species in 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). Thus, 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 the mating preparation.

Interestingly, the minimum temperature reduces the effect of reproductive parameters on protandry in two models. This seems to confirm a constraint to emergence from harsh environmental conditions. However, adaptations may have evolved to overcome this, such as food hoarding and feeding before emergence. However, as no model included food-storing, 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 gender that immerges first varies among species. Body mass loss in males before and during mating increases the active time after mating and delays the immergence of males 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 that explains the order of immergence. This is in line with observations made at the population level, which show that individuals (males or females), who invest less or not at all in reproduction accumulate reserves earlier and immerge before others (Millesi et al., 1998; Murie and Harris, 1982; Neuhaus, 2000; Nicol and Morrow, 2012).

Bats were not included in this meta-analysis but represent an interesting model because the sex difference in reproduction phenology is very different from most hibernators and thus is supposed to induce other patterns in hibernation phenology (Willis, 2017). In temperate bats, mating takes place just before hibernation during "fall swarming" (Thomas et al., 1979). Females store sperm during winter and ovulation takes place shortly after emergence (Buchanan, 1987). In *Myotis lucifugus* (the little brown bat), males immerge after females probably to increase mating opportunities and recover from body mass loss during mating (Norquay and Willis, 2014). On the contrary, females emerge first, probably because early parturition increases juvenile survival. The patterns observed are consistent with the trade-offs hypothesis outlined in this study. Although few data are currently available, future comparative studies between bat species may enhance our understanding of this hypothesis.

ii. Ectotherms dormancy

Ectotherms have similarities to the dormancy phenology in endotherms (Fig. 4). In ectotherms as well as endotherms, some reproductive parameters seem to be in trade-off with the survival benefits of dormancy and may explain the variations in dormancy phenology between the sexes, especially in emergence date.

Male lizards generally emerge earlier than females, providing time to establish a territory (Hibbitts et al., 2012) and/or mature their testes before mating (Breedveld and Fitze, 2016). Interestingly, protandry disappeared when mating occurs later in the active season (Olsson et al., 1999). The sex difference does not seem to be explained by a difference in the maturation duration of the reproductive organs but rather in timing. Indeed, *Zootoca vivipara* (the viviparous lizard), females do not have developed follicles at emergence and ovulation occurs several weeks after mating (Bauwens and Verheyen, 1985). 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).

In *Gonepteryx rhamni* (the common brimstone), butterfly males emerge from dormancy 3 weeks before females at a time when there is "ample nectar supply". 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). In contrast, females delay emergence despite favorable energetic conditions to coincide with the phenology of the host plant consumed by the larvae. Unlike hibernators, both protandry and protogyny (females emerge before males) are found in insects. Interestingly, it is hypothesized

that protandry is favored when the first male to mate is more likely to fertilize the eggs, a phenomenon present in species where females only breed once just after reaching sexual maturity (Van Timmerman et al., 2001). Males therefore benefit greatly from being ready for reproduction as soon as the females emerge (Alcock et al., 1978; Fagerström and Wiklund, 1982; Wiklund and Fagerström, 1977). In contrast, protogyny is favored in species where the last mating male is more likely to fertilize eggs (Kawakami et al., 2017; Van Timmerman et al., 2001). In this case, there would be greater survival benefits for males than costs to reproduction from staying dormant longer and emerging after females.

This trade-off between survival and reproduction may explain the sex difference in dormancy of up to several months (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.

b) Adaptive role of seasonal dormancy

i. Endotherms dormancy

Hibernation is widely considered to occur in periods of negative energy balance. In our study, several elements might suggest that hibernation occurs even when environmental conditions allow for a positive energy balance. Gains in body mass 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 month more) while males were gaining body mass 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 both species with a sexual dimorphism biased towards males or females (Table 3). Moreover, in some species, all adult individuals immerse 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.

Of course, hibernation may produce energy savings during extremely harsh climatic conditions. However, the phenology of seasonal hibernation may have multiple evolutionary causes. Thus, as proposed by Ruf *et al.* (2012), hibernation may increase survival during environmental conditions that are not otherwise life-threatening, but it does not favor reproduction. This broader view of the adaptive role of hibernation is also consistent with the fact that some hibernators emerge under unfavorable conditions (Johns and Armitage, 1979; Morton and Sherman, 1978) that may result in a greater loss of body mass after emergence than during hibernation (Snyder et al., 1961). Species with a short active season are constrained to emerge and copulate early in the season to allow sufficient time for the young to grow. Thus, a hibernation 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).

From a broad perspective, hibernation use should be explained by a global cost/benefit approach (Willis, 2017), combining at least two major trade-offs. The first one would be

between reproduction and survival, which should be a good indicator of the time spent underground and thus the beginning and end of heterothermy. The second one would be between the costs and benefits of torpor, which explains especially the duration, the depth and frequency of torpor (Humphries et al., 2003). Future investigations may uncover other trade-offs.

Studying these trade-offs under different environmental conditions would allow a better understanding and ability to predict the impact of climate change on hibernators. For example, our study suggests that hibernation phenology is largely dependent on the annual cycle of body mass variation, especially for males. Although these cycles have an endogenous component in seasonal species (John, 2005), environmental conditions may play an important role in the magnitudes of seasonal changes in body mass. Inter-annual variation in food availability and concurrent droughts, that are expected to be exacerbated by climate change (Trenberth et al., 2014), are already showing different effects on the trade-off between reproduction and survival. For some species, years with reduced food availability are associated with an early emergence (Kawamichi, 1996), which can be further significant when reproduction is skipped (Hoelzl et al., 2015; Munro et al., 2008). But low productivity can also lead to later emergence (Alcorn, 1940; Harris and Leitner, 2004; O'Farrell et al., 1975), probably due to a delay in the accumulation of reserves. This contradicts the view that hibernation duration should necessarily increase with energetic constraints. In *Uroditellus mollis* (the Piute ground squirrel), food-poor years can either result in a delay (Alcorn, 1940) or in an early emergence when reproduction is skipped (Smith and Johnson, 1985). These observations highlight, on the one hand, the complex interaction between environmental conditions, reproduction and the cycle of in body mass change, which determines

immergence. On the other hand, it pinpoints the phenotypic plasticity in the phenology of certain obligatory hibernators in response to environmental variations.

Our study included two non-Holarctic species. Although they represent a very small minority of hibernating species, 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 (Bintz 1984; 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, it is questionable whether the survival benefits of hibernation are limited to energetic benefits for large hibernators (Ruf et al., 2012; Turbill et al., 2011). 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 kind of study demonstrates the influence of hibernation on ecosystem dynamics. But it also raises the question of whether interspecific competition may influence hibernation phenology.

ii. Ectotherms dormancy

It is assumed that dormancy in ectotherms is a simple inactivity phase induced by cold. Although this has already been contested for some species (Gregory, 1982; Mayhew, 1965), only few evolutionary perspectives have been presented. The following observations of a temperature-independent dormancy phenology may be explained by other benefits for survival such as avoiding predators (Ji, 2011; Kroon et al., 2008; Slusarczyk, 1995) or intra- (Tougeron et al., 2018) and interspecific competition (Dyugmedzhiev et al., 2019).

Several observations show that reptiles enter dormancy while ambient temperature is still high enough to promote activity (Jameson and Allison, 1976; Jameson Jr, 1974). A good example is the case of *Aspidoscelis sexlineatus* (the six-lined racerunner), where adult lizards enter hibernation 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. Trade-offs (here between survival and reproduction) are factors responsible for maintaining inter-individual differences within populations (Roff, 2002). 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. A similar phenomenon has been demonstrated in an heterothermic endotherm, *Glis glis* (the edible dormouse), in which younger individuals that have a greater chance of reproducing in subsequent years, delay their emergence for survival benefit at the expense of their reproductive success (Bieber et al., 2018). Other large inter-individual differences may also be explained by the occurrence of both risk-taking and risk-averse strategies within a population (Nussey 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 (Košťál, 2006; Tauber and Tauber, 1976; Tougeron et al., 2020). This strategy is 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 diapause 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). Reproduction may also have an important influence on dormancy phenology of insects. For example, in species for which larvae develop only on one or a few specific host plants, emergence is largely influenced by the phenology of those plants (Diamond et al., 2011; Navarro-Cano et al., 2015; Pratt and Ballmer, 1993). In this case, dormancy may allow survival until the most favorable time for reproduction.

It has been widely demonstrated that dormancy phenology in many ectotherms is influenced by harsh conditions, especially decreasing ambient temperatures or winter duration (e.g. Sexton and Hunt, 1980; Strain et al., 2012; Wilsterman et al., 2021). However, evidence presented above suggests that, in some ectotherms, dormancy phenology may also be part of a strategy to increase survival in unfavorable conditions for reproduction. This kind of strategy has been extensively theorized and modelled to explain the phenology of dormancy in some invertebrates (Cohen, 1970; Hairston Jr and Munns Jr, 1984; Hopper, 1999;

Ji, 2011). Several physiological and behavioral mechanism may allow to enter in 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.

5) 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. Other non-exclusive hypotheses have also been proposed (Morbey and Ydenberg, 2001) and further studies are needed to test them. However, this trade-off seems also to explain dormancy phenology at other scales and highlights important similarities between endotherms and ectotherms. Thus, dormancy in non-life-threatening 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 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 impact on ecosystems.

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7) 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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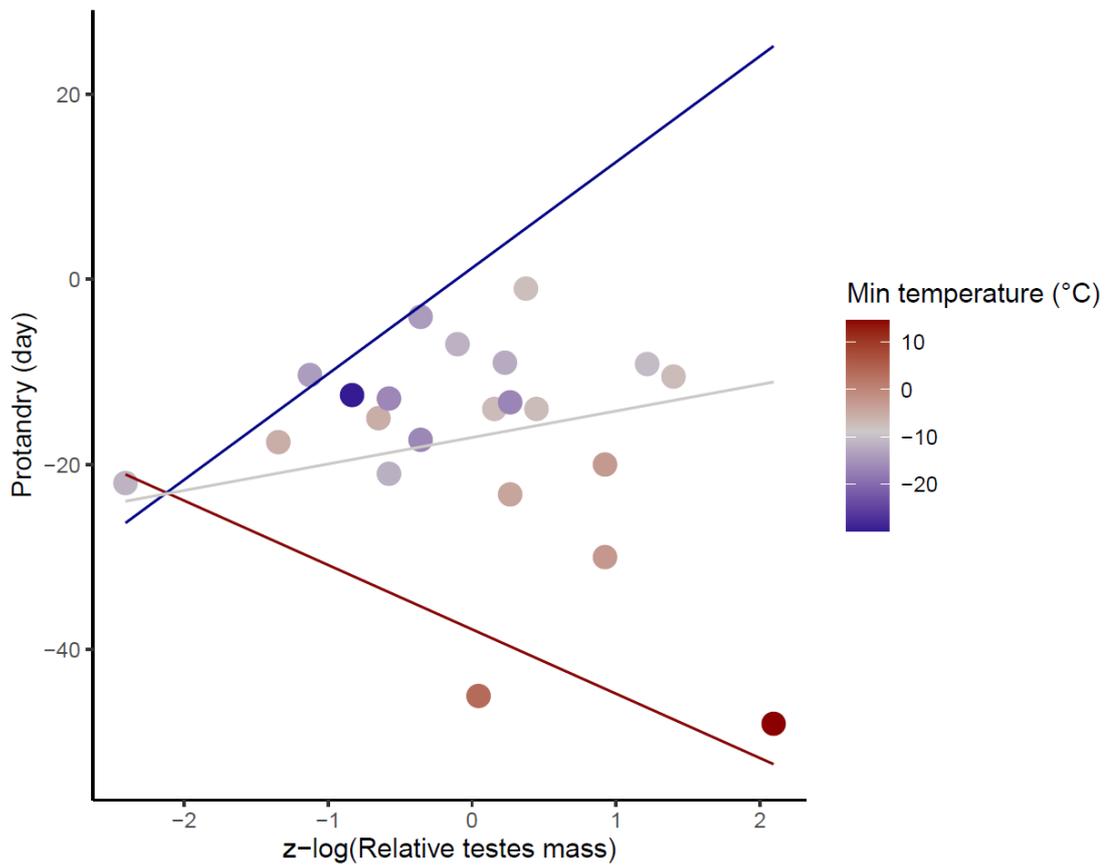
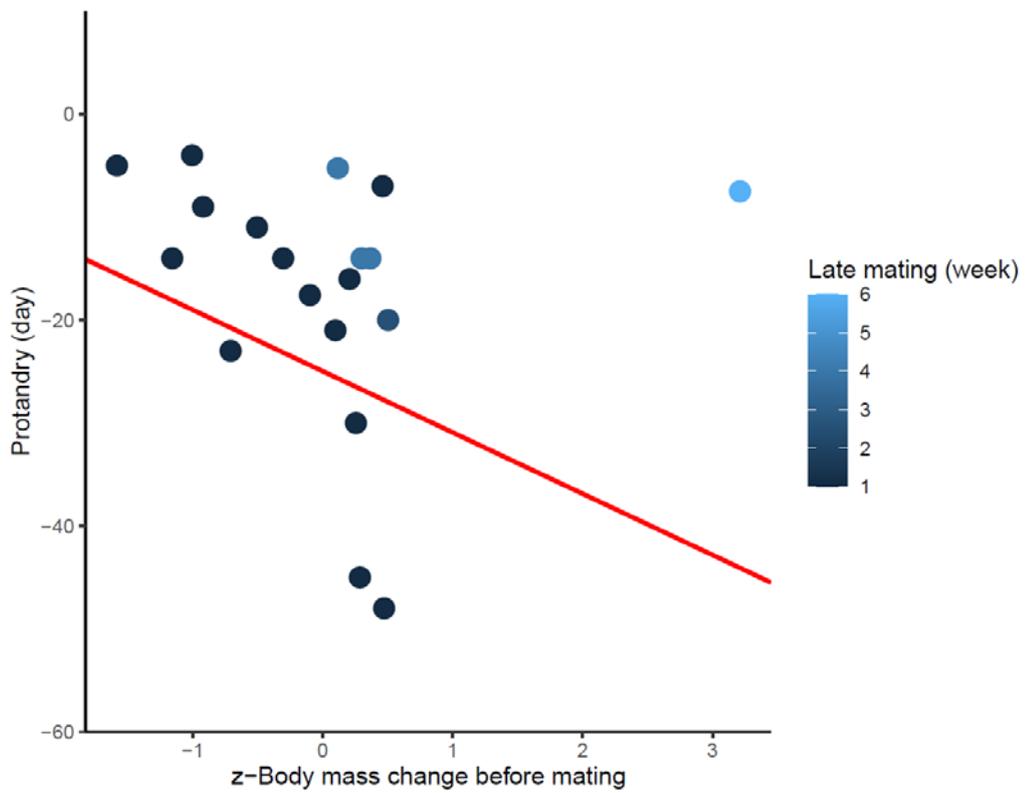


Figure 1 Effects of relative testes mass (standardized and log-transformed) on protandry. The minimum temperatures of the study sites are indicated by a color gradient with the warmest temperatures in red. The regression lines in red, white and blue indicate respectively the effect of log-transformed relative testes mass on protandry when the annual minimum temperature is equal to the max, mean and min value among study sites.



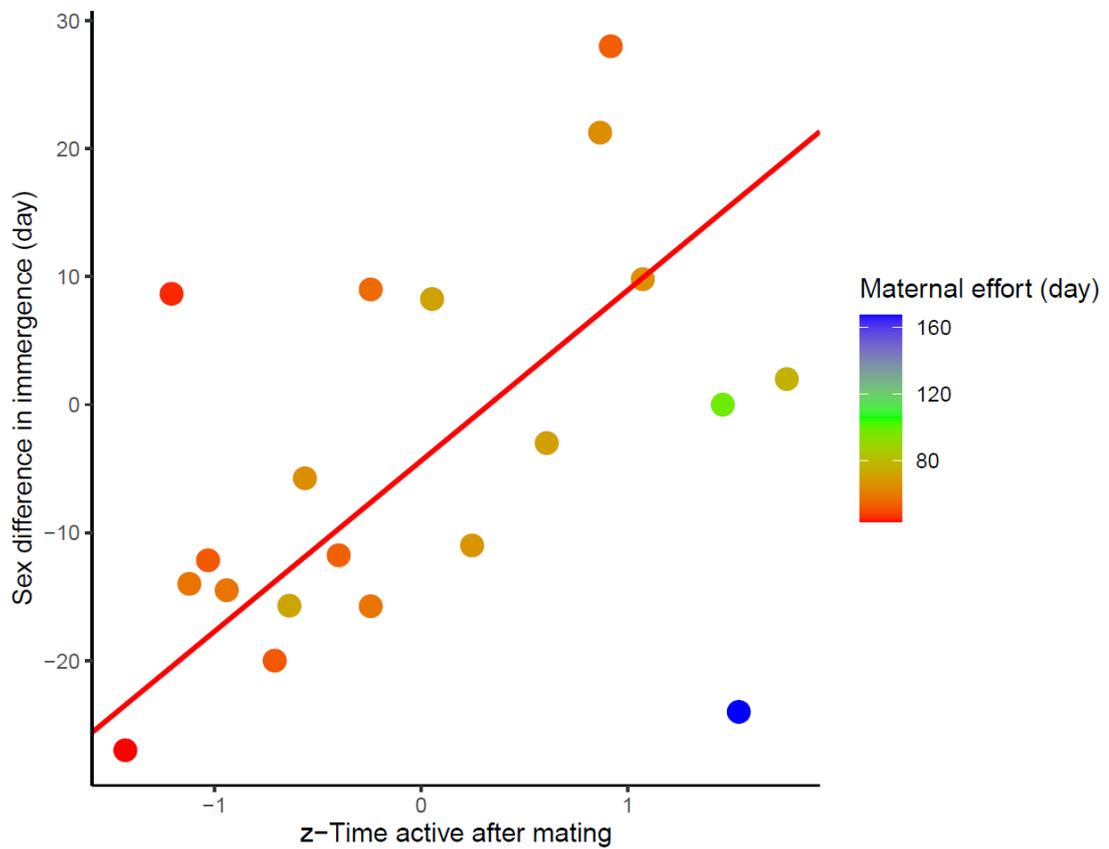


Figure 3 Effects of active time spent by males after mating (standardized) on the sex difference in emergence date. The regression line in red indicates the effect of active time after mating for the same maternal effort. The duration of the maternal effort is represented by a color gradient with the longest effort in blue.

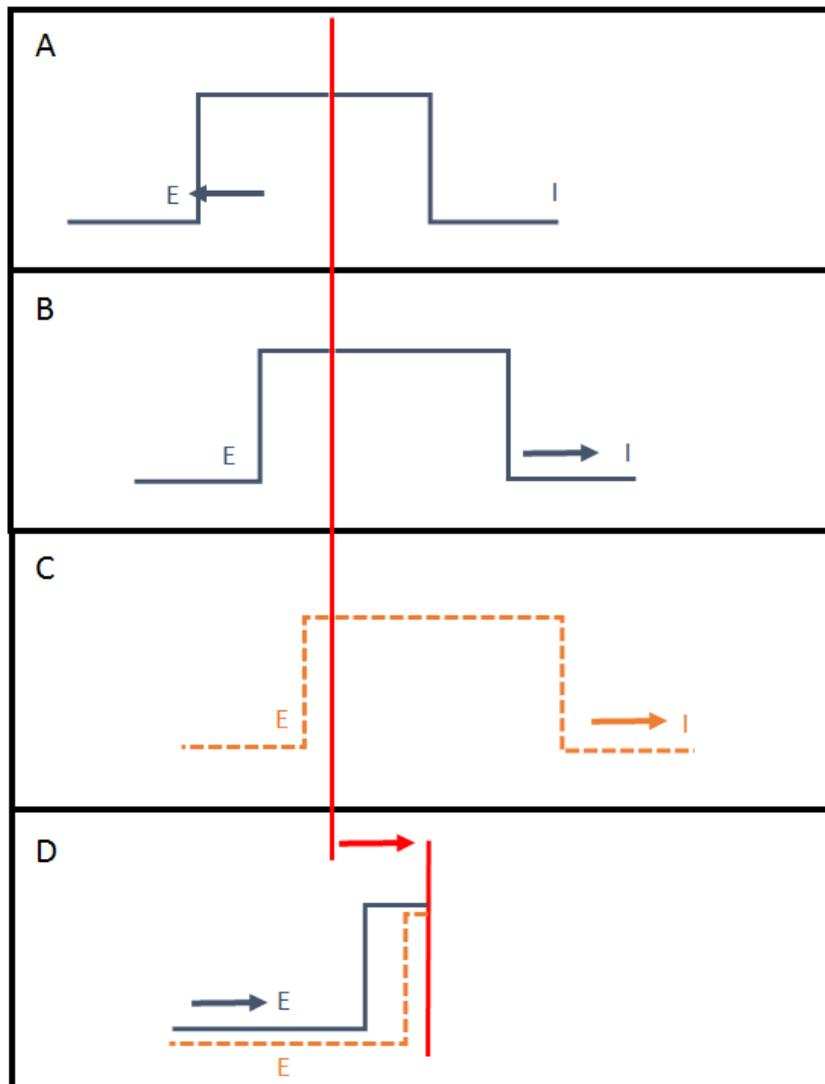
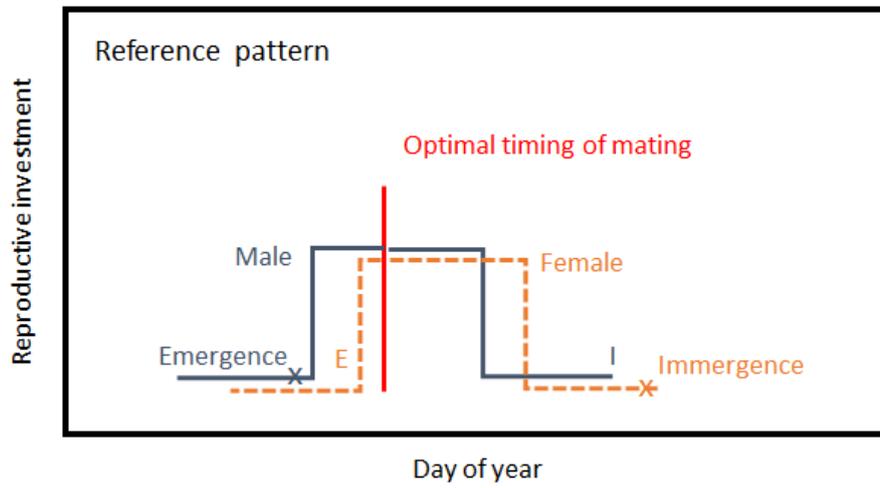


Figure 4 Different patterns of reproductive investment and their influence on sex difference in dormancy phenology. The reference pattern is a hypothetical investment used to illustrate the effect of (A) longer physiological preparation before mating on male emergence (B) a

longer recovery period from mating stress on male immergence (C) a longer maternal effort on female immergence (D) a later optimal mating period compared to female emergence on the sex difference in emergence. Patterns A, B, C, D illustrate the effects of reproductive investment on hibernation phenology measured in this study. Effects of patterns A and D on ectotherm dormancy are also observed (Breedveld and Fitze, 2016; Graves and Duvall, 1990; Hibbitts et al., 2012; Olsson et al., 1999; Wiklund et al., 1996) but B and C remain open questions. Note, the sex difference in the magnitude of the reproductive investment is not to scale. Figure inspired by Willis (2017).

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. The abbreviation "Diff" and "Bmc", stands respectively for "Difference" and "Body mass change".

	Model number	1	2	3	4	5	6	7
	Sample size	11	11	19	15	22	19	20
Dependent variable	Protandry					X	X	
	Sex diff in immergence							X
	Body mass gain before mating	X	X					
	Active time after mating			X	X			
Independent variable	Log(Relative testes mass)		X			X*		
	Bmc before mating						X*	
	Bmc during mating	X		X				
	Bmc before and during mating				X			
	Active time after mating							X
	Maternal effort							X
	Minimum temperature					X*	X*	
	Food-storing					X*	X*	
	Late mating season [Mean mating delay (week)]					X* [1.52]	X* [1.82]	

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", "Bmc", "rel" and "Min temper" stands respectively for "Difference", "Body mass change", "relative" and "Minimum temperature".

	Y_{ML}							$Y = 0$			
	R^2	Y_{ML}	Dependent variable	Independent variable	$\beta \pm SE$	t-value	p-value	R^2	$\beta \pm SE$	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***				
				Bmc 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)	Active time after mating	Intercept	98.25 ± 20.38	4.82	< 0.001***	0.13	90.59 ± 11.31	8.01	< 0.001***
				Bmc 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)	Active time after mating	Intercept	99.15 ± 16.24	6.10	< 0.001***	0.33	89.76 ± 9.01	9.96	< 0.001***
				Bmc before and during 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-Bmc 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 (20 species)	0.47	0.000 (NA, 0.333)	Sex diff in immergence	Intercept	-4.38 ± 2.42	-1.81	0.130				
				z-Active time after mating	13.34 ± 3.18	4.20	< 0.001***				
				z-Maternal effort	-11.20 ± 3.18	-3.53	0.003**				
Model 8 (14 species)	0.79	0.00 (NA, 0.980)	Protandry	Intercept	-17.34 ± 1.82	-9.53	< 0.001***				
				z-Body mass variation before mating	-6.02 ± 1.81	-3.34	0.008**				
				z-Min temperature	-5.25 ± 2.41	-2.17	0.055.				
				z-Body mass variation before mating : z-Min temperature	-6.30 ± 2.84	-2.22	0.051.				

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⁾.

<i>Species</i>	<i>Body size dimorphism</i>	<i>Male body mass gain before mating (% of emergence body mass)</i>	<i>The end of reserve accumulation before hibernation for females</i>
<i>Cricetus cricetus</i>	1,14 ⁽¹⁾	9,35 ⁽²⁾	27 day after male ⁽³⁾
<i>Cynomys leucurus</i>	1,04 ⁽⁴⁾	4,89 ⁽⁵⁾	11 day after male ⁽⁶⁾
<i>Glis glis</i>	0,97 ⁽⁷⁾	6,63 ⁽⁸⁾	14 day after male ⁽⁹⁾
<i>Microcebus murinus</i>	0,96 ⁽¹⁰⁾	9,01 ⁽¹¹⁾	Same time as male ⁽¹²⁾
<i>Uroditellus parryi</i>	0,97 ⁽¹³⁾	0,49 ⁽¹⁴⁾	35 days before male ⁽¹⁵⁾