Running head: Trade-offs in dormancy phenology

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

Théo Constant [1] , F. Stephen Dobson[1,2] , Caroline Habold[1] * & Sylvain Giroud[3,4] *

[1] UMR 7178, Centre National de la Recherche Scientifique, Institut Pluridisciplinaire Hubert CURIEN, Université de Strasbourg, Strasbourg, France

[2] Department of Biological Sciences, Auburn University, Auburn, AL, United States

[3] Department of Interdisciplinary Life Sciences, Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Vienna, Austria

[4] Energetic Lab, Department of Biology, Northern Michigan University, Marquette, MI, USA

***** Co-senior authorship

Corresponding authors: Sylvain Giroud

Address: department of Interdisciplinary Life Sciences, Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Vienna, Austria

E-mail: sgiroud@nmu.edu

Data accessibility statement: the data and computer code supporting the results are available at https://github.com/Theo-Constant/Trade-offs-in-dormancy-phenology.git

Acknowledgments: the authors are grateful to the researchers for providing specific information on previous studies including published data, in particular to Carina Siutz, Danielle Levesque, Andrey Tchabovsky, Eric Rickart, Philip Leitner and John Hoogland for sharing data, some of which have been used in the meta-analysis of this article. The authors are also grateful to John Drake who provided excellent suggestions for manuscript improvements. SG was financially supported by the Austrian Science Fund (FWF, Grant No. P31577-B25) and the Austrian Agency for International Cooperation in Education and Research (OeAD – Scientific and Technological Cooperation, Grant No. FR 09/2020).

Abstract

Seasonal animal dormancy, hibernation or diapause, is widely interpreted as a physiological response for surviving energetic challenges during the harshest times of the year. However, there are other mutually non-exclusive hypotheses to explain the timing of animal dormancy over time, that is, entry into and emergence from hibernation (i.e. dormancy phenology). Other survival advantages of dormancy that have been proposed are reduced risks of predation and competition (the "life-history" hypothesis), but comparative tests across animal species are not yet available. Under this hypothesis, dormancy phenology is influenced by a trade-off between the reproductive advantages of being active and the survival benefits of being in dormancy. Thus, species may emerge from dormancy when reproductive benefits occur, regardless of the environmental conditions for obtaining energy. Species may go into dormancy when these environmental conditions would allow continued activity, if there were benefits from reduced predation or competition. Within a species, males and females differ in the amount of time and energy they invest in reproduction. Thus, the trade-off between reproduction and survival may be reflected in sex differences in phenology of dormancy.

Using a phylogenetic comparative method applied to more than 20 hibernating mammalian species, we predicted that differences between the sexes in hibernation phenology should be associated with differences in reproductive investment, regardless of energetic status. Consistent with the life-history hypothesis, the sex that spent the less time in activities directly associated with reproduction (e.g. testicular maturation, gestation) or indirectly (e.g. recovery from reproductive stress) spent more time in hibernation. This was not expected if hibernation phenology were solely influenced by energetic constraints. Moreover, hibernation sometimes took place at times when the environment would allow the maintenance of a positive energy balance.

We also compiled, initial evidence consistent with the life history hypothesis to explain the dormancy phenology of ectotherms (invertebrates and reptiles). Thus, dormancy during non-life-threatening periods that are unfavorable for reproduction may be more widespread than previously appreciated.

Keywords: annual cycle, dormancy, energy balance, hibernation, metabolic suppression, overwintering, protandry, reproductive investment, risk spreading.

1) Introduction

A large number of species across the tree of life enter prolonged dormancy each year (Wilsterman et al. 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 (Hoehler and Jørgensen 2013, Staples 2016). From an evolutionary perspective, dormancy improves survival during stressful environmental periods, until subsequent better conditions that favor reproduction (Watts and Tenhumberg 2021). The evolutionary tactic of dormancy has been studied independently among different major phylogenetic groups (Wilsterman et al. 2021), and these separate considerations have limited the development of a global evolutionary framework to explain dormancy.

The dormancy of plants, micro-organisms and some invertebrates 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 that reduce competition and predation (Danks 1992, Satterthwaite 2010, Blath and Tóbiás 2020). The evolution of dormancy is explained as based, for example, on “evolutionarily stable strategies” (Hairston Jr and Munns Jr 1984, Kortessis and Chesson 2019), “life history theory” (Ji 2011, Watts and Tenhumberg 2021), or as a “bet hedging strategy” (Hopper 1999, Joschinski and Bonte 2021).

In most animals, however, the topic of prolonged dormancy has primarily focused on ecophysiological rather than evolutionary biology. Dormancy duration increases with energy constraints in the environment, demonstrating its adaptive role in response to harsh conditions (Pianka 1970, Turbill and Prior 2016, Wilsterman et al. 2021). However, some animals immerge in dormancy while energy availability would allow them to continue their activity, suggesting improved survival and perhaps fitness benefits of being dormant (Jameson and Allison 1976,

Wiklund et al. 1996, Humphries et al. 2002). A reduction in the risk of predation or competition during animal dormancy has been suggested mainly based on increased survival during hibernation compared to the active season (Turbill et al. 2011, Ruf et al. 2012, Constant et al. 2020), in particular from studies of the hibernating edible dormouse (*Glis glis*) (Bieber and Ruf 2009, Bieber et al. 2014, Hoelzl et al. 2015, Ruf and Bieber 2022). To date, however, the generality of an influence of these factors on the evolution of prolonged dormancy lacks attention. This raises the question of whether the timing of animal dormancy, i.e. dormancy phenology, might be exclusively explained by energy constraint or whether other ecological factors may be involved.

In animals, a distinction is made between heterothermic endotherms (mammals and birds) that are able to actively influence their metabolic rate via oxidative metabolism and ectotherms (invertebrates, fish, amphibians, and reptiles) whose metabolic rates are more subject to microclimatic fluctuations (Staples 2016). In both cases, although dormancy drastically reduces energy expenditure, some energy is nonetheless lost in the absence of an external source. 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). If, however, 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 when not investing in reproduction *versus* being dormant at that time to increase survival (the life-history hypothesis). Within species, this trade-off may be reflected by sex differences in the phenology of dormancy.

In a recent study, predation avoidance and sexual selection received support for explaining intraspecific variation in hibernation phenology in the northern Idaho ground squirrel (*Urocitellus*

brunneus, Allison et al. n.d.) 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 (Michener 1983, 1984). Sexual selection may favor a life history in which relatively early-emerging males benefit from greater reproductive success (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 (Manno and Dobson 2008, Hibbitts et al. 2012) prior to mating are likely to have greater reproductive success (Michener 1983, 1984). Thus, greater protandry is assumed to have evolved with longer periods of mating preparation. For females, emergence phenology may promote breeding and/or care of offspring during the most favorable annual period (e.g., a match of the peak in lactational energy demand and maximum 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). During the rest of the year, both sexes are expected to prepare and enter dormancy based on survival benefits when they are no longer investing in or recovering from reproduction.

In the present study, we investigated the “life-history hypothesis”, a non-mutually exclusive hypothesis with the “energy limitation hypothesis” for explaining the phenology of dormancy, especially sex differences within species. To begin with, we predicted from the life-history hypothesis that the sex that invests the least time in reproduction, will spend more time in dormancy, regardless of energy shortage (Fig. 1d). On the contrary, if only “energy limitation hypothesis” is true then the sex difference in dormancy phenology is explained by sex differences in energy balance and not by past or future reproductive investment. (Fig. 1c). To examine these predictions, we used two complementary approaches: (i) a set of phylogenetic comparative

analyses, and (ii) a comparison between endotherm and ectotherm dormancy via the conducted analyses (on endotherms) and the existing literature (on ectotherms).

First, using phylogenetic comparative analyses, we compared reproductive and hibernation traits that might tradeoff and coevolve in more than 20 hibernating mammals. We examined types of sex-specific physiological constraints that have been suggested to influence sex differences 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 greater body mass gain. We tested whether one or both of 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 the timing of immergence, with the sex that spends more time in their post-mating reproductive activity also being the one that immerges the latest. This is predicted by the life-history hypothesis, but not by the energy limitation hypothesis (compare Fig 1c and 1d).

Secondly, there is a need to unify the study of dormancy across ectotherms and endotherms for answering fundamental questions (Wilsterman et al. 2021). While there are insufficient data on dormancy phenology and reproductive investment in ectotherms to allow a comparative analysis, we examined, as a second step, the relationships between reproductive investment, energy balance, and dormancy phenology of ectotherms that are already available in the literature. We compared these studies for ectotherms to our results for endotherms. Finally, we highlighted evidence from the literature for the independence of dormancy phenology from energy balance.

2) Materials and methods

a) Review Criteria

Our literature review was based on 152 hibernating species of mammals (see supplementary material 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). This implies different trade-offs between hibernation and reproduction that require separate analyses. In addition, there were few data available on both reproduction and hibernation for hibernating bat species (see below for traits needed for inclusion; also the Discussion for hypotheses applied to these groups).

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. In total, our literature search allowed inclusion of 29 hibernating mammals in the analyses for which we have both reproduction and hibernation data including mainly rodents, a monotreme, a primate and an *Eulipotyphla* species.

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 (see supplementary material S1 for search criteria).

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

c) Sex differences in reproductive investment

i. Emergence

Males are expected to emerge before females to be physically ready before the emergence of the females and the subsequent reproduction. We expected that maturation of higher relative testes mass (see table 4 in Kenagy and Trombulak, 1986) and a higher accumulation of body mass (Humphries et al. 2002) take more time (see supplementary material S1 for search criteria). The data on testes mass corresponded to the maximum mass reached during the mating season. Relative testes mass was calculated as follows: testes mass/body mass. For males, relative body mass changes between emergence and mating are hereafter referred to as "Δ body mass before mating," and were 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 for males was 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 recently emerged males lost body mass before females emerged from hibernation, which may have resulted in physiological stress. Thus, 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.

Maternal effort duration was calculated as the sum of the gestation and lactation periods(see supplementary material S1 for search criteria).

d) Climate data

Species living in harsh conditions may be constrained by a shorter active season that might influence 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 recorded, and when not provided we determined their location using Google Earth and the location description. Then the location data were used to extract values of the mean temperature of the coldest month (known as "BIO6" in the database and 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 (see supplementary materials S1 for details and phylogenetic mammalian) 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).

The PGLS models used an average datum per species for each factor. For hibernation phenology, body mass change, post-mating activity time 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 during 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 for recovery.

To test for a sex difference in hibernation phenology, protandry and sex difference in immergence were the dependent variables in all our models and relative testes mass, Δ body mass before mating, post mating activity time and maternal effort were independent variables in separate models. 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 more greatly delayed 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 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 change in body mass before mating or with relative testes mass.

Table 1 describes the models tested, with their respective sample sizes (see supplementary materials 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 the 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 improve the fit to 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 was no significant relationship between body mass gain for males before mating and Δ body mass during mating, as would be expected for capital breeding species (model 1 in table 2). However, body mass gain before mating increased significantly with higher relative testes mass (model 2 in table 2). In these models, there was little or no influence of phylogeny.

The change in male 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 loss from emergence until the end of reproduction by males (model 4 in table 2). This result supports 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 appeared strong. Nevertheless, similar results were found when influences of phylogeny were not considered (lambda = 0 in table 2).

b) Emergence

The relationship between 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 in Table 3 and Fig. 2).

Protandry increased significantly with the increase in body mass before mating (model 6 in Table 3 and Fig. 3). At the same time, this pattern was strongest in species for which mating occurred 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 showed different covariate influences. 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 was lower in model 5 compared to model 6 (Table 1). Minimum temperature was not included in model 6 (Table 3), 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. The influence of phylogeny varied greatly among models, with lambda ranging from 0 to 1. By constraining the model to ignore the influence of phylogeny (lambda=0), variable estimates were preserved in model 5.

c) Immergence

The sex difference in immergence date was associated with post-mating activity time for males and maternal effort (model 7 in Fig. 4, Table 3). The sex that spent the most time in these activities

immerged 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 (see supplementary materials S3). Finally, phylogeny had trivial or no influence on this model.

4) Discussion

a) Sex difference in dormancy phenology

In this study, we constrasted two mutually non-exclusive hypotheses about dormancy phenology. Energy limitation hypothesis, which predicts that body sexes should immerge into and emerge from hibernation when food resources are sufficient to support metabolic needs. The life-history hypothesis, on the other hand, suggests that males and females time these events with respect to reproductive advantages. 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 predicts that sex difference in hibernation phenology is related to relatively small sex differences in energy balance regardless of reproductive investment during the active annual period. The life-history hypothesis, however, predicts that the sex with lesser investment of time and energy in reproduction should spend more time in hibernation, regardless of its energy balance. Based on phylogenetic comparative analyses, we compared reproductive traits and dormancy phenology that were 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 for reproduction was less important, protandry diminished. As well, the sex that spent the least amount

of time in post mating activity (maternal effort or recovery from reproductive stress) immerged first. The comparative method, however, did not allow assignment of causation of one variable on the other; that is, of the causal direction of selection pressures between reproductive investments and hibernation phenology.

In response to sexual selection, protandry seems to be higher in species for which mating preparation takes longer for males. Males with greater accumulation of energy reserve before mating showed longer protandry. Contrary to our expectations, this did not serve to compensate for the loss of body mass during the mating period. Rather, body mass gain before mating increased significantly with relative testes mass, a proxy for sperm competition (Harcourt et al. 1995). Thus, in addition to being used as a reserve, males with higher body mass could also have a competitive advantage in gaining access to mating females. Further, 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 evaluation of 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 (Pra et al. 2022) or pre-emergence euthermic period (Barnes et al. 1988, Millesi et al. 2008b). The duration of testes maturation may 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 (Barnes et al. 1986, 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 of investment in testes maturation or maintenance in a harsh environment. To avoid this, males of some fat-storing species hoard 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 (Turbill et al. 2011, Constant et al. 2020).

In ectotherms, testes maturation has also been proposed as a major influence on protandry. In *Zootoca vivipara* (a viviparous lizard), male lizards generally emerged 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. In this species, females did not have developed follicles at emergence and ovulation occured 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 order of 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).

Similar to 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, but rather a substantial accumulation of fat for both sexes, at least in some species (e.g., *Ictidomys parvidens*, Schwanz, 2006). According to the life history hypothesis, 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, as assumed by the energetic limitation hypothesis. A measurement of energy balance at the time of emergence for these species would therefore be necessary to discriminate the hypotheses.

In the results for mammalian species, minimum overwinter 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 was not by itself likely to keep males of some species from emerging earlier (e.g. *Cricetus cricetus*, Siutz et al., 2016). Early emerging males may benefit from consuming higher quality food or in competition with other males (e.g., dominance assertion or territory establishment, Manno and Dobson 2008).

Unlike emergence, the sex that immerges into hibernation first varies among species. Body mass loss in males before and during mating increases the post-mating activity time which was associated with a delays 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) did 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 immerged for the same date of male immergence.

Therefore, it was the sex difference in time spend in reproduction or recovery from reproduction which was correlated with the order of immergence. While this was expected under the life-history hypothesis, the energy hypothesis suggests a fairly close correaspondance between immergence dates of males and females, and no particular pattern with respect to such variables as the length of gestatin and lactation for females. In ectotherms, very few data are available on sex difference in immergence date and therefore do not allow evaluation of this hypothesis.

Bats were not included in this meta-analysis but represent an interesting model for hibernation biology, because the sex difference in reproduction phenology is very different from most hibernators. Thus, bats introduce varied and unique patterns to an understanding of 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, likely increasing their mating opportunities, and then recover from body mass lost during mating (Norquay and Willis 2014). The female bats usually emerge first, probably because early parturition increases juvenile survival. The patterns observed are consistent with the life-history hypothesis. Although few data are currently available, future comparative studies between bat species should enhance our understanding of this hypothesis.

Although the sex difference in dormancy phenology seems to be the most widespread support for a trade-off between survival and reproduction, evidence exists at other scales of life. In mammals, males and females that invest little or not at all in reproduction exhibit advances in energy reserve accumulation and earlier immergence for up to several weeks, while reproductive congeners continue activity (Neuhaus 2000, Millesi et al. 2008a). 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 ectotherms, several studies suggest that the benefits for reproduction (Diamond et al. 2011, Navarro-Cano et al. 2015) and the benefits for survival 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), influence dormancy phenology at the species level. Thus, the life history hypothesis finds important support to explain the phenology of dormancy at different scales (e.g. individual scale, different between sexes). Although the energy limitation hypothesis seems to explain part of dormancy duration (Pianka 1970, Turbill and Prior 2016, Wilsterman et al. 2021) and thus its phenology, in the next section, we presented elements from the study and the literature based on the energy balance that are incompatible with the "energy limitation hypothesis". In the next section, we presented other elements of the study and the literature based on the energy balance that are incompatible with the "energy limitation hypothesis.

b) Dormancy and energy balance

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. Any deviation from this principle may highlight a balance rather in favor of reproduction (by sexual or non-sexual forms of natural selection) or survival (Fig. 1) as expected by the life history hypothesis. 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 (Snyder et al. 1961). 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 adult survival (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 the environment allows a positive energy balance for individuals with comparable energy demands, such as different sexe or age groups. In several species, females stay in hibernation (up to almost 2 months more) while males gain body mass of up to 9% after emergence, or one sex immerges while the second continues to accumulate energy reserves (Table 4). Sexual dimorphism may be responsible for sex differences in energy expenditure (Kenagy et al. 1989) and therefore energy balance. However, these observations concern species with a sexual size dimorphism biased towards both males or females (Table 4). To our knowledge, the only study that measured energy balance at the time of immergence showed that *Tamias striatus* (the eastern chipmunk) immerged while a positive energy balance could be maintained (Humphries et al. 2002). Observations of other species suggest immergence when little food is available, but supposedly enough to support activity (Dobson et al. 1992, Grigg and Beard 2000, Munro et al. 2008, Hoelzl et al. 2015). On the contrary, low productivity can lead to later immergence (Alcorn 1940, 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 ectotherms as well, some observations confirmed a dormancy phenology staggered with respect to the harsh season. In some reptiles and insects, individuals enter dormancy while ambient

temperature and food were still high enough to promote activity (Jameson Jr 1974, Jameson and Allison 1976, Etheridge et al. 1983, Wiklund et al. 1996). In *Elaphe obsoleta* (the black rat snake), part of the variation in emergence date was explained by the fact that smaller and younger individuals emerged 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 proposed, on the contrary, that small individuals, subjected to a higher predation rate in spring, benefited from increased survival while remaining inactive. On the contrary, because of the reproductive benefits of early emergence, males of *Vipera berus* (the common European adder) emerge before females in thermally unfavorable periods, leading to significant mass loss (Herczeg et al. 2007).

In the same way, the majority of insects enter dormancy long before environmental conditions deteriorate, and remain dormant sometimes long after favorable conditions return (Tauber and Tauber 1976, Koštál 2006). 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 (Hopper 1999).

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) (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.

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 constraints explain a part of dormancy phenology in both endotherms and ectotherms (Wilsterman et al. 2021), but a large body of evidence from our study shows some independence of energy balance at the specific times of emergence and immergence into

hibernation. Thus, we expect that dormancy phenology will exhibit multiple evolutionary causes, especially when many species are studied and compared. The occurance of dormancy at high altitude and latitude where few or no energy resources are available over part of the year appears to be a support for the energy limitation hypothesis (Ruf et al. 2012), although this hypothesis could yet be of limited importance in explaining the phenology of the transition from dormancy to activity and *vice-versa*. 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).

5) References

Abdi, H. 2007. Z-scores. Encyclopedia of measurement and statistics 3:1055–1058.

Alcorn, J. R. 1940. Life History Notes on the Piute Ground Squirrel. Journal of Mammalogy 21:160–170.

Allison, A. Z., C. J. Conway, and A. E. Morris. (n.d.). Why hibernate? Tests of four hypotheses to explain intraspecific variation in hibernation phenology. Functional Ecology.

Ancona, S., A. Liker, M. C. Carmona-Isunza, and T. Székely. 2020. Sex differences in age-to-maturation relate to sexual selection and adult sex ratios in birds. Evolution letters 4:44–53.

Barnes, B. M., M. Kretzmann, P. Licht, and I. Zucker. 1986. The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, Spermophilus lateralis. Biology of Reproduction 35:1289–1297.

Barnes, B. M., M. Kretzmann, I. Zucker, and P. Licht. 1988. Plasma androgen and gonadotropin levels during hibernation and testicular maturation in golden-mantled ground squirrels. Biology of reproduction 38:616–622.

Barto, K. 2020. MuMIn: multi-model inference, R package version 1.43. 17.

Bauwens, D., and R. F. Verheyen. 1985. The timing of reproduction in the lizard Lacerata vivipara: differences between individual females. Journal of Herpetology:353–364.

Bieber, C., K. Lebl, G. Stalder, F. Geiser, and T. Ruf. 2014. Body mass dependent use of hibernation: why not prolong the active season, if they can? Functional Ecology:167–177.

534 Bieber, C., and T. Ruf. 2004. Seasonal timing of reproduction and hibernation in the edible dormouse
535 (Glis glis). Life in the cold: Evolution, mechanism, adaptation, and application:113–125.

536 Bieber, C., and T. Ruf. 2009. Summer dormancy in edible dormice (Glis glis) without energetic
537 constraints. Naturwissenschaften 96:165–171.

538 Bieber, C., C. Turbill, and T. Ruf. 2018. Effects of aging on timing of hibernation and reproduction.
539 Scientific Reports 8:1–11.

540 Blath, J., and A. Tóbiás. 2020. Invasion and fixation of microbial dormancy traits under competitive
541 pressure. Stochastic Processes and their Applications 130:7363–7395.

542 Blouin-Demers, G., K. A. Prior, and P. J. Weatherhead. 2000. Patterns of variation in spring emergence by
543 black rat snakes (Elaphe obsoleta obsoleta). Herpetologica:175–188.

544 Breedveld, M. C., and P. S. Fitze. 2016. Experimental evidence that sperm maturation drives protandry in
545 an ectotherm. Oecologia 182:129–137.

546 Buchanan, G. D. 1987. Timing of ovulation and early embryonic development in Myotis lucifugus
547 (Chiroptera: Vespertilionidae) from northern central Ontario. American Journal of Anatomy 178:335–
548 340.

549 Constant, T., S. Giroud, V. A. Viblanc, M. L. Tissier, P. Bergeron, F. S. Dobson, and C. Habold. 2020.
550 Integrating Mortality Risk and the Adaptiveness of Hibernation. Frontiers in Physiology 11.

551 Danks, H. V. 1992. LONG LIFE CYCLES IN INSECTS. The Canadian Entomologist 124:167–187.

552 Diamond, S. E., A. M. Frame, R. A. Martin, and L. B. Buckley. 2011. Species' traits predict phenological
553 responses to climate change in butterflies. Ecology 92:1005–1012.

554 Dobson, F. S., M. J. Badry, and C. Geddes. 1992. Seasonal activity and body mass of Columbian ground
555 squirrels. Canadian Journal of Zoology 70:1364–1368.

556 Dyugmedzhiev, A., M. Slavchev, and B. Naumov. 2019. Emergence and dispersal of snakes after syntopic
557 hibernation. Herpetozoa 32:149.

558 Etheridge, K., L. C. Wit, and J. C. Sellers. 1983. Hibernation in the lizard Cnemidophorus sexlineatus
559 (Lacertilia: Teiidae). Copeia:206–214.

560 Graves, B. M., and D. Duvall. 1990. Spring emergence patterns of wandering garter snakes and prairie
561 rattlesnakes in Wyoming. Journal of Herpetology:351–356.

562 Grigg, G., and L. Beard. 2000. Hibernation by Echidnas in Mild Climates: Hints about the Evolution of
563 Endothermy? Pages 5–19 *in* G. Heldmaier and M. Klingenspor, editors. Life in the Cold. Springer Berlin
564 Heidelberg.

565 Gunderson, A. R., and M. Leal. 2016. A conceptual framework for understanding thermal constraints on
566 ectotherm activity with implications for predicting responses to global change. Ecology Letters 19:111–
567 120.

Hairston Jr, N. G., and W. R. Munns Jr. 1984. The timing of copepod diapause as an evolutionarily stable strategy. The American Naturalist 123:733–751.

Harcourt, H., A. Purvis, and L. Liles. 1995. Sperm competition: mating system, not breeding season, affects testes size of primates. Functional Ecology:468–476.

Herczeg, G., J. SAARIKIVI, A. GONDA, J. PERÄLÄ, A. TUOMOLA, and J. MERILÄ. 2007. Suboptimal thermoregulation in male adders (Vipera berus) after hibernation imposed by spermiogenesis. Biological Journal of the Linnean Society 92:19–27.

Hibbitts, T. J., W. E. Cooper, and M. J. Whiting. 2012. Spatial distribution and activity patterns in African barking geckos: implications for mating system and reproduction. Journal of Herpetology 46:456–460.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology: A Journal of the Royal Meteorological Society 25:1965–1978.

Hoehler, T. M., and B. B. Jørgensen. 2013. Microbial life under extreme energy limitation. Nature Reviews Microbiology 11:83–94.

Hoelzl, F., C. Bieber, J. S. Cornils, H. Gerritsmann, G. L. Stalder, C. Walzer, and T. Ruf. 2015. How to spend the summer? Free-living dormice (Glis glis) can hibernate for 11 months in non-reproductive years. Journal of Comparative Physiology B 185:931–939.

Hopper, K. R. 1999. Risk-spreading and bet-hedging in insect population biology. Annual review of entomology 44:535–560.

Humphries, M. M., D. W. Thomas, C. L. Hall, J. R. Speakman, and D. L. Kramer. 2002. The energetics of autumn mast hoarding in eastern chipmunks. Oecologia 133:30–37.

Jameson, E. W., and A. Allison. 1976. Fat and Breeding Cycles in Two Montane Populations of Sceloporus occidentalis (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 10:211.

Jameson Jr, E. W. 1974. Fat and breeding cycles in a montane population of Sceloporus graciosus. Journal of Herpetology:311–322.

Ji, R. 2011. Calanus finmarchicus diapause initiation: new view from traditional life history-based model. Marine Ecology Progress Series 440:105–114.

Joschinski, J., and D. Bonte. 2021. Diapause and bet-hedging strategies in insects: a meta-analysis of reaction norm shapes. Oikos.

Kawamichi, M. 1996. Ecological Factors Affecting Annual Variation in Commencement of Hibernation in Wild Chipmunks (Tamias sibiricus). Journal of Mammalogy 77:731–744.

Kenagy, G. J., S. M. Sharbaugh, and K. A. Nagy. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269–282.

Kenagy, G. J., and S. C. Trombulak. 1986. Size and Function of Mammalian Testes in Relation to Body Size. Journal of Mammalogy 67:1–22.

Kortessis, N., and P. Chesson. 2019. Germination variation facilitates the evolution of seed dormancy when coupled with seedling competition. Theoretical Population Biology 130:60–73.

Koštál, V. 2006. Eco-physiological phases of insect diapause. Journal of insect physiology 52:113–127.

Kroon, A., R. L. Veenendaal, J. Bruin, M. Egas, and M. W. Sabelis. 2008. "Sleeping with the enemy"—predator-induced diapause in a mite. Naturwissenschaften 95:1195–1198.

Levesque, D. L., O. M. A. Lovasoa, S. N. Rakotoharimalala, and B. G. Lovegrove. 2013. High mortality and annual fecundity in a free-ranging basal placental mammal, Setifer setosus (Tenrecidae: Afrosoricida). Journal of Zoology 291:205–212.

Manno, T. G., and F. S. Dobson. 2008. Why are male Columbian ground squirrels territorial? Ethology 114:1049–1060.

Michener, G. R. 1983. Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? Behavioral Ecology and Sociobiology 14:29–38.

Michener, G. R. 1984. Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality.

Michener, G. R. 1992. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. Oecologia 89:397–406.

Millesi, E., A. Divjak, and A. Strauss. 2008a. Seasonal timing and pre-hibernation fattening in breeding and non-breeding European Ground Squirrels. In: Lovegrove BG, McKechnie AE (eds) Hypometabo-lism in animals: hibernation, torpor and cryobiology. University of KwaZulu-Natal, Pietermaritzburg,:p 289-294.

Millesi, E., S. Huber, J. Dittami, I. Hoffmann, and S. Daan. 1998. Parameters of Mating Effort and Success in Male European Ground Squirrels, Spermophilus citellus. Ethology 104:298–313.

Millesi, E., A. Strauss, T. Burger, I. E. Hoffmann, and M. Walzl. 2008b. Follicular development in European ground squirrels (Spermophilus citellus) in different phases of the annual cycle. Reproduction 136:205–210.

Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673.

Morrow, G., N. A. Andersen, and S. C. Nicol. 2009. Reproductive strategies of the short-beaked echidna–a review with new data from a long-term study on the Tasmanian subspecies (Tachyglossus aculeatus setosus). Australian Journal of Zoology 57:275–282.

Munro, D., D. W. Thomas, and M. M. Humphries. 2008. Extreme suppression of aboveground activity by a food-storing hibernator, the eastern chipmunk (Tamias striatus). Canadian Journal of Zoology 86:364–370.

Navarro-Cano, J. A., B. Karlsson, D. Posledovich, T. Toftegaard, C. Wiklund, J. Ehrlén, and K. Gotthard. 2015. Climate change, phenology, and butterfly host plant utilization. AMBIO 44:78–88.

Neuhaus, P. 2000. Timing of Hibernation and Molt in Female Columbian Ground Squirrels. Journal of Mammalogy 81:571–577.

Norquay, K. J. O., and C. K. R. Willis. 2014. Hibernation phenology of M yotis lucifugus. Journal of Zoology 294:85–92.

O'Farrell, T. P., R. J. Olson, R. O. Gilbert, and J. D. Hedlund. 1975. A Population of Great Basin Pocket Mice, Perognathus parvus, in the Shrub-Steppe of South-Central Washington. Ecological Monographs 45:1–28.

Olsson, M., T. Birkead, and R. Shine. 1999. Can relaxed time constraints on sperm production eliminate protandry in an ectotherm? Biological Journal of the Linnean Society 66:159–170.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, and S. Fritz. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version 5:1–36.

Paradis, E. 2011. Analysis of Phylogenetics and Evolution with R. Springer Science & Business Media.

Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Pianka, E. R. 1970. Comparative Autecology of the Lizard Cnemidophorus Tigris in Different Parts of Its Georgraphic Range. Ecology 51:703–720.

Pinder, A. W., K. B. Storey, and G. R. Ultsch. 1992. Estivation and Hibernation. Environmental physiology of the amphibians:250.

Pra, R. D., S. M. Mohr, D. K. Merriman, S. N. Bagriantsev, and E. O. Gracheva. 2022. Ground squirrels initiate sexual maturation during hibernation. Current Biology 0.

Ruf, T., and C. Bieber. 2022. Why hibernate? Predator avoidance in the edible dormouse. Mammal Research:1–11.

Ruf, T., C. Bieber, and C. Turbill. 2012. Survival, Aging, and Life-History Tactics in Mammalian Hibernators. Pages 123–132 *in* T. Ruf, C. Bieber, W. Arnold, and E. Millesi, editors. Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations. Springer Berlin Heidelberg, Berlin, Heidelberg.

Sandell, M. 1990. The Evolution of Seasonal Delayed Implantation. The Quarterly Review of Biology 65:23–42.

Satterthwaite, W. H. 2010. Competition for space can drive the evolution of dormancy in a temporally invariant environment. Plant Ecology 208:167–185.

Schwanz, L. E. 2006. Annual cycle of activity, reproduction, and body mass in Mexican ground squirrels (Spermophilus mexicanus). Journal of Mammalogy 87:1086–1095.

669 Siutz, C., C. Franceschini, and E. Millesi. 2016. Sex and age differences in hibernation patterns of
670 common hamsters: adult females hibernate for shorter periods than males. Journal of Comparative
671 Physiology B 186:801–811.

672 Slusarczyk, M. 1995. Predator-induced diapause in Daphnia. Ecology 76:1008–1013.

673 Snyder, R. L., D. E. Davis, and J. J. Christian. 1961. Seasonal Changes in the Weights of Woodchucks.
674 Journal of Mammalogy 42:297–312.

675 Staples, J. F. 2016. Metabolic Flexibility: Hibernation, Torpor, and Estivation. Pages 737–771
676 Comprehensive Physiology. American Cancer Society.

677 Stevenson, R. D. 1985. Body Size and Limits to the Daily Range of Body Temperature in Terrestrial
678 Ectotherms. The American Naturalist 125:102–117.

679 Tauber, M. J., and C. A. Tauber. 1976. Insect seasonality: diapause maintenance, termination, and
680 postdiapause development. Annual review of entomology 21:81–107.

681 Thomas, D. W., M. B. Fenton, and R. M. Barclay. 1979. Social behavior of the little brown bat, Myotis
682 lucifugus: I. Mating behavior. Behavioral Ecology and Sociobiology:129–136.

683 Tougeron, K., G. Hraoui, C. Le Lann, J. van Baaren, and J. Brodeur. 2018. Intraspecific maternal
684 competition induces summer diapause in insect parasitoids. Insect science 25:1080–1088.

685 Turbill, C., C. Bieber, and T. Ruf. 2011. Hibernation is associated with increased survival and the
686 evolution of slow life histories among mammals. Proceedings of the Royal Society B: Biological Sciences
687 278:3355–3363.

688 Turbill, C., and S. Prior. 2016. Thermal climate-linked variation in annual survival rate of hibernating
689 rodents: shorter winter dormancy and lower survival in warmer climates. Functional Ecology 30:1366–
690 1372.

691 Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, USA.

692 Wartel, A., P. Lindenfors, and J. Lind. 2019. Whatever you want: Inconsistent results are the rule, not the
693 exception, in the study of primate brain evolution. PloS one 14:e0218655.

694 Watts, J. C., and B. Tenhumberg. 2021. Optimal resource allocation and prolonged dormancy strategies
695 in herbaceous plants. Journal of Ecology 109:218–233.

696 Wiklund, C., V. Lindfors, and J. Forsberg. 1996. Early male emergence and reproductive phenology of the
697 adult overwintering butterfly Gonepteryx rhamni in Sweden. Oikos:227–240.

698 Williams, C. T., B. M. Barnes, G. J. Kenagy, and C. L. Buck. 2014. Phenology of hibernation and
699 reproduction in ground squirrels: integration of environmental cues with endogenous programming.
700 Journal of Zoology 292:112–124.

701 Willis, C. K. R. 2017. Trade-offs Influencing the Physiological Ecology of Hibernation in Temperate-Zone
702 Bats. Integrative and Comparative Biology 57:1214–1224.

Wilsterman, K., M. A. Ballinger, and C. M. Williams. 2021. A unifying, eco-physiological framework for animal dormancy. Functional Ecology 35:11–31.

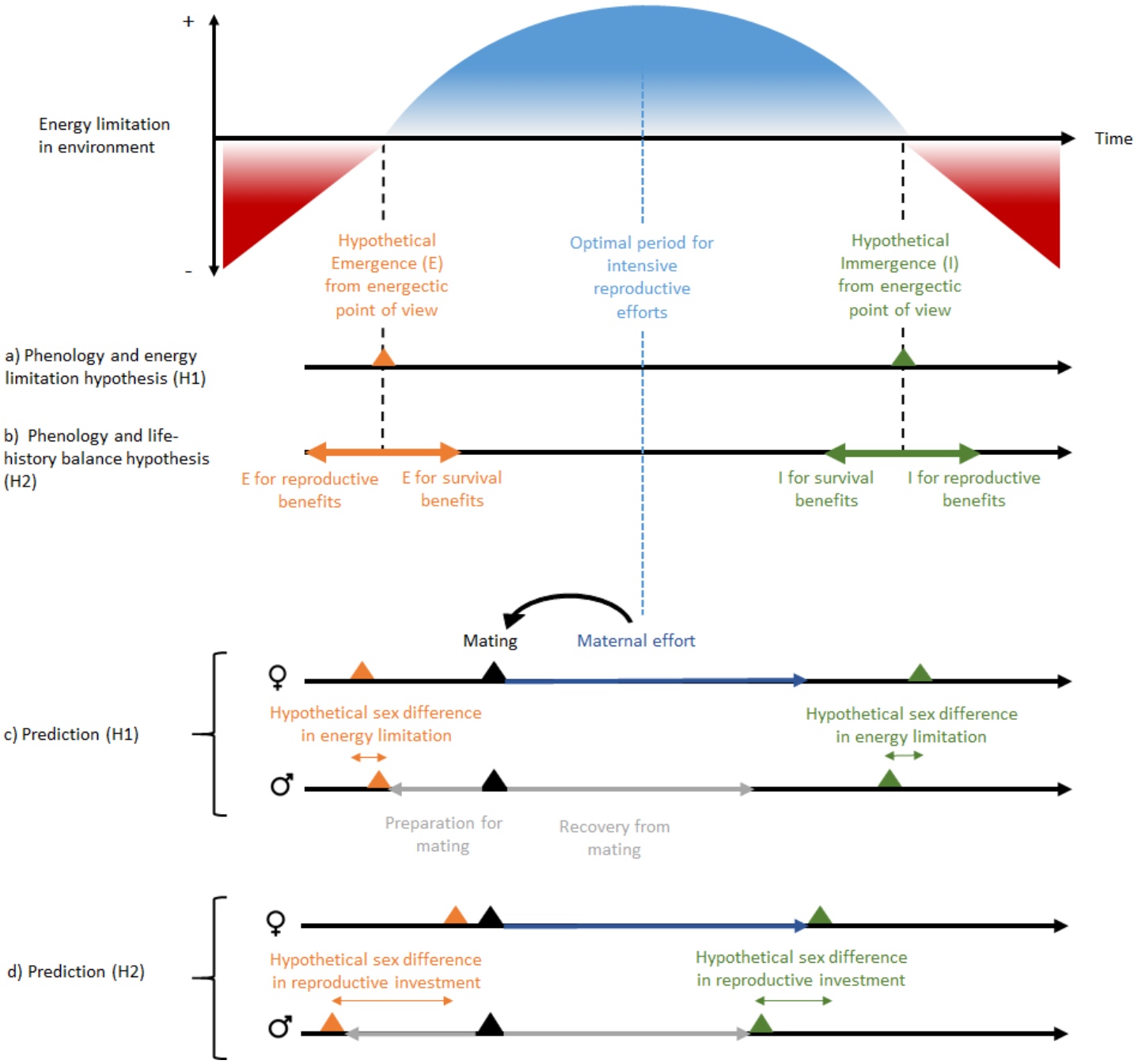

Figure 1 Schematic representation of “the phenology and energy limitation hypothesis” and “the phenology and life-history balance hypothesis” and their predictions. Energetic limitation in the environment refers to variation over time of the energetic balance (mainly for endotherms) and the thermal window 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 explained by differences in energy limitation, and reproductive investment should 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 is expected for species without paternal effort. But the concept can be applied to other types of mating strategies. The hibernation phenology presented for prediction (H1) are 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 is less sex difference 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.

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" stands for "difference".

	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					
	Post-mating activity time			X	X			
Independent variable	Log(relative testes mass)		X			X		
	Δ body mass before mating						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*	
	Food-storing					X*	X*	
	Delay in mating [Mean mating delay (week)]					X* [1.52]	X* [1.82]	

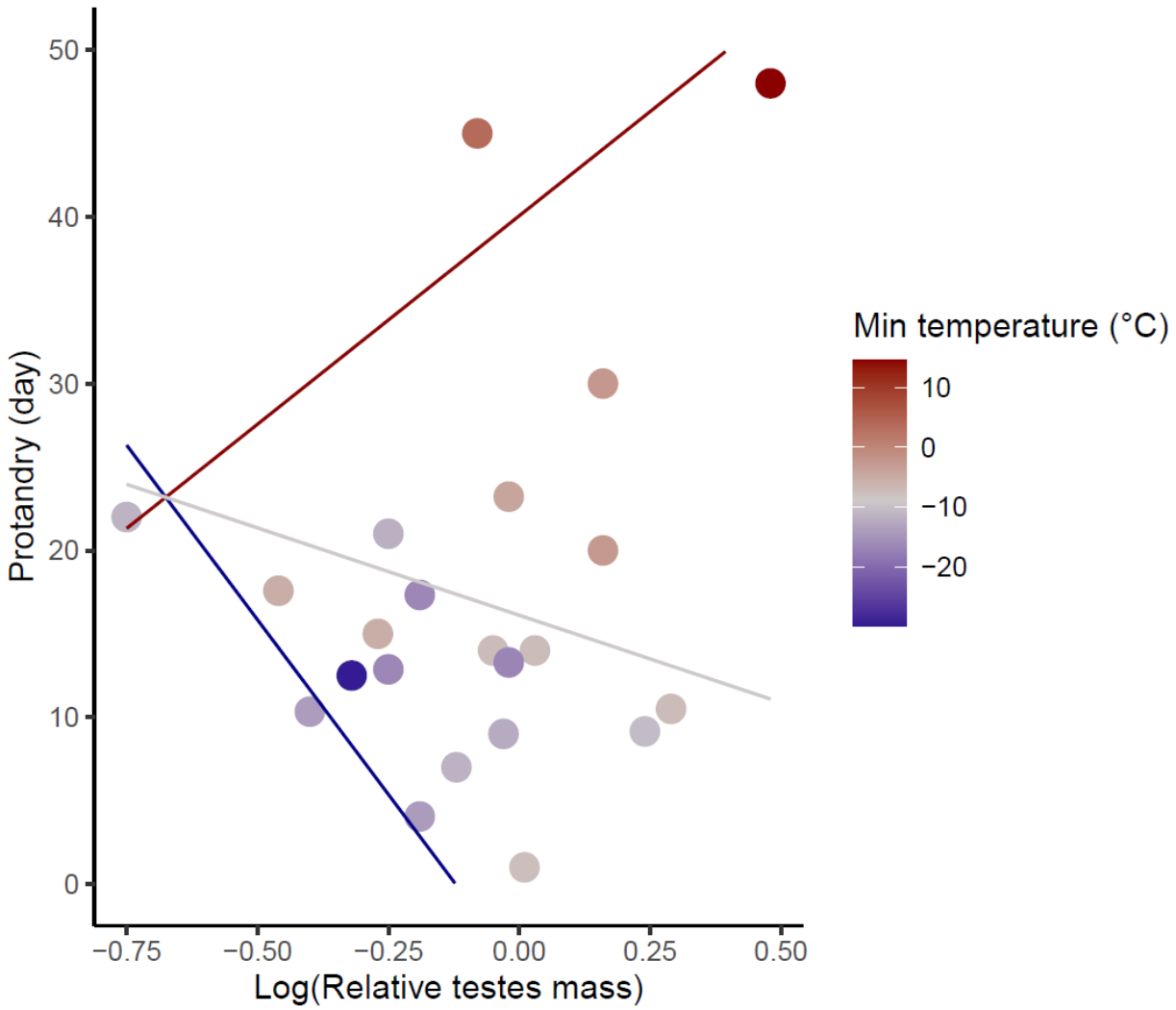

Figure 2 Effects of relative testes mass (log-transformed) on protandry. The minimum temperatures of the study sites are indicated by a color gradient with the warmest temperatures in red. The regression lines in red, light grey and blue indicate respectively the effect of log-transformed relative testes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

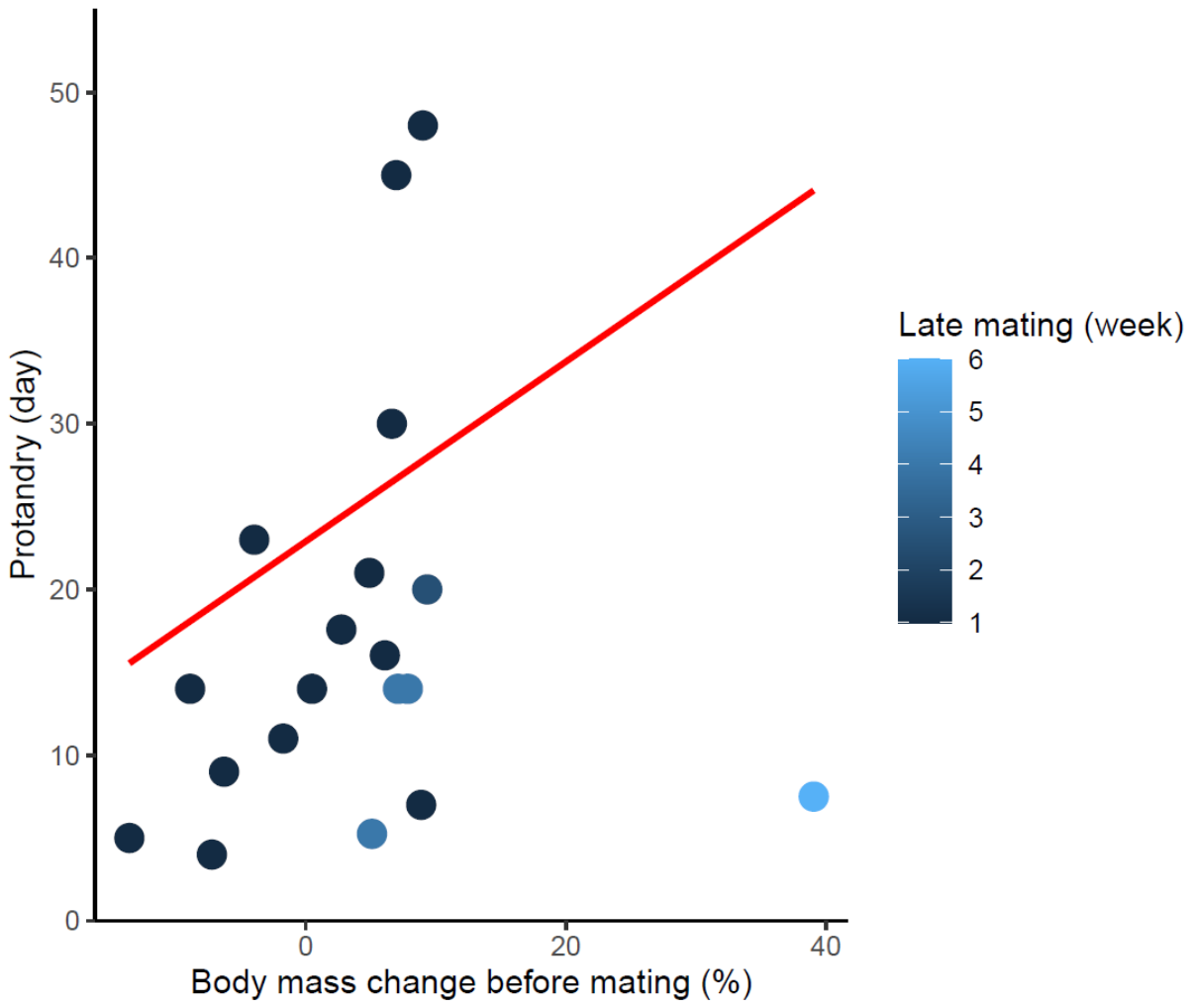

Figure 3 Effects of Δ body mass before mating on protandry. The delay between female emergence and the beginning of the mating period is represented by a color gradient with the greatest delay in light blue. The regression line in red indicates the effect of Δ body mass before mating for the mean mating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

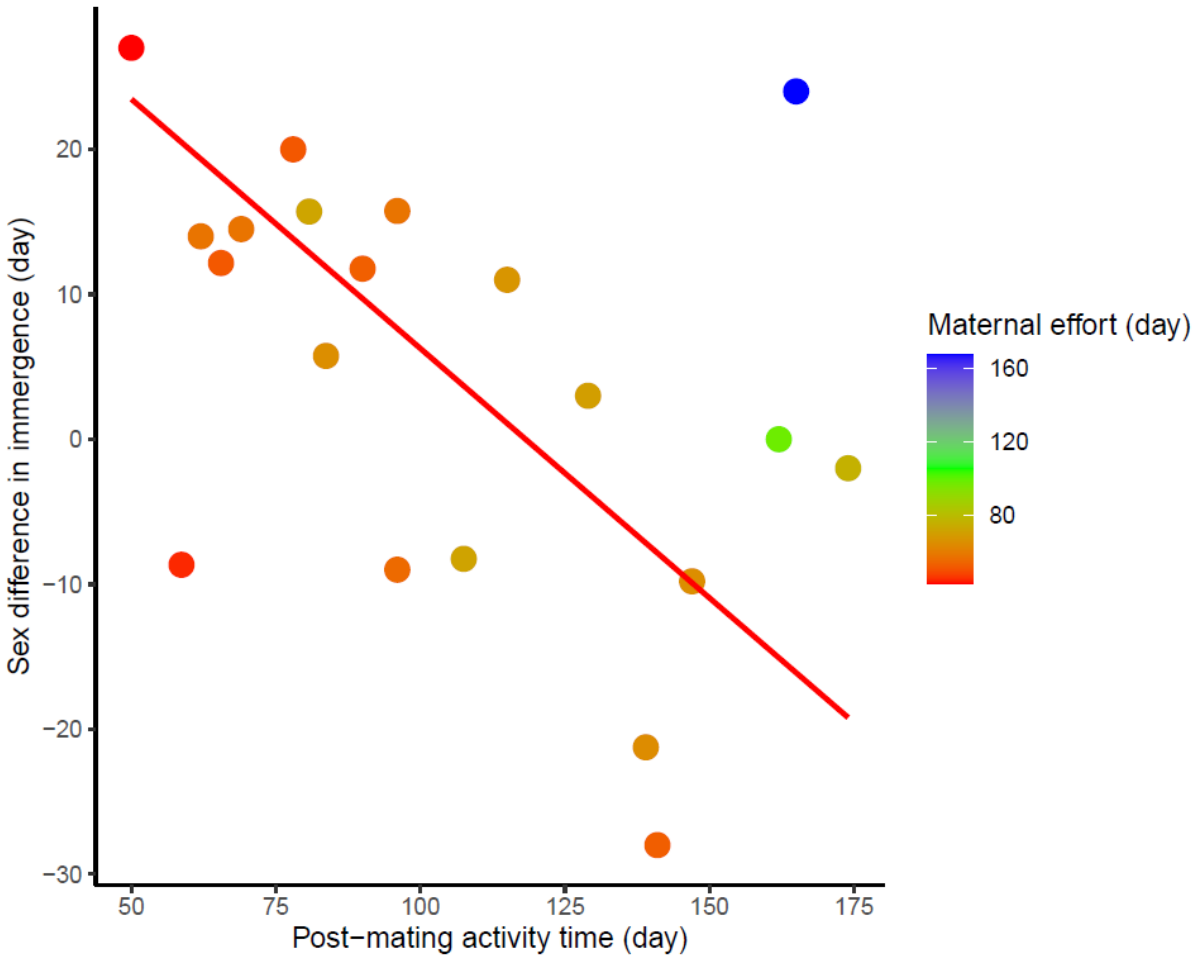

Figure 4 Effects of active time spent by males after mating on the sex difference in immergence date. The regression line in red indicates the effect of post-mating activity time for the mean maternal effort. The duration of the maternal effort is represented by a color gradient with the longest effort 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 preliminary assumption. The Z standardized model estimates and the phylogenetic effect are reciprocally estimated by β and γ_M. 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". 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	0.00 (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	0.00 (NA, 0.56)	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	0.76 (NA, 0.99)	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 *

Table 3 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" and "rel" "Min" stand respectively for "difference", "relative" and "Minimum". 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. 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}	ependent variab	Independent variable	β ± SE	*t*-value	*p*-value	R^2	β ± SE	*t*-value	*p*-value
Model 5 (22 species)	0.47	0.47 (NA, 0.89)	Protandry	Intercept	17.08 ± 3.51	4.87	< 0.001***	0.58	15.34 ± 1.76	8.72	< 0.001***
				z-Log rel testes mass	-2.86 ± 1.79	-1.60	0.126		-2.97 ± 1.97	-1.51	0.167
				z-Min temperature	7.55 ± 2.22	3.40	0.003**		7.88 ± 2.00	3.94	< 0.001***
				z-Log rel testes mass : Min temperature	3.54 ± 1.44	2.46	0.024*		3.56 ± 1.42	2.50	0.022*
Model 6 (19 species)	0.47	1.00 (0.84, 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 (20 species)	0.47	0.00 (NA, 0.33)	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**				

Table 4 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 (See supplementary materials S4 for references).

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	9.35	27 days after male
Cynomys leucurus	1.04	4.89	11 days after male
Glis glis	0.97	6.63	14 days after male
Microcebus murinus	0.96	9.01	Same time as male
Urocitellus parryii	0.97	0.49	35 days before male

Supplementary materials S1

Materials and methods

a) Review Criteria

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 [1]. For example, bears are the only mammals with gestation, parturition and lactation during hibernation [2]. 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.

b) Sex difference in hibernation phenology

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 (see supplementary materials S1 for details). 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 (see supplementary materials S1 for details). This excluded four studies [3–6]. 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 [7] 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 [8,9]. These data were therefore not included in this study.

c) Sex differences in reproductive investment

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). We favored data measured at the same study site as the hibernation phenology data. Otherwise, different data obtained for the same species were averaged.

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 [10] to extract the data from graphs. This software has recently been validated for this use [11]. 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).

d) Statistics

For each PGLS 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 [15]. For each consensus trees (see Figure 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.

References

1. Sandell, M. (1990). The Evolution of Seasonal Delayed Implantation. Q. Rev. Biol. *65*, 23–42. 10.1086/416583.

2. Friebe, A., Evans, A.L., Arnemo, J.M., Blanc, S., Brunberg, S., Fleissner, G., Swenson, J.E., and Zedrosser, A. (2014). Factors Affecting Date of Implantation, Parturition, and Den Entry Estimated from Activity and Body Temperature in Free-Ranging Brown Bears. PLOS ONE *9*, e101410. 10.1371/journal.pone.0101410.

3. Dunford, C. (1974). Annual cycle of cliff chipmunks in the Santa Catalina Mountains, Arizona. J. Mammal. *55*, 401–416.

4. Gashwiler, J.S. (1976). Biology of Townsend's chipmunks in western Oregon. The Murrelet *57*, 26–31.

5. Mouhoub sayah, C., Robin, J.-P., Pévet, P., Monecke, S., Doumandji, S., and Saboureau, M. (2009). Road mortality of the Algerian hedgehog (Atelerix algirus) in the Soummam Valley (Algeria). Rev. Décologie.

6. Randrianambinina, B., Rakotondravony, D., Radespiel, U., and Zimmermann, E. (2003). Seasonal changes in general activity, body mass and reproduction of two small nocturnal primates: a comparison of the golden brown mouse lemur (Microcebus ravelobensis) in Northwestern Madagascar and the brown mouse lemur (Microcebus rufus) in Eastern Madagascar. Primates *44*, 321–331.

7. Munroe, K.E. (2011). The Socioecology, Mating System and Behavior of Round-Tailed Ground Squirrels (Xerospermophilus tereticaudus).

8. Dobson, F.S., and Davis, D.E. (1986). Hibernation and Sociality in the California Ground Squirrel. J. Mammal. *67*, 416–421. 10.2307/1380902.

9. Holekamp, K.E., Nunes, S., and Talamantes, F. (1988). Circulating prolactin in free-living California ground squirrels (Spermophilus beecheyi). Gen. Comp. Endocrinol. *71*, 484–492.

10. Huwaldt, J.A., and Steinhorst, S. (2015). Plot Digitizer, version 2.6. 8 (Software).

11. Aydin, O., and Yassikaya, M.Y. (2021). Validity and reliability analysis of the PlotDigitizer software program for data extraction from single-case graphs. Perspect. Behav. Sci., 1–19.

12. Magalhães, J.P.D., and Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. J. Evol. Biol. *22*, 1770–1774. 10.1111/j.1420-9101.2009.01783.x.

13. Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., et al. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology *90*, 2648–2648. 10.1890/08-1494.1.

14. Upham, N.S., Esselstyn, J.A., and Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol. *17*. 10.1371/journal.pbio.3000494.

15. Paradis, E. (2011). Analysis of Phylogenetics and Evolution with R (Springer Science & Business Media).

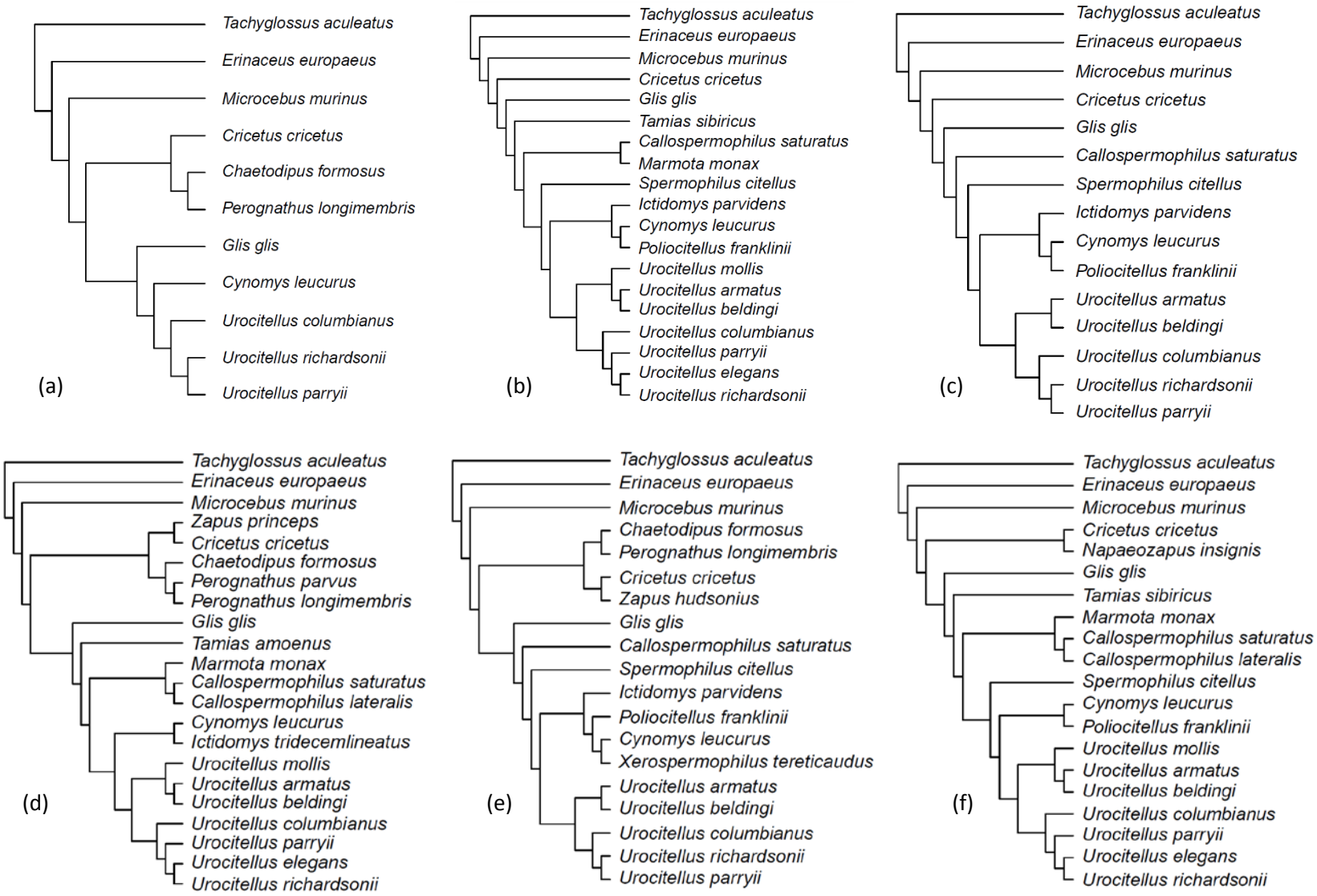

Figure S1. Consensus phylogenetic trees for the species under study: (a) model 1 and 2 (b) model 3 (c) model 4 (d) model 5 (e) model 6 (f) model 7 (g) model 8. Each consensus tree was built from 100 trees obtained from http://vertlife.org/phylosubsets/. Branch lengths were calculated using Grafen's computations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

Supplementary materials 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]

References

1. Kenagy, G. J. & Bartholomew, G. A. Seasonal Reproductive Patterns in Five Coexisting California Desert Rodent Species: Ecological Archives M055-002. *Ecological Monographs* **55**, 371–397 (1985).

2. Kenagy, G. J. & Trombulak, S. C. Size and Function of Mammalian Testes in Relation to Body Size. *Journal of Mammalogy* **67**, 1–22 (1986).

3. Lebl, K. & Millesi, E. *Yearling male Common hamsters and the trade-off between growth and reproduction*. (2008).

4. Pévet, P., Buijs, R. M. & Masson-Pévet, M. Effect of pinealectomy and a constant high level of circulating melatonin or of 5-methoxytryptamine on the vasopressinergic innervation in the brain of the European hamster (Cricetus cricetus, L). *Journal of neural transmission* **70**, 287–294 (1987).

5. Bakko, E. B. & Brown, L. N. Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. *Journal of Mammalogy* **48**, 100–112 (1967).

6. Haigh, A., O'Riordan, R. M. & Butler, F. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). *Acta Theriologica* **57**, 321–331 (2012).

7. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. *Acta theriologica* **59**, 173–181 (2014).

8. Bieber, C. & Ruf, T. Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). *Life in the cold: Evolution, mechanism, adaptation, and application* 113–125 (2004).

9. Kryštufek, B. Compartmentalization of body of a fat dormouse Glis glis. *Trakya Üniversitesi Fen Bilimleri Dergisi* (2001).

10. Schmid, J. & Kappeler, P. M. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (Microcebus murinus). *Behavioral Ecology and Sociobiology* **43**, 125–132 (1998).

11. Lemaître, J.-F., Ramm, S. A., Barton, R. A. & Stockley, P. Sperm competition and brain size evolution in mammals. *Journal of Evolutionary Biology* **22**, 2215–2221 (2009).

12. Soulsbury, C. D. Genetic patterns of paternity and testes size in mammals. *PLoS One* **5**, e9581 (2010).

13. Nicol, S. C., Andersen, N. A., Morrow, G. E. & Harris, R. L. Spurs, sexual dimorphism and reproductive maturity in Tasmanian echidnas (Tachyglossus aculeatus setosus). *Australian Mammalogy* **41**, 161–169 (2018).

14. Morrow, G. E., Jones, S. M. & Nicol, S. C. Interaction of hibernation and male reproductive function in wild Tasmanian echidnas Tachyglossus aculeatus setosus. *Journal of Mammalogy* **97**, 852–860 (2016).

15. Raveh, S. *et al.* Mating order and reproductive success in male Columbian ground squirrels (Urocitellus columbianus). *Behavioral Ecology* **21**, 537–547 (2010).

16. Boonstra, R., Bradley, A. J. & Delehanty, B. Preparing for hibernation in ground squirrels: adrenal androgen production in summer linked to environmental severity in winter. *Functional Ecology* **25**, 1348–1359 (2011).

17. Buck, C. L. & Barnes, B. M. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy* **80**, 430–442 (1999).

18. Michener, G. R. Sexual differences in reproductive effort of Richardson's ground squirrels. *Journal of Mammalogy* **79**, 1–19 (1998).

19. Michener, G. R. & Locklear, L. Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* **71**, 855–868 (1990).

20. Delehanty, B. & Boonstra, R. Impact of live trapping on stress profiles of Richardson's ground squirrel (Spermophilus richardsonii). *General and Comparative Endocrinology* **160**, 176–182 (2009).

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]

References

1. Kenagy, G. J., Sharbaugh, S. M. & Nagy, K. A. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269–282 (1989).

2. Siutz, C., Franceschini, C. & Millesi, E. Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. *J Comp Physiol B* **186**, 801–811 (2016).

3. Lebl, K. & Millesi, E. *Yearling male Common hamsters and the trade-off between growth and reproduction*. (2008).

4. Clark, T. W. Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus). (1977).

5. Bakko, E. B. & Brown, L. N. Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. *Journal of Mammalogy* **48**, 100–112 (1967).

6. Haigh, A., O'Riordan, R. M. & Butler, F. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). *Acta Theriologica* **57**, 321–331 (2012).

7. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. *Acta theriologica* **59**, 173–181 (2014).

8. Rautio, A., Valtonen, A. & Kunnasranta, M. The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. in *Annales Zoologici Fennici* vol. 50 107–123 (BioOne, 2013).

9. Haigh, A. The ecology of the European hedgehog (Erinaceus europaeus) in rural Ireland. (University College Cork, 2011).

10. Bieber, C. & Ruf, T. Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). *Life in the cold: Evolution, mechanism, adaptation, and application* 113–125 (2004).

11. Maher, C. R. Social organization in woodchucks (Marmota monax) and its relationship to growing season. *Ethology* **112**, 313–324 (2006).

12. Schmid, J. & Kappeler, P. M. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (Microcebus murinus). *Behavioral Ecology and Sociobiology* **43**, 125–132 (1998).

13. Iverson, S. L. & Turner, B. N. Natural history of a Manitoba population of Franklin's ground squirrels. *Canadian Field-Naturalist* **86**, 145–149 (1972).

14. Choromanski-Norris, J., Fritzell, E. K. & Sargeant, A. B. Seasonal Activity Cycle and Weight Changes of the Franklin's Ground Squirrel. *American Midland Naturalist* **116**, 101 (1986).

15. Millesi, E., Strijkstra, A. M., Hoffmann, I. E., Dittami, J. P. & Daan, S. Sex and Age Differences in Mass, Morphology, and Annual Cycle in European Ground Squirrels, Spermophilus citellus. *J Mammal* **80**, 218–231 (1999).

16. Nicol, S. C., Morrow, G. E. & Harris, R. L. Energetics meets sexual conflict: The phenology of hibernation in Tasmanian echidnas. *Functional Ecology* **33**, 2150–2160 (2019).

17. Nicol, S. C., Andersen, N. A., Morrow, G. E. & Harris, R. L. Spurs, sexual dimorphism and reproductive maturity in Tasmanian echidnas (Tachyglossus aculeatus setosus). *Australian Mammalogy* **41**, 161–169 (2018).

18. Kawamichi, M. Ecological Factors Affecting Annual Variation in Commencement of Hibernation in Wild Chipmunks (Tamias sibiricus). *J Mammal* **77**, 731–744 (1996).

19. Morton, M. L. & Gallup, J. S. Reproductive cycle of the Belding ground squirrel (Spermophilus beldingi beldingi): seasonal and age differences. *The Great Basin Naturalist* 427–433 (1975).

20. Morton, M. L. Seasonal Cycles of Body Weights and Lipids in Belding Ground Squirrels. *Body Weights and Lipids in Ground Squirrels* (1975).

21. Morton, M. L. & Sherman, P. W. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. *Canadian Journal of Zoology* **56**, 2578–2590 (1978).

22. Murie, J. O. & Harris, M. A. Annual Variation of Spring Emergence and Breeding in Columbian Ground Squirrels (Spermophilus columbianus). *J Mammal* **63**, 431–439 (1982).

23. Young, P. J. Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* **83**, 504–511 (1990).

24. Raveh, S. *et al.* Mating order and reproductive success in male Columbian ground squirrels (Urocitellus columbianus). *Behavioral Ecology* **21**, 537–547 (2010).

25. Fagerstone, K. A. The annual cycle of Wyoming ground squirrels in Colorado. *Journal of Mammalogy* **69**, 678–687 (1988).

26. Rickart, E. A. Annual cycles of activity and body composition in Spermophilus townsendii mollis. *Canadian Journal of Zoology* **60**, 3298–3306 (1982).

27. Sheriff, M. J. *et al.* Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2369–2375 (2011).

28. Buck, C. L. & Barnes, B. M. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy* **80**, 430–442 (1999).

29. Michener, G. R. & Locklear, L. Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* **71**, 855–868 (1990).

30. Michener, G. R. Sexual differences in reproductive effort of Richardson's ground squirrels. *Journal of Mammalogy* **79**, 1–19 (1998).

31. Schwanz, L. E. Annual cycle of activity, reproduction, and body mass in Mexican ground squirrels (Spermophilus mexicanus). *Journal of Mammalogy* **87**, 1086–1095 (2006).

32. Knopf, F. L. & Balph, D. F. Annual Periodicity of Uinta Ground Squirrels. *The Southwestern Naturalist* **22**, 213–224 (1977).

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

References

1. Bronson, M. T. Altitudinal variation in emergence time of golden-mantled ground squirrels (Spermophilus lateralis). *Journal of Mammalogy* **61**, 124–126 (1980).

2. Skryja, D. D. & Clark, T. W. Reproduction, Seasonal Changes in Body Weight, Fat Deposition, Spleen and Adrenal Gland Weight of the Golden-Mantled Ground Squirrel, Spermophilus lateralis lateralis, (Sciuridae) in the Laramie Mountains, Wyoming. *The Southwestern Naturalist* **15**, 201–208 (1970).

3. McKeever, S. The biology of the golden-mantled ground squirrel, Citellus lateralis. *Ecological Monographs* **34**, 383–401 (1964).

4. Vander Wall, S. B. Food hoarding in animals. (1990).

5. Kenagy, G. J. & Trombulak, S. C. Size and Function of Mammalian Testes in Relation to Body Size. *Journal of Mammalogy* **67**, 1–22 (1986).

6. Trombulak, S. C. Life history of the Cascade golden-mantled ground squirrel (Spermophilus saturatus). *Journal of mammalogy* **68**, 544–554 (1987).

7. Kenagy, G. J., Sharbaugh, S. M. & Nagy, K. A. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269–282 (1989).

8. Michener, G. R. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. *Oecologia* **89**, 397–406 (1992).

9. Kenagy, G. J. & Bartholomew, G. A. Seasonal Reproductive Patterns in Five Coexisting California Desert Rodent Species: Ecological Archives M055-002. *Ecological Monographs* **55**, 371–397 (1985).

10. Siutz, C., Franceschini, C. & Millesi, E. Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. *J Comp Physiol B* **186**, 801–811 (2016).

11. Siutz, C., Valent, M., Ammann, V., Niebauer, A. & Millesi, E. Sex-specific effects of food supplementation on hibernation performance and reproductive timing in free-ranging common hamsters. *Sci Rep* **8**, 1–10 (2018).

12. Hufnagl, S., Franceschini-Zink, C. & Millesi, E. Seasonal constraints and reproductive performance in female Common hamsters (Cricetus cricetus). *Mammalian Biology* **76**, 124–128 (2011).

13. Pévet, P., Buijs, R. M. & Masson-Pévet, M. Effect of pinealectomy and a constant high level of circulating melatonin or of 5-methoxytryptamine on the vasopressinergic innervation in the brain of the European hamster (Cricetus cricetus, L). *Journal of neural transmission* **70**, 287–294 (1987).

14. Bakko, E. B. & Brown, L. N. Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. *Journal of Mammalogy* **48**, 100–112 (1967).

15. Clark, T. W. Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus). (1977).

16. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. *Acta theriologica* **59**, 173–181 (2014).

17. Haigh, A., O'Riordan, R. M. & Butler, F. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). *Acta Theriologica* **57**, 321–331 (2012).

18. Rautio, A., Valtonen, A. & Kunnasranta, M. The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. in *Annales Zoologici Fennici* vol. 50 107–123 (BioOne, 2013).

19. Bieber, C. & Ruf, T. Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). *Life in the cold: Evolution, mechanism, adaptation, and application* 113–125 (2004).

20. Bieber, C. Population dynamics, sexual activity, and reproduction failure in the fat dormouse (Myoxus glis). *Journal of Zoology* **244**, 223–229 (1998).

21. Kryštufek, B. Compartmentalization of body of a fat dormouse Glis glis. *Trakya Üniversitesi Fen Bilimleri Dergisi* (2001).

22. Clark, T. W. Notes on the biology of the thirteen-lined ground squirrel in the Laramie Plains, Wyoming. *The Southwestern Naturalist* **15**, 499–502 (1971).

23. Wells, L. J. The Fibro-Muscular Scrotal Sac Under Normal and Experimental Conditions in an Annual Breeder (Citellus). *Proceedings of the Society for Experimental Biology and Medicine* **36**, 625–629 (1937).

24. Maher, C. R. Social organization in woodchucks (Marmota monax) and its relationship to growing season. *Ethology* **112**, 313–324 (2006).

25. Maher, C. R. & Duron, M. Mating system and paternity in woodchucks (Marmota monax). *Journal of Mammalogy* **91**, 628–635 (2010).

26. Kenagy, G. J. & Barnes, B. M. Seasonal Reproductive Patterns in Four Coexisting Rodent Species from the Cascade Mountains, Washington. *J Mammal* **69**, 274–292 (1988).

27. O'Farrell, T. P., Olson, R. J., Gilbert, R. O. & Hedlund, J. D. A Population of Great Basin Pocket Mice, Perognathus parvus, in the Shrub-Steppe of South-Central Washington. *Ecological Monographs* **45**, 1–28 (1975).

28. Nicol, S. C., Morrow, G. E. & Harris, R. L. Energetics meets sexual conflict: The phenology of hibernation in Tasmanian echidnas. *Functional Ecology* **33**, 2150–2160 (2019).

29. Morrow, G. E., Jones, S. M. & Nicol, S. C. Interaction of hibernation and male reproductive function in wild Tasmanian echidnas Tachyglossus aculeatus setosus. *Journal of Mammalogy* **97**, 852–860 (2016).

30. Soulsbury, C. D. Genetic patterns of paternity and testes size in mammals. *PLoS One* **5**, e9581 (2010).

31. Knopf, F. L. & Balph, D. F. Annual Periodicity of Uinta Ground Squirrels. *The Southwestern Naturalist* **22**, 213–224 (1977).

32. Amend, S. R. On the population ecology of Uinta ground squirrels. (1970).

33. Rieger, J. F. Body size, litter size, timing of reproduction, and juvenile survival in the Unita ground squirrel, Spermophilus armatus. *Oecologia* **107**, 463–468 (1996).

34. Gür, H. & Gür, M. K. Annual cycle of activity, reproduction, and body mass of Anatolian ground squirrels (Spermophilus xanthoprymnus) in Turkey. *Journal of Mammalogy* **86**, 7–14 (2005).

35. Ellis, L. C. & Balph, D. F. Age and seasonal differences in the synthesis and metabolism of testosterone by testicular tissue and pineal HIOMT activity of Uinta ground squirrels (Spermophilus armatus). *General and comparative endocrinology* **28**, 42–51 (1976).

36. Morton, M. L. & Sherman, P. W. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. *Canadian Journal of Zoology* **56**, 2578–2590 (1978).

37. Morton, M. L. & Gallup, J. S. Reproductive cycle of the Belding ground squirrel (Spermophilus beldingi beldingi): seasonal and age differences. *The Great Basin Naturalist* 427–433 (1975).

38. Young, P. J. Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* **83**, 504–511 (1990).

39. Raveh, S. *et al.* Mating order and reproductive success in male Columbian ground squirrels (Urocitellus columbianus). *Behavioral Ecology* **21**, 537–547 (2010).

40. Boonstra, R., Bradley, A. J. & Delehanty, B. Preparing for hibernation in ground squirrels: adrenal androgen production in summer linked to environmental severity in winter. *Functional Ecology* **25**, 1348–1359 (2011).

41. Van Horne, B., Schooley, R. L., Olson, G. S. & Burnham, K. P. Patterns of density, reproduction, and survival in Townsend's ground squirrels. *Snake River Birds of Prey Area, research and monitoring, annual report. Edited by K. Steenhof. US Department of the Interior, Bureau of Land Management, Boise, Idaho* 158 (1993).

42. Rickart, E. A. Annual cycles of activity and body composition in Spermophilus townsendii mollis. *Canadian Journal of Zoology* **60**, 3298–3306 (1982).

43. Rickart, E. A. Spermophilus townsendii. *Mammalian Species* 1–6 (1987) doi:10.2307/0.268.1.

44. Sheriff, M. J. *et al.* Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2369–2375 (2011).

45. Buck, C. L. & Barnes, B. M. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy* **80**, 430–442 (1999).

46. Michener, G. R. & Locklear, L. Over-winter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. *Journal of Mammalogy* **71**, 489–499 (1990).

47. Michener, G. R. Sexual differences in reproductive effort of Richardson's ground squirrels. *Journal of Mammalogy* **79**, 1–19 (1998).

48. Michener, G. R. & Locklear, L. Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* **71**, 855–868 (1990).

49. Yeaton, R. I. Social behavior and social organization in Richardson's ground squirrel (Spermophilus richardsonii) in Saskatchewan. *Journal of Mammalogy* **53**, 139–147 (1972).

50. Davis, L. S. & Murie, J. O. Male territoriality and the mating system of Richardson's ground squirrels (Spermophilus richardsonii). *Journal of Mammalogy* **66**, 268–279 (1985).

51. Schmutz, S. M., Boag, D. A. & Schmutz, J. K. Causes of the unequal sex ratio in populations of adult Richardson's ground squirrels. *Can. J. Zool.* **57**, 1849–1855 (1979).

52. Delehanty, B. & Boonstra, R. Impact of live trapping on stress profiles of Richardson's ground squirrel (Spermophilus richardsonii). *General and Comparative Endocrinology* **160**, 176–182 (2009).

53. Brown, L. N. Seasonal activity patterns and breeding of the western jumping mouse (Zapus princeps) in Wyoming. *American Midland Naturalist* 460–470 (1967).

54. Fagerstone, K. A. The annual cycle of Wyoming ground squirrels in Colorado. *Journal of Mammalogy* **69**, 678–687 (1988).

55. Clark, T. W. Richardson's ground squirrel (Spermophilus richardsonii) in the Laramie Basin, Wyoming. *The Great Basin Naturalist* 55–70 (1970).

56. Schmid, J. Sex-specific differences in activity patterns and fattening in the gray mouse lemur (Microcebus murinus) in Madagascar. *Journal of Mammalogy* **80**, 749–757 (1999).

57. Lemaître, J.-F., Ramm, S. A., Barton, R. A. & Stockley, P. Sperm competition and brain size evolution in mammals. *Journal of Evolutionary Biology* **22**, 2215–2221 (2009).

Table S4 Data on dependent and independent factors used in models 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. 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

References

1. Kenagy, G. J., Sharbaugh, S. M. & Nagy, K. A. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269–282 (1989).

2. Siutz, C., Franceschini, C. & Millesi, E. Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. *J Comp Physiol B* **186**, 801–811 (2016).

3. Siutz, C., Valent, M., Ammann, V., Niebauer, A. & Millesi, E. Sex-specific effects of food supplementation on hibernation performance and reproductive timing in free-ranging common hamsters. *Sci Rep* **8**, 1–10 (2018).

4. Hufnagl, S., Franceschini-Zink, C. & Millesi, E. Seasonal constraints and reproductive performance in female Common hamsters (Cricetus cricetus). *Mammalian Biology* **76**, 124–128 (2011).

5. Lebl, K. & Millesi, E. *Yearling male Common hamsters and the trade-off between growth and reproduction*. (2008).

6. Bakko, E. B. & Brown, L. N. Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. *Journal of Mammalogy* **48**, 100–112 (1967).

7. Clark, T. W. Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus). (1977).

8. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. *Acta theriologica* **59**, 173–181 (2014).

9. Haigh, A., O'Riordan, R. M. & Butler, F. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). *Acta Theriologica* **57**, 321–331 (2012).

10. Rautio, A., Valtonen, A. & Kunnasranta, M. The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. in *Annales Zoologici Fennici* vol. 50 107–123 (BioOne, 2013).

11. Bieber, C. & Ruf, T. Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). *Life in the cold: Evolution, mechanism, adaptation, and application* 113–125 (2004).

12. Bieber, C. Population dynamics, sexual activity, and reproduction failure in the fat dormouse (Myoxus glis). *Journal of Zoology* **244**, 223–229 (1998).

13. Schmid, J. Sex-specific differences in activity patterns and fattening in the gray mouse lemur (Microcebus murinus) in Madagascar. *Journal of Mammalogy* **80**, 749–757 (1999).

14. Schmid, J. & Kappeler, P. M. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (Microcebus murinus). *Behavioral Ecology and Sociobiology* **43**, 125–132 (1998).

15. Choromanski-Norris, J., Fritzell, E. K. & Sargeant, A. B. Seasonal Activity Cycle and Weight Changes of the Franklin's Ground Squirrel. *American Midland Naturalist* **116**, 101 (1986).

16. Iverson, S. L. & Turner, B. N. Natural history of a Manitoba population of Franklin's ground squirrels. *Canadian Field-Naturalist* **86**, 145–149 (1972).

17. Millesi, E., Strijkstra, A. M., Hoffmann, I. E., Dittami, J. P. & Daan, S. Sex and Age Differences in Mass, Morphology, and Annual Cycle in European Ground Squirrels, Spermophilus citellus. *J Mammal* **80**, 218–231 (1999).

18. Gür, H. & Gür, M. K. Annual cycle of activity, reproduction, and body mass of Anatolian ground squirrels (Spermophilus xanthoprymnus) in Turkey. *Journal of Mammalogy* **86**, 7–14 (2005).

19. Nicol, S. C., Morrow, G. E. & Harris, R. L. Energetics meets sexual conflict: The phenology of hibernation in Tasmanian echidnas. *Functional Ecology* **33**, 2150–2160 (2019).

20. Nicol, S. C., Andersen, N. A., Morrow, G. E. & Harris, R. L. Spurs, sexual dimorphism and reproductive maturity in Tasmanian echidnas (Tachyglossus aculeatus setosus). *Australian Mammalogy* **41**, 161–169 (2018).

21. Morton, M. L. & Sherman, P. W. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. *Canadian Journal of Zoology* **56**, 2578–2590 (1978).

22. Raveh, S. *et al.* Mating order and reproductive success in male Columbian ground squirrels (Urocitellus columbianus). *Behavioral Ecology* **21**, 537–547 (2010).

23. Sheriff, M. J. *et al.* Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2369–2375 (2011).

24. Buck, C. L. & Barnes, B. M. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy* **80**, 430–442 (1999).

25. Michener, G. R. & Locklear, L. Over-winter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. *Journal of Mammalogy* **71**, 489–499 (1990).

26. Michener, G. R. Sexual differences in reproductive effort of Richardson's ground squirrels. *Journal of Mammalogy* **79**, 1–19 (1998).

27. Michener, G. R. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. *Oecologia* **89**, 397–406 (1992).

28. Michener, G. R. & Locklear, L. Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* **71**, 855–868 (1990).

29. Hoyle, J. & Boonstra, R. Life history traits of the meadow jumping mouse, Zapus hudsonius, in southern Ontario. (1986).

30. Knopf, F. L. & Balph, D. F. Annual Periodicity of Uinta Ground Squirrels. *The Southwestern Naturalist* **22**, 213–224 (1977).

31. Kenagy, G. J. & Bartholomew, G. A. Seasonal Reproductive Patterns in Five Coexisting California Desert Rodent Species: Ecological Archives M055-002. *Ecological Monographs* **55**, 371–397 (1985).

32. Schwanz, L. E. Annual cycle of activity, reproduction, and body mass in Mexican ground squirrels (Spermophilus mexicanus). *Journal of Mammalogy* **87**, 1086–1095 (2006).

33. Kenagy, G. J. & Barnes, B. M. Seasonal Reproductive Patterns in Four Coexisting Rodent Species from the Cascade Mountains, Washington. *J Mammal* **69**, 274–292 (1988).

34. Munroe, K. E. & Koprowski, J. L. Annual cycles in the desert: body mass, activity and reproduction in round-tailed ground squirrels (Xerospermophilus tereticaudus). *THE SOCIOECOLOGY, MATING SYSTEM AND BEHAVIOR OF ROUND-TAILED GROUND SQUIRRELS (XEROSPERMOPHILUS TERETICAUDUS)* 29 (2011).

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]

References

1. Kenagy, G. J., Sharbaugh, S. M. & Nagy, K. A. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* **78**, 269–282 (1989).

2. Hayssen, V. Reproductive Effort in Squirrels: Ecological, Phylogenetic, Allometric, and Latitudinal Patterns. *J Mammal* **89**, 582–606 (2008).

3. Magalhães, J. P. D. & Costa, J. A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology* **22**, 1770–1774 (2009).

4. Siutz, C., Franceschini, C. & Millesi, E. Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. *J Comp Physiol B* **186**, 801–811 (2016).

5. Lebl, K. & Millesi, E. *Yearling male Common hamsters and the trade-off between growth and reproduction*. (2008).

6. Clark, T. W. Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus). (1977).

7. Bakko, E. B. & Brown, L. N. Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. *Journal of Mammalogy* **48**, 100–112 (1967).

8. Haigh, A., O'Riordan, R. M. & Butler, F. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). *Acta Theriologica* **57**, 321–331 (2012).

9. Rautio, A., Valtonen, A., Auttila, M. & Kunnasranta, M. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. *Acta theriologica* **59**, 173–181 (2014).

10. Rautio, A., Valtonen, A. & Kunnasranta, M. The effects of sex and season on home range in European hedgehogs at the northern edge of the species range. in *Annales Zoologici Fennici* vol. 50 107–123 (BioOne, 2013).

11. Haigh, A. The ecology of the European hedgehog (Erinaceus europaeus) in rural Ireland. (University College Cork, 2011).

12. Bieber, C. & Ruf, T. Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). *Life in the cold: Evolution, mechanism, adaptation, and application* 113–125 (2004).

13. Maher, C. R. Social organization in woodchucks (Marmota monax) and its relationship to growing season. *Ethology* **112**, 313–324 (2006).

14. Schmid, J. Sex-specific differences in activity patterns and fattening in the gray mouse lemur (Microcebus murinus) in Madagascar. *Journal of Mammalogy* **80**, 749–757 (1999).

15. Iverson, S. L. & Turner, B. N. Natural history of a Manitoba population of Franklin's ground squirrels. *Canadian Field-Naturalist* **86**, 145–149 (1972).

16. Choromanski-Norris, J., Fritzell, E. K. & Sargeant, A. B. Seasonal Activity Cycle and Weight Changes of the Franklin's Ground Squirrel. *American Midland Naturalist* **116**, 101 (1986).

17. Millesi, E., Strijkstra, A. M., Hoffmann, I. E., Dittami, J. P. & Daan, S. Sex and Age Differences in Mass, Morphology, and Annual Cycle in European Ground Squirrels, Spermophilus citellus. *J Mammal* **80**, 218–231 (1999).

18. Nicol, S. C., Morrow, G. E. & Harris, R. L. Energetics meets sexual conflict: The phenology of hibernation in Tasmanian echidnas. *Functional Ecology* **33**, 2150–2160 (2019).

19. Kawamichi, M. Ecological Factors Affecting Annual Variation in Commencement of Hibernation in Wild Chipmunks (Tamias sibiricus). *J Mammal* **77**, 731–744 (1996).

20. Morton, M. L. & Gallup, J. S. Reproductive cycle of the Belding ground squirrel (Spermophilus beldingi beldingi): seasonal and age differences. *The Great Basin Naturalist* 427–433 (1975).

21. Morton, M. L. Seasonal Cycles of Body Weights and Lipids in Belding Ground Squirrels. *Body Weights and Lipids in Ground Squirrels* (1975).

22. Morton, M. L. & Sherman, P. W. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. *Canadian Journal of Zoology* **56**, 2578–2590 (1978).

23. Murie, J. O. & Harris, M. A. Annual Variation of Spring Emergence and Breeding in Columbian Ground Squirrels (Spermophilus columbianus). *J Mammal* **63**, 431–439 (1982).

24. Young, P. J. Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* **83**, 504–511 (1990).

25. Fagerstone, K. A. The annual cycle of Wyoming ground squirrels in Colorado. *Journal of Mammalogy* **69**, 678–687 (1988).

26. Rickart, E. A. Annual cycles of activity and body composition in Spermophilus townsendii mollis. *Canadian Journal of Zoology* **60**, 3298–3306 (1982).

27. Sheriff, M. J. *et al.* Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2369–2375 (2011).

28. Michener, G. R. & Locklear, L. Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* **71**, 855–868 (1990).

29. Michener, G. R. Sexual differences in reproductive effort of Richardson's ground squirrels. *Journal of Mammalogy* **79**, 1–19 (1998).

30. Michener, G. R. & Locklear, L. Over-winter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. *Journal of Mammalogy* **71**, 489–499 (1990).

31. Michener, G. R. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. *Oecologia* **89**, 397–406 (1992).

32. Ovaska, K. & Herman, T. B. Life history characteristics and movements of the woodland jumping mouse, Napaeozapus insignis, in Nova Scotia. *Canadian journal of zoology* **66**, 1752–1762 (1988).

33. Bronson, M. T. Altitudinal variation in emergence time of golden-mantled ground squirrels (Spermophilus lateralis). *Journal of Mammalogy* **61**, 124–126 (1980).

34. Knopf, F. L. & Balph, D. F. Annual Periodicity of Uinta Ground Squirrels. *The Southwestern Naturalist* **22**, 213–224 (1977).

35. Amend, S. R. On the population ecology of Uinta ground squirrels. (1970).

Supplementary materials S3

Table S1 Regression results for the best models explaining sex difference in immergence without outlier. The Z standardized model estimates and the phylogenetic effect are reciprocally estimated by β and γ_M. The abbreviations "Diff" stands for "Difference".

	γ_{ML}						
	R^2	γ_{ML}	**Dependent variable**	**Independent variable**	**β ± SE**	***t*-value**	***p*-value**
Model 9 (20 species)	0.47	0.000 (NA, 0.341)	Sex diff in immergence	Intercept	3.35 ± 2.55	1.31	0.207
				z-Post-mating activity time	-13.69 ± 3.65	-3.74	< 0.001***
				z-Maternal effort	6.93 ± 3.65	1.90	0.076.

Supplementary materials S4

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. Superscript numbers indicate bibliographic references

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 days after male (3)
Cynomys leucurus	1.04 (4)	4.89 (5)	11 days after male (6)
Glis glis	0.97 (7)	6.63 (8)	14 days after male (9)
Microcebus murinus	0.96 (10)	9.01 (11)	Same time as male (12)
Urocitellus parryii	0.97 (4)	0.49 (13)	35 days before male (14)

References

1. Kryštufek, B., Hoffmann, I.E., Nedyalkov, N., Pozdnyakov, A., and Vohralík, V. (2020). Cricetus cricetus (Rodentia: Cricetidae). Mamm. Species *52*, 10–26. 10.1093/mspecies/seaa001.

2. Lebl, K., and Millesi, E. (2008). Yearling male Common hamsters and the trade-off between growth and reproduction. Biosyst. Ecol. Ser. *25*, 115–126.

3. Siutz, C., Franceschini, C., and Millesi, E. (2016). Sex and age differences in hibernation patterns of common hamsters: adult females hibernate for shorter periods than males. J. Comp. Physiol. B *186*, 801–811. 10.1007/s00360-016-0995-z.

4. Hayssen, V. (2008). Patterns of Body and Tail Length and Body Mass in Sciuridae. J. Mammal. *89*, 852–873. 10.1644/07-MAMM-A-217.1.

5. Bakko, E.B., and Brown, L.N. (1967). Breeding Biology of The White-Tailed Prairie Dog, Cynomys Leucurus, in Wyoming. J. Mammal. *48*, 100–112. 10.2307/1378174.

6. Clark, T.W. (1977). Ecology and ethology of the white-tailed prairie dog (Cynomys leucurus). Milwaukee Public Mus. Publ. Biol. Geol. *3*, 1–96.

7. Matějů, J., and Kratochvíl, L. (2013). Sexual size dimorphism in ground squirrels (Rodentia: Sciuridae: Marmotini) does not correlate with body size and sociality. Front. Zool. *10*, 27. 10.1186/1742-9994-10-27.

8. Bieber, C. (1998). Population dynamics, sexual activity, and reproduction failure in the fat dormouse (Myoxus glis). J. Zool. *244*, 223–229.

9. Bieber, C., and Ruf, T. (2004). Seasonal timing of reproduction and hibernation in the edible dormouse (Glis glis). Life Cold Evol. Mech. Adapt. Appl., 113–125.

10. Rakotondranary, S.J., Hapke, A., and Ganzhorn, J.U. (2011). Distribution and Morphological Variation of Microcebus spp. Along an Environmental Gradient in Southeastern Madagascar. Int. J. Primatol. *32*, 1037. 10.1007/s10764-011-9521-z.

11. Schmid, J., and Kappeler, P.M. (1998). Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (Microcebus murinus). Behav. Ecol. Sociobiol. *43*, 125–132.

12. Schmid, J. (1999). Sex-specific differences in activity patterns and fattening in the gray mouse lemur (Microcebus murinus) in Madagascar. J. Mammal. *80*, 749–757.

13. Buck, C.L., and Barnes, B.M. (1999). Annual cycle of body composition and hibernation in free-living arctic ground squirrels. J. Mammal. *80*, 430–442.

14. Sheriff, M.J., Kenagy, G.J., Richter, M., Lee, T., Tøien, Ø., Kohl, F., Buck, C.L., and Barnes, B.M. (2011). Phenological variation in annual timing of hibernation and breeding in

nearby populations of Arctic ground squirrels. Proc. R. Soc. B Biol. Sci. *278*, 2369–2375. 10.1098/rspb.2010.2482.