Ecology
Evolutionary Biology

Evolutionary trade-offs in dormancy phenology

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Reviewed Preprint

Revised by authors after peer review.

About eLife's process

Reviewed preprint version 2
April 10, 2024 (this version)

Reviewed preprint version 1
November 29, 2023

Posted to preprint server
October 6, 2023

Sent for peer review
June 26, 2023

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 (the physiological constraint hypothesis). However, there are other mutually non-exclusive hypotheses to explain the timing of animal dormancy, 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 reproductive advantages of being active and survival benefits of dormancy. 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 by within-species sex differences in the phenology of dormancy. To examine this hypothesis, we used two complementary approaches: (i) a set of phylogenetic comparative analyses on mammals (mainly holarctic rodents), and (ii) a comparison between endotherm and ectotherm dormancy, via analyses of endotherms (including mainly holoarctic rodents) and the existing literature on ectotherms.

Using the phylogenetic comparative method applied to more than 20 hibernating mammalian species, we found support for both hypotheses as explanations for the phenology of dormancy. In accordance with the life history hypotheses, sex differences in emergence and immergence were favored by the sex difference in reproductive effort. In addition, physiological constraint may influence the trade-off between survival and reproduction such that, low temperature and precipitation as well as smaller body mass influence sex differences in phenology. We also compiled initial evidence that ectotherm dormancy (invertebrates and reptiles) may be 1) less temperature dependent than previously thought and 2) associated with trade-offs consistent with the life history hypothesis. Dormancy in some endotherms and ectotherms show staggered phenology with respect to the growing season (earlier emergence and immergence than expected) which illustrates the selection pressure exerted by the trade-off between reproduction (earlier emergence than expected) and adult survival (earlier immergence than expected). Thus, dormancy during non-life-threatening periods that are unfavorable for reproduction may be more widespread than previously appreciated.

eLife assessment

This **valuable** and ambitious review examines seasonal dormancy in various species, including hibernating mammals (excluding bats and bears) and ectotherms. It provides a **solid** test of hypotheses on dormancy timing, considering energetic constraints and life history as alternative drivers. The review will be of interest to evolutionary biologists.

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 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 ecophysiology rather than evolutionary biology. Dormancy duration increases with physiological constraints in the environment (e.g. energy shortage, thermic, or water constraints), demonstrating its adaptive role in response to short growing season (Pianka 1970, Turbill and Prior 2016, Wilsterman et al. 2021). However, some animals immerge into dormancy while environnemental conditions would allow (from a physiological point of view) a continuation of activity, suggesting other survival benefits than coping with a short growing season (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 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, that is dormancy phenology, might be exclusively explained by physiological constraint or whether other ecological factors may be involved.

Among dormant animals, a general distinction is made between heterothermic endotherms (some 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 of heterothermy, 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 physiological issues (the physiological constraint hypothesis), selection should 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 to dormancy such as improved survival due to a reduction of predation risk, these survival benefits may produce a trade-off between being active and investing in reproduction *versus* being dormant for a time to increase survival (the life-history hypothesis). Nevertheless, these two hypotheses are not mutually exclusive, since harsh climatic conditions and low food availability may reduce the benefits of being active for reproductive success and thus influence this trade-off. Within species, this trade-off may be reflected by sex differences in the phenology of dormancy, since males and females exhibit differences in reproductive timing and investment (Emlen and Oring 1977).

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 emerged from dormancy and arrived at mating sites some days or weeks before females (termed "protandry"), and mating occurred shortly after female emergenced from dormancy. 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 intraspecific competition and 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**) or beginning early to afford long active seasons for offspring while not compromising the survival of parents. 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). Later in the year, both sexes are expected to enter dormancy when they are no longer investing in or recovering from reproduction, and after acquiring adequate energy stores for overwintering.

In the present study, we investigated the "physiological constraints" and "life-history" hypotheses, two non-mutually exclusive evolutionary explanations for the phenology of dormancy, especially in regard to sex differences within species. To examine these hypotheses, 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 (from endotherms, including mainly holoarctic rodents) and the existing literature (from ectotherms).

First, using phylogenetic comparative analyses, we compared traits associated with climat, reproduction, body mass, and hibernation to explain sex differences in phenology in more than 20 hibernating mammals (**Fig. 2**). To begin with, we predicted from the life history hypothesis that (1) males of species with high energetic cost of reproduction would exhibit greater protandry due to longer mating preparation. We tested whether body mass lost during mating was associated with greater protandry. For immergence, males were expected to be constrained by the long-term negative effects of reproductive stress (Millesi et al. 1998), whereas female immergence was contrained by maternal effort (Levesque et al. 2013). Thus, we expected that (2) the species with higher sex differences in energetic cost of reproduction would have a greater sex difference in the timing of immergence, with the sex that invested more energy or time in reproduction also being the one that immerged last. If sex differences in hibernation phenology were solely explain by the physiological constraint hypothesis, then we would predict that species with high sexual dimophism (proxy of sex difference in energetic demand) in body mass would exhibit greater sex differences in hibernation phenology. On the contrary, if physiological constraints influenced the

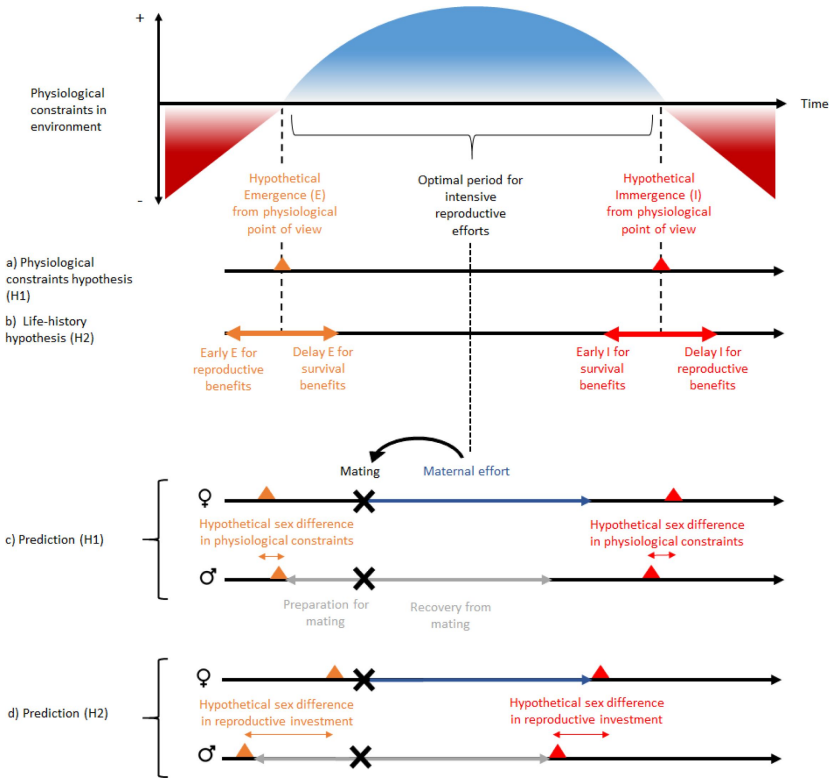

Figure 1

Schematic representation of “the physiological constraint hypothesis” and “the life-history hypothesis” and their predictions. Physiological constraints in the environment refers to variation over time of the energetic balance (mainly for heterothermic 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 or thermal conditions or *vice versa*. It predicts that the sex difference in dormancy phenology is explained by sex differences in physiological constraints, and that 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 the 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 beneficial envioronmental conditions for 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. Black, grey and dark blue horizontal arrows represent respectively time over the year, reproductive investment in males and reproductive investment in females. Red and orange triangles represent respectively immergence and emergence timing and black cross represent mating timing.

trade-off between survival and reproduction, then we would predict that that species living in short growing seasons (low temperature and precipitation) and smaller species would exhibit lower sex differences in hibernation phenology due to higher cost of thermoregulation during activity.

Secondly, there is a need to unify the study of dormancy across ectotherms and endotherms for answering fundamental evolutionary questions (Wilsterman et al. 2021). While there are insufficient data on dormancy phenology and reproductive investment in ectotherms to allow a statistical comparative analysis, we examined, as a second step, the relationships between reproductive investment, energy balance, thermal contraints, 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.

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). In this study, we addressed what can be called ecological hibernation, i.e. the seasonal duration that an animal remains sequestered in its burrow or den, which is assumed to be directly linked to the reduced risk of predation. In contrast, we did not consider heterothermic hibernation, which corresponds to the time between the beginning and end of the use of torpor. So when we mention hibernation, emergence or immergence, the specific reference is to ecological hibernation. 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). Only one bird species is considered to be a hibernator, and no information is available on sex differences in hibernation phenology (Woods and Brigham 2004, Woods et al. 2019).

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.

We have excluded immergence data for *Tamias sibericus* because this species does not follow the general phenology of other species (see “Study limitations” section for details).

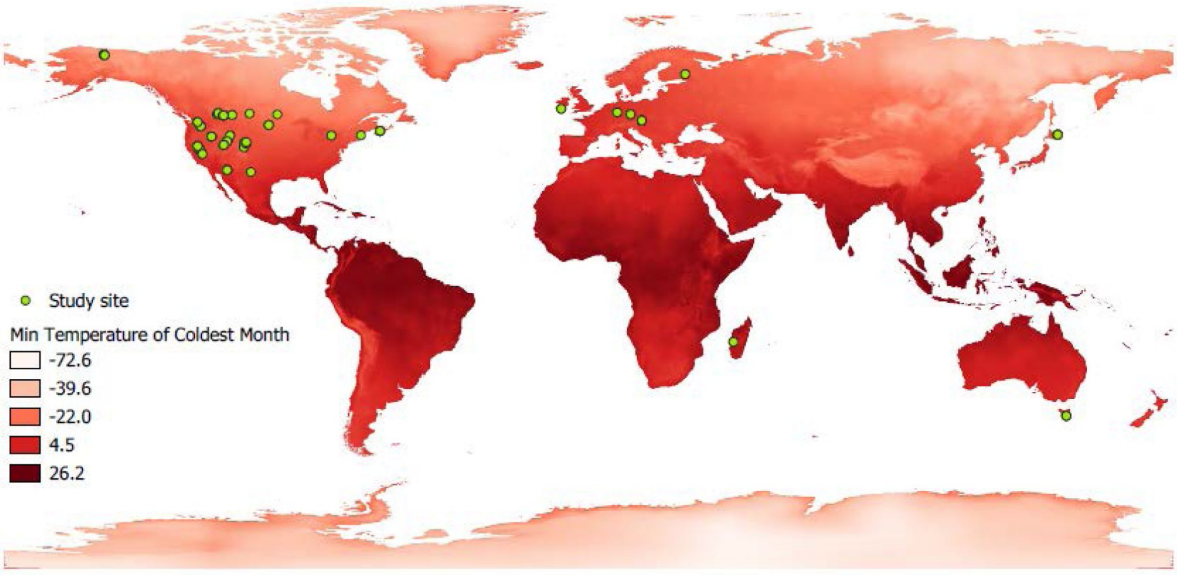

Figure 2

World map showing the study sites of the hibernating species studied. Green dots indicate the location of study sites. A red gradient represents the variation in minimum ambient temperature, a parameter used in this study.

c) Sex differences in reproductive investment and sexual dimorphism

For males, relative body mass changes during the mating period **(**hereafter referred to as "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. Male immergence is expected to be constrained by the long-term negative effects of reproductive stress (Millesi et al. 1998). In addition to energetic costs of mating, 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 may have contrained female immergence in two ways: the duration and energy cost of maternal care. Maternal effort duration was calculated as the sum of the gestation and lactation periods. Energy cost of reproductive effort also known as "specific reproductive effort" is calculated as the mean annual litter size times juvenile body mass at weaning divided by the body mass of adult female before reproduction (Armitage 1981).

For the analyses, we only accepted reproductive and body mass data from the same or very close study sites as the hibernation phenology data. We extracted body mass at immergence and emergence for both sexes and calculated sexual dimorphism as female body mass divided by male body mass. We made a few exceptions for juvenile body mass at weaning, for which some data were obtained in Hayssen (2008). As maternal effort duration and lactation data were not available in the literature for *Urocitellus brunneus* and *Ictidomys parvidens* respectively, we used averages for the clade *Marmotini* obtained from Hayssen (2008).

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) and annual precipitation (known as "BIO12" in the database) 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 mammalian phylogeny) 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). Each PGLS model produces a λ parameter representing the effect of phylogeny ranging between 0 (no phylogeny effect) and 1 (covariance entirely explained by co-ancestry).

The PGLS models used only one value per species for each factor. For hibernation phenology, body mass, reproductive effort and climatic variable, 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.

To test the life history and physiological constraint hypotheses on emergence, protandry was the dependent variable while, Δ body mass during mating, male body mass at emergence, sexual dimorphism at emergence, minimum temperature, annual precipitation, foodstoring and late mating were independent variables. The “late mating” factor aims to test 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 ». The “food-storing” factor 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). To test the life history and physiological constraint hypotheses on immergence, sex difference in immergence was the dependent variable while Δ body mass through the end of mating, duration of maternal effort, specific reproductive effort of female, sexual dimorphism in impmergence, minimum temperature and annual precipitation were independent variables. In both models, we tested for a “two factor interaction” between either minimum temperature, annual precipitation male and female reproductive effort. were independent variables.

The two models are described hereafter (see supplementary materials S2 for datasets):

Protandry ~ late_mating + foodstoring + male body mass + dimorphisme body mass at emergence + Δ body mass during mating * Minimum temperature + Δ body mass during mating * annual precipitation

Sex difference in immergence ~ log(specific reproductive effort) * Minimum temperature + log(specific reproductive effort) * precipitation + Δ body mass through the end of mating * Minimum temperature + Δ body mass through the end of mating * Precipitation + Maternal effort duration* Precipitation + Maternal effort duration * Minimum temperature + Body mass immergence + Dimorphisme at immergence

For both 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 variance inflation factors (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). Female-specific reproductive effort was log-transformed 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).

Results

a) Emergence

Protandry increased significantly with male body mass loss during mating and increased ambient temperature (model 1 in **Table 1** and **Fig. 3**). At the same time, protandry decreased in species for which males are smaller. The effect of ambient temperature on protandry is almost 2 times greater than male body mass and body mass loss during mating. There is also a trend towards lower protandry with increasing time between female emergence and the start of mating but this relationship is not significant (“late mating” in model 1, **Table 1**). This model showed no influence of phylogeny.

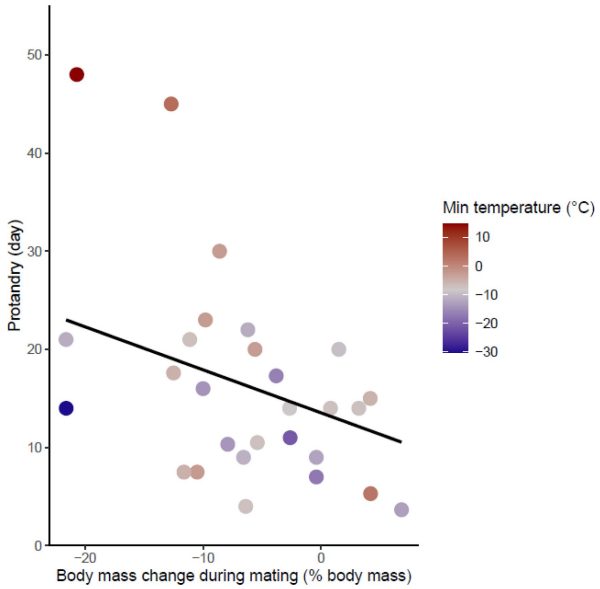

Figure 3

Effects of body mass variation during mating on protandry. The minimum temperatures of the study sites are indicated by a color gradient with the warmest temperatures in red. The regression line in black indicates the effect of body mass variation during mating on protandry. Body mass variation during mating was represented as a percentage of body mass before mating.

	γ_{ML}						
	R^2	γ_{ML}	Dependent variable	Independent variable	β ± SE	*t* -value	*p*- value
Model 1 (28 species)	0.59	0.00 (NA, 0.69)	Protandry	Intercept	16.31 ± 1.27	12.76	< 0.001***
				z- Male body mass at emergence	3.25 ± 1.37	2.37	0.02*
				z-Δ body mass during mating	-3.32 ± 1.39	-2.38	0.02*
				z-Min temperature	5.94 ± 1.36	4.34	< 0.001***
				z- late mating	-2.58 ± 1.41	-1.83	0.08 .
Model 2 (21 species)	0.50	0.00 (NA, 0.38)	Sex diff in immergence	Intercept	-5.18 ± 2.18	-2.36	0.03*
				z- log specific reproductive effort	-13.77 ± 3.88	-3.54	0.002**
				z-Δ body mass through the end of mating	-9.07 ± 2.37	-3.81	0.001**
				z- precipitation	-7.67 ± 2.59	-2.95	0.009**
				z- Maternal effort duration	-12.66 ± 3.58	-3.52	0.002**
Model 3 (20 species)	0.63	0.00 (NA, 0.73)	Sex diff in immergence	Intercept	-4.24 ± 1.89	-2.23	0.04*
				z- log specific reproductive effort	-10.20 ± 2.34	-4.35	< 0.001***
				z-Δ body mass through the end of mating	-7.05 ± 2.05	-3.42	0.003**
				z- precipitation	-12.48 ± 2.70	-4.61	< 0.001***
				z-dimorphism at immergence	-4.75 ± 2.42	-1.96	0.06 .

Table 1

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.

b) Immergence

The sex difference in immergence date was associated with maternal effort duration, specific reproductive effort of female, Δ body mass through the end of mating and precipitation (model 2, **Table 1**). High reproductive effort for both males and females delayed their immergence (**Fig. 4** and **5**). At the same time, males immerged before females for species living in an environment with high annual precipitation. The effect of maternal effort duration was influenced by an outlier, *Tachyglossus aculeatus,* a species for which gestation and lactation for females was an extremely long period (*i.e.* 167 day). Maternal effort duration was not conserved in the best model when the outlier was removed (model 3, **Table 1**). There is also a trend towards early male immergence in species with male biaised body mass dimorphism at immergence but this relationship is not significant (model 3, **Table 1**). Finally, phylogeny had no influence on this model.

Discussion

a) Sex difference in dormancy phenology

In this study, we investigated two mutually non-exclusive hypotheses about dormancy phenology: the physiological contraints and life history hypotheses. 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 life-history hypothesis predicts a trade-off between the survival benefit of hibernation and the reproductive benefit of activity, such that the sex with lesser investment of time and energy in reproduction should spend more time in hibernation. If the physiological constraints hypothesis was the sole explanation for hibernation phenology, then species with high sexual dimorphism (proxy for energy demand) should show a large sex difference in hibernation phenology. As well, if physiological constraints influence the trade-off between survival and reproduction, then small species and species living in short growing season should show lower sex differences due to the higher costs of being active. Based on phylogenetic comparative analyses, we found supports for both hypotheses. In accordance with the life history hypothesis, sex difference in emergence and immergence seem to reflect sex differences in reproductive effort. 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 addition, physiological constraint may influence the trade off between survival and reproduction such that, low temperature and precipitation as well as smaller body mass influence sex differences in phenology.

Males with higher body mass loss during mating showed higher protandry. The males of some species increased locomotion and are subject to strong competition during mating, which greatly reduces their foraging time (Millesi et al. 1998). Thus, an early emergence of males may have evolved in response to sexual selection to accumulate energy reserves in anticipation of reproductive efforts. Females, on the contrary, are not subject to intraspecific competition for reproduction and may have sufficient time before (generally one week after emergence) and during the breeding period to improve their body condition. Protandry may also allow the maturation of the reproductive system or monopolization of territories (Barnes et al. 1988, Millesi et al. 2008b, Thompson et al. 2023). In addition, protandry decreases in species living in cold environments and in species with lower male body mass in accordance with the physiological contraints hypothesis. Despite the reproductive benefits of early emergence, the cost of activity may be too high for these species, probably due to excessive heat loss in a cold environment.

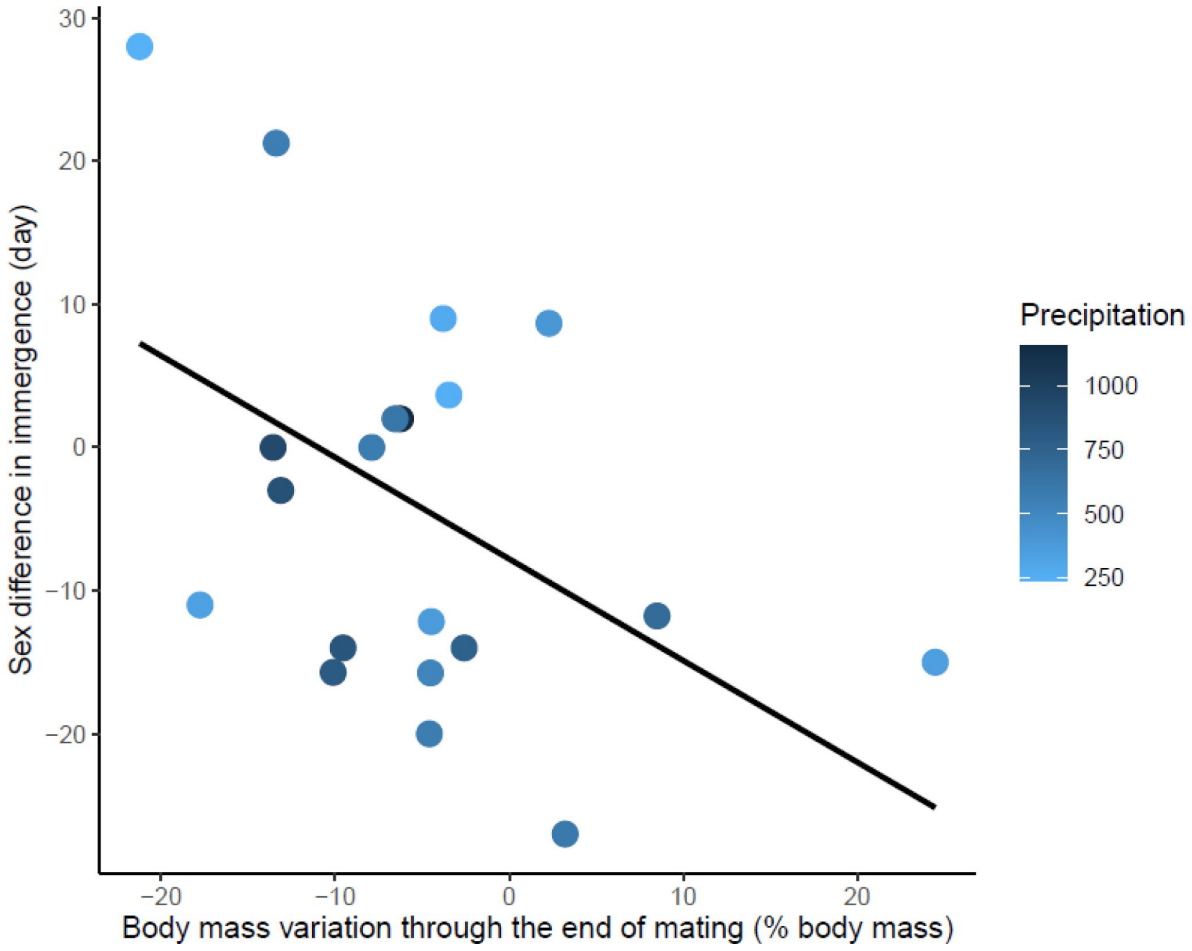

Figure 4

Effects of body mass variation through the end of mating on sex differences in immergence. Annual precipitation at the study sites are indicated by a color gradient with the highest precipitation in dark blue. The regression line in black indicates the effect of body mass variation through the end of mating on sex difference in immergence. Body mass variation through the end of mating was represented as a percentage of body mass at emergence. Males immerged earlier in species living in an environment with high precipitation (dark blue dots).

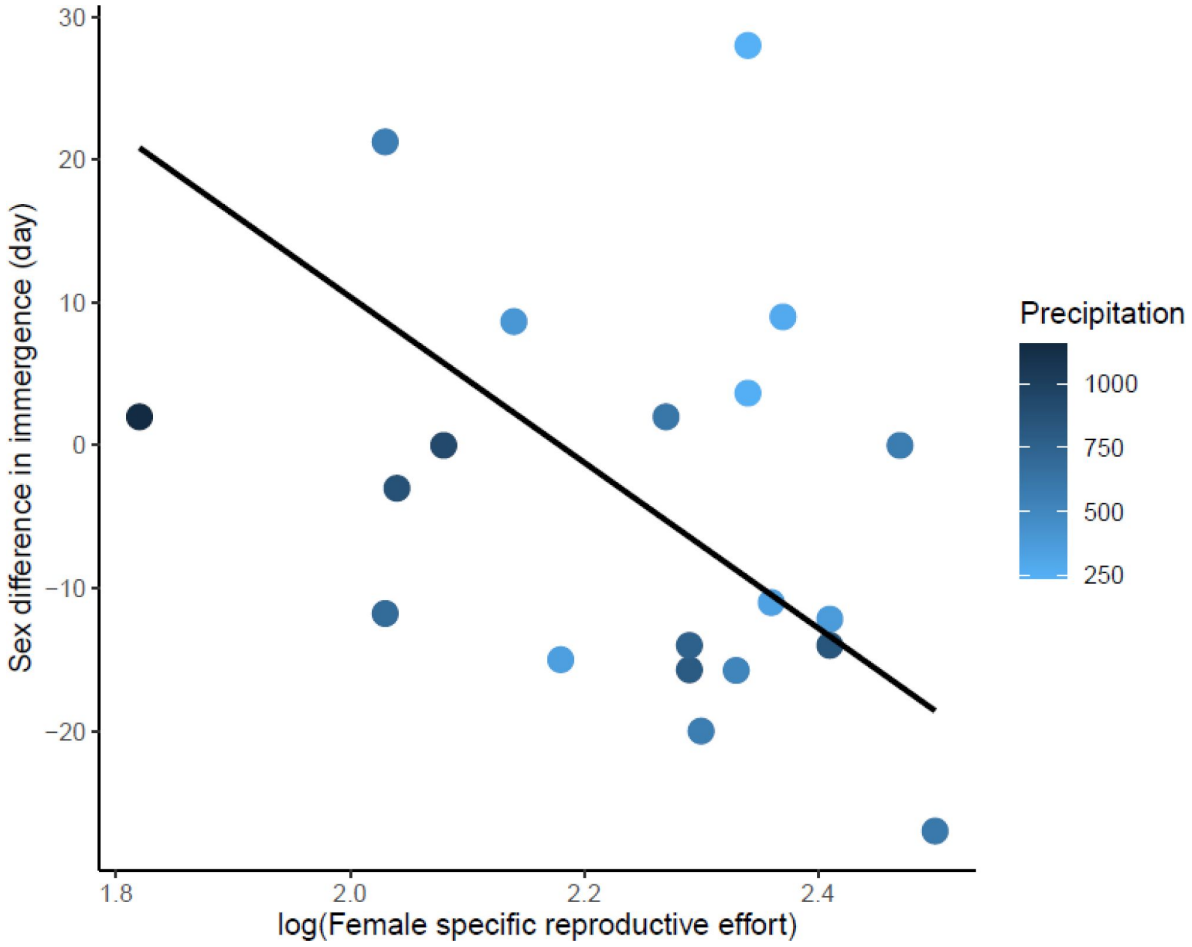

Figure 5

Effects of female specific reproductive effort on sex difference in immergence. The annual precipitation of the study sites are indicated by a color gradient with the highest precipitation in dark blue. The regression line in black indicates the effect of female specific reproductive effort on sex difference in immergence. Males immerged earlier in species living in an environment with high precipitation (dark blue dots).

In some species, males may have adaptations that improve their physical condition before reproduction without early emergence in cold climate. For example, males of some fat-storing species (e.g. *Urocitellus Parryii)* 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). Although food storage in the burrow may have evolved to overcome short growing season or predation, 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*, protandry: 20 day, 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, Thompson et al. 2023).

There is a trend for decrease protandry in species for which reproduction occurs several weeks after female emergence, as demonstrated in lizards and snakes (Graves and Duvall 1990, Olsson et al. 1999). 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. This phenomenon concerns only a few species in our comparative analysis, which may explain its non-significant effect.

In ectotherms, testes maturation has 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 have increased the chances of fertilizing eggs for males and decreased the probability of copulating with an infertile male for females (Breedveld and Fitze 2016). In *Gonepteryx rhamni* (the common brimstone butterfly), males emerged from dormancy 3 weeks before females. Males were quickly ready to reproduce, but this delay would have allowed them to increase their amount of sperm before mating and thus reproduce more successfully (Wiklund et al. 1996).

Unlike emergence, the sex that immerges into hibernation first varies among species. For males, high body mass loss before and during mating was associated with a delays in male immergence (for the same date of female 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). For females, the higher the specific reproductive effort, the later the females immerged for the same date of male immergence. As for males, high reproductive investment by females may induce stress that delays immergence. The duration of maternal effort may also delay entry into hibernation, but its influence seems to result from an extreme value (*Tachyglossus aculeatus,* maternal effort duration: 167 day). Therefore, it was the sex difference in the time and energy invested in reproduction which was associated with the order of immergence. As for emergence, physiological constraints due to short growing season may influence immergence. High precipitation seem to favor early immerge of males compared to females. High precipitation may be associated with high water and food availability enable a fast recovery from reproductive effort. However, female are constrained by maternal effort duration (gestation and lactation) which may result in early immergence of males compared to females. On the contrary, low precipitation may constrain recovery, and thus delay male immergence to a greater extent

than females in comparison with an environment with high precipitation (in both environments, female are constrained by maternal care). In ectotherms, very few data are available on sex differences in immergence date and therefore do not allow evaluation of this hypothesis.

Although the sex difference in dormancy phenology seems to be widely supported 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 had a greater chance of reproducing in subsequent years, they delayed 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. the individual scale, differences between sexes). Although the energy limitation hypothesis seems to explain part of dormancy duration (Pianka 1970, Turbill and Prior 2016, Wilsterman et al. 2021), it cannot, by itself, explain the sex differences in dormancy phenology. In the next section, we examine how physiological constraints may be integrated into the life history hypothesis framework, that is, the trade-off between reproduction and survival, to explain the phenology of dormancy in endotherms and ectotherms.

b) Dormancy and physiological constraints

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 growing 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 observed for some individuals, even in species not known to hoard food, may indicate that the environment allows a positive energy balance for other individuals with comparable energy demands. 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 2**). Sexual dimorphism may not be responsible for this sex differences as 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, years of 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.

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

Table 2

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 S2 for references).

In ectotherms as well, some observations confirmed a dormancy phenology staggered with respect to the growing 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 is 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. Males of *Vipera berus* (the common European adder) emerge before females in thermally unfavorable periods, leading to significant body mass loss because of the reproductive benefits of early emergence (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 supposedly 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.

c) Study limits

Our statistical analyses were based on a limited number of hibernators, and we have accepted approximations concerning the phenology data for some species (e.g., date at which first/last individuals of each sex were observed) due to the limited data in the literature. The analysis included mainly Holarctic rodents except for *Erinaceus europaeus, Microcebus murinus* and *Tachyglossus aculeatus.* Our analyses included two non-Holarctic species (*Microcebus murinus* and *Tachyglossus aculeatus).* Although they represent a very small minority of hibernating species, the results obtained seem to be consistent with Holarctic species. Hibernation in non-Holarctic species is supposed to have evolved in response to other environmental factors than food shortage, such as water shortage (Bintz 1984; Nowack et al., 2020). However, similar selection pressures may therefore exist and should encourage further comparative research on hibernation in non-Holarctic and Holarctic species.

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 subsequently recovering from body mass lost during mating (Norquay and Willis 2014). Female bats likely emerged first because early parturition increased juvenile survival. The patterns observed were consistent with the life-history hypothesis. Although few data are currently available, future comparative studies between bat species should enhance our understanding of the life-history hypothesis. *Tamias sibericus* was also excluded from the analyse of immergence. Chipmunks are food storing hibernators and wait until autumn to fill the hibernaculum with acorns (from masting in autumn) for winter feeding. Thus, reproductive effort may no longer have an impact on immergence at this time, but rather males may wait until all females hibernate in order to confirm the location of female burrows and increase mating success in the spring (Kawamichi 1996). Thus, chipmunks may delay their immergence for reproductive benefits, in line with the life-history hypothesis. Although the analyses performed in this study only included some of hibernators, the available information suggested that the life history hypothesis may apply to the phenology of other hibernators.

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 and context-specific 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 evidence from our study shows some independence of energy balance at the specific times of emergence and immergence into hibernation. This study shows that physiological constraints must be integrated into the survival-reproduction trade-off of hibernation phenology to be meaningful. 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 supported for the physiological constraints hypothesis (Ruf et al. 2012), although this hypothesis appears to be of limited or partial 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).

Data accessibility statement

the data and computer code supporting the results are available at *https://github.com/Theo-Constant/Evolutionary-trade-offs-in-dormancy-phenology.git*

Acknowledgements

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 and two referees 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).

Supplementary materials S1

Materials and methods

a) 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. Because of their imprecision, we excluded the studies for which hibernation season phenology was deduced from the presence of active individuals on a monthly basis. This excluded four studies [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.

b) Sex differences in reproductive investment

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.

For the analyses, we give priority to reproductive and body mass data from the same or very close study sites as the hibernation phenology data. We made a few exceptions for juvenile body mass at weaning, for which some data were obtained in Hayssen (2008), male reproductive effort for *Spermophilus brunneus* and *Zapus princeps* and the length of gestation and lactation. 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 a specific search combining the following terms: (scientific OR common names of species) AND (lactation duration OR gestation duration). As maternal effort duration and lactation data were not available in the

literature for *Urocitellus brunneus* and *Ictidomys parvidens* respectively, we used averages for the clade *Marmotini* obtained from Hayssen (2008). The body mass at weaning for *Urocitellus brunneus* correpsonds to the body mass at weaning of *Urocitellus townsendii* (phylogenetically close species) corrected for the difference in body mass of the females from Hayssen (2008) as body mass accounts for 76–84% of the variation in weaning mass in the clade *Marmotini* (Hayssen, 2008)

c) 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.

Supplementary materials S2

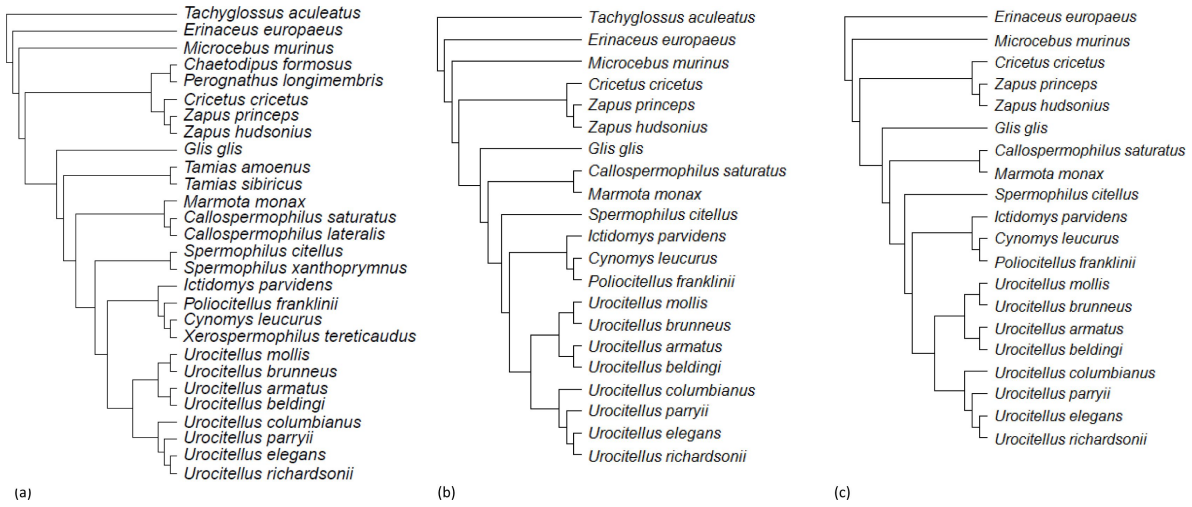

Figure S1.

Consensus phylogenetic trees for the species under study: (a) model 1 (b) model 2 and (c) model 3. 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).

species	Late mating	Food/ Fat	protandry	Body mass change during mating	Body mass male	Dimorphism body mass emergence	precipitation	Min temperature
Callospermophilus lateralis	1[1]	Fat	21[1]	-11,126[2]	173[2]	1,26[2]	411	-7
Callospermophilus saturatus	1[3]	Food	4[3]	-6,38[3]	248[3]	1,45[3]	863	-7,3
Chaetodipus formosus	4[4]	Food	14[4]	0,8[4]	18,6[4]	1,12[4]	863	-7,3
Cricetus cricetus	2,5[5,6]	Food	20[7]	-5,6[8]	400,9[8]	1,58[6,8]	595	-2,7
Cynomys leucurus	1[9]	Fat	21[9,10]	-21,61[9]	829,4[9]	1,69[9]	337	-11,5
Erinaceus europaeus	1[11,12]	Fat	17,6[12,13]	-12,5[12,13]	1028,67[12,13]	1,32[12,13]	803	-5,3
Glis glis	1[14]	Fat	30[15]	-8,6[14]	105,5[14]	1,1[14]	758	-2,5
Ictidomys parvidens	6[16]	Fat	7,5[16]	-10,5[16]	192[16]	1,27[16]	347	-2,4
Marmota monax	1[17]	Fat	22[18]	-6,2[17]	2701[17]	1,03[17]	1156	-11,5
Microcebus murinus	1[19]	Fat	48[19]	-20,7[20]	62[20]	1,02[20]	922	14,6
Perognathus longimembris	4[4]	Food	14[21]	3,2[21]	7[21]	1,06[21]	863	-7,3
Poliocitellus franklinii	1[22,23]	Fat	11[22,23]	-2,62[22,23]	417,1[22,23]	1,27[22,23]	517	-21,1
Spermophilus citellus	1[24]	Fat	23[25]	-9,8[25]	316,26[25]	1,68[25]	556	-2,5
Spermophilus xanthoprymnus	1[24]	Fat	7,5[24]	-11,62[24]	292[24]	1,69[24]	407	-5,2
Tachyglossus aculeatus	1[26]	Fat	45[26]	-12,7[27]	3950[27]	1,06[27]	625	3,6
Tamias amoenus	1[21]	Food	10,5[21]	-5,4[21]	42,3[21]	0,91[21]	846	-7,3
Tamias sibiricus	1[28]	Food	20[28]	1,5[29]	90,6[29]	0,96[29]	942	-9,4
Urocitellus armatus	1[24]	Fat	3,66[30]	6,82[30]	333,7[30]	1,25[30]	402	-13
Urocitellus beldingi	1[24]	Fat	9[31]	-0,4[31]	240,1[31]	1,14[31]	568	-12,4
Urocitellus brunneus	1[32]	Fat	9[32]	-6,57[33]	175[33]	1,44[33]	610	-11
Urocitellus columbianus	1[24]	Fat	7[34]	-0,4[34]	430[34]	1,18[34]	346	-17,5
Urocitellus elegans	1[35]	Fat	17,3[35]	-3,8[35]	249,3[35]	1,37[35]	281	-16,6
Urocitellus mollis	1[36]	Fat	15[36]	4,17[37]	181[37]	1,49[37]	248	-5,4
Urocitellus parryii	1[24]	Food	14[38]	-21,6[39]	941[39]	1,58[39]	237	-30,2
Urocitellus richardsonii	1[24]	Food	16[40–43]	-10[41,43]	392,5[41,43]	1,7[41,43]	371,5	-14,4
Xerospermophilus tereticaudus	4[44]	Fat	5,3[44]	4,2[44]	142[44]	1,27[44]	250	2,4
Zapus hudsonius	1[45]	Fat	14[38]	-2,67[45]	17[45]	1,02[45]	837	-8,5
Zapus princeps	1[46]	Fat	10,33[46]	-7,91[47]	22,48[47]	0,95[47]	570	-14,1

Table S1

Data on dependent and independent factors used in models 1. Protandry was used as the dependent factor and Body mass change during mating, late mating, body mass male, strategy fatstoring or foodstoring, minimum temperature, precipitation and dimorphism of body mass at emergence were considered as independent factors. Protandry was calculated as follows: Female Julian date – male Julian date. 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	Food/ Fat-	Sex diff immerg	Minimum temper	Body mass change end of mating	Precipitation	Body mass immerg	Maternal effort duration	Littersize	Weaning mass	Body mass femelle	Dimorphism immergence	Specific reprod effort
Callospermophilus saturatus	Food	3[2]	-7,3	-13,1[2]	863	273[2]	70[1,3]	2,7[2]	76[2]	185[2]	0,97[2]	110,7
Cricetus cricetus	Food	27[4]	-2,7	3,2[8]	595	344[5,6]	43[3]	7,31[5]	105[5]	245[6]	1,44[5,6]	313,2
Cynomys leucurus	Fat	11[10]	-11,5	-17,7[7]	337	1288[7]	67[1]	5,64[7]	198,5[7]	491[7]	1,55[7]	227,6
Erinaceus europaeus	Fat	15,7[8,9]	-5,2	-10,1[8,9]	803,5	1152[8,9]	72[2]	5[10]	235[11]	606[8,9]	1,16[8,9]	193,8
Glis glis	Fat	14[12]	-2,5	-2,5[13]	758	122,26[13]	58[3]	4,9[14]	39,2[15]	99,32[13]	1,21[13]	193,3
Ictidomys parvidens	Fat	15[16]	-2,4	24,4[16]	347	282,5[16]	68[1]	6,4[16]	43,8[16]	187[16]	1,24[16]	149,9
Marmota monax	Fat	-2[17]	-11,5	-6,2[18]	1156	3798,7[18]	76,05[1]	3,5[19]	490[17]	2610[18]	1,08[18]	65,7
Microcebus murinus	Fat	0[20]	14,6	-13,5[21]	922	74,5[21]	98[3]	2[22]	36,6[23]	60[21]	0,71[21]	121,6
Poliocitellus franklinii	Fat	15,75[24,25]	-21,1	-4,5[24,25]	517	577,88[24,25]	58[1]	6,75[25]	101,33[1]	322[24,25]	1,26[24,25]	211,7
Spermophilus citellus	Fat	-21,25[26]	-2,5	-13,3[26]	556	352,47[26]	64,5[1]	3,9[26]	51,5[27]	188[26]	1,31[26]	106,8
Tachyglossus aculeatus	Fat	24[28]	3,5	-6,6[29]	625	4180[29]	167,5[30]	1[31]	1650[31]	3806[29]	1,13[29]	43,3
Urocitellus armatus	Fat	-8,6[32]	-13	2,2[32]	402	521,83[32]	45[1]	6[33]	60,3[34]	262[32]	1,32[32]	137,7
Urocitellus beldingi	Fat	20[35]	-12,3	-4,5[35]	568	381,8[35]	51,53[1]	6,31[36]	69[37]	217[35]	1,21[35]	200,6
Urocitellus brunneus	Fat	-2[38]	-11	-6,5[39]	610	269,5[39]	66,5[1]	6,2[40]	36,55[1]	121[39]	1,35[39]	186,7
Urocitellus columbianus	Fat	11,7[41]	-16,1	8,4[41]	693	579[41]	53,2[1]	3,6[42]	112,6[43]	380[41]	1,32[41]	106,6
Urocitellus elegans	Fat	-9[44]	-16,6	-3,8[44]	281	363,68[44]	55,58[1]	5,88[45]	80,5[46]	203[44]	1,25[44]	233,1
Urocitellus mollis	Fat	-3,66[47]	-5,4	-3,4[48]	248	227,83[48]	58[1]	8,1[47]	32,8[47]	122,5[48]	1,38[48]	216,8
Urocitellus parryii	Food	-28[49]	-30,2	-21,2[50]	237	1034,74[50]	53	5,8	234,5	615[50]	1,05[50]	221,1
Urocitellus richardsonii	Food	12,16[51–54]	-14,42	-4,4[52,54]	370	524,52[52,54]	51,79	7,1	83,75	229[52,54]	1,30[52,54]	259,6
Zapus hudsonius	Fat	14[49]	-8,5	-9,5[55]	837	22,78[55]	47	5,5	7,8	16,7[55]	0,92[55]	256,8
Zapus princeps	Fat	0[56]	-14,1	-7,9[57]	570	35,24[57]	48	5,4	12,9	23[57]	1[57]	296,9

Table S2

Data on dependent and independent factors used in models 2 and 3 (same data base without *Tachyglossus aculeatus*). Sex difference in immergence was used as the dependent factor whereas strategy fatstoring or foodstoring, body mass change through the end of mating, body mass immergence, dimorphism at immergence maternal effort, maternal effort duration, female specific reproductive effort, minimum temperature and precipitation were considered as independent factors. The exact hibernation phenology data for *Cricetus cricetus* have been confirmed by the authors. Weaning body mass for *Zapus princeps* and *Urocitellus mollis* was calculated from body mass data at 52-60 days and 29 days, respectively, and corrected at 48 and 34 days, corresponding to weaning dates. For maternal effort duration of *Urocitellus brunneus* and *Ictidomys parvidens*, we used respectively the averages for the clade *Marmotini* obtained from Hayssen (2008). The body mass at weaning for *Urocitellus brunneus* correpsonds to the body mass at weaning of *Urocitellus townsendii* (phylogenetically close species) corrected for the difference in body mass of the females from Hayssen (2008) as body mass accounts for 76–84% of the variation in weaning mass in the clade *Marmotini* (Hayssen, 2008) Sex difference in immergence was calculated as follows: female Julian date – male Julian date.

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Reviewer #2 (Public Review):

Summary:

An article with lots of interesting ideas and questions regarding the evolution of timing of dormancy, emphasizing mammalian hibernation but also including ectotherms. The authors compare selective forces of constraints due to energy availability versus predator avoidance and requirements and consequences of reproduction in a review of between and within species (sex) differences in the seasonal timing of entry and exit from dormancy.

Strengths:

The multispecies approach including endotherms and ectotherms is ambitious. This review is rich with ideas if not in convincing conclusions. Limitations are discussed yet are impactful, namely that differences among and within species are contrast only for ecological hibernation (the duration of remaining sequestered) and not for "heterothermic hibernation" the period between first and last torpor. Differences between the two can have significant energetic consequences, especially for mammals returning to euthermic levels of body temperature whilst remaining in their cold burrows before emerging, eg. reproductively developing males in spring.

Weaknesses:

The differences between physiological requirements for gameatogenesis between sexes that affect the timing of heterothermy and need for euthermy during mammalian hibernator are significant issues that underlie, but are under discussed, in this contrast of selective pressures that determine seasonal timing of dormancy. Some additional discussion of the effects of rapid rapid climate change on between and within species phenologies of dormancy would have been interesting.

https://doi.org/10.7554/eLife.89644.2.sa0

Author response:

The following is the authors' response to the original reviews.

> ***Public Reviews***
>
> ***Reviewer #1 (Public Review):***
>
> *Summary:*
>
> *Dormancy/diapause/hibernation (depending on how the terms are defined) is a key life history strategy that allows the temporal escape from unfavorable conditions. Although environmental conditions do play a major role in inducing and terminating dormancy*

> *(authors call this energy limitation hypothesis), the authors test a mutually non-exclusive hypothesis (life-history hypothesis) that sex-specific selection pressures, at least to some extent, would further shape the timing of these life-history events. Authors use a metanalytic approach to collect data (mainly on rodents) on various life-history traits to test trade-offs among these traits between sexes and how they affect entry and termination of dormancy.*
>
> *Strengths:*
>
> *I found the theoretical background in the Introduction quite interesting, to the point and the arguments were well-placed. How sex-specific selection pressures would drive entry and termination of diapause in insects (e.g. protandry), especially in temperate butterflies, is very well investigated. Authors attempt to extend these ideas to endotherms and trying to find general patterns across ectotherms and endotherms is particularly exciting. This work and similar evidence could make a great contribution to the life-history theory, specifically understanding factors that drive the regulation of life cycle timing.*
>
> *Weaknesses:*
>
> *(1) I felt that including 'ectotherms' in the title is a bit misleading as there is hardly (in fact any?) any data presented on ectotherms. Also, most of the focus of the discussion is heavily mammal (rodent) focussed. I believe saying endotherms in the title as well is a bit misleading as the data is mammalfocused.*

We change the title to : "Evolutionnary trade-offs in dormancy phenology". This is a hybrid article comprising both a meta-analysis and a literature review. Each of these parts brings new elements to the hypotheses presented. The statistical analyses only concern mammals and especially rodent species. But the literature review highlighted links between the evolution of dormancy in ectotherms and endotherms that have not been linked in previous studies. We feel it is important for readers to know that much of the discussion will focus on the comparison of these two groups. But we understand that placing the term ectotherms in the title might suggest a meta-analysis including these two groups.

In addition, we indicated more specifically in the abstract and at the end of the introduction that the article includes two approaches associated with different groups of animals.

We also specified in the section « review criteria » that:

Only one bird species is considered to be a hibernator, and no information is available on sex differences in hibernation phenology (Woods and Brigham 2004, Woods et al. 2019).

We have also added a "study limitations" section, which explains that although the meta-analysis is limited by the data available in the literature, the information available for the species groups not studied seems to support our results.

> *(2) I think more information needs to be provided early on to make readers aware of the diversity of animals included in the study and their geographic distribution. Are they mostly temperate or tropical? What is the span of the latitude as day length can have a major influence on dormancy timings? I think it is important to point out that data is more rodent-centric. Along the line of this point, is there a reason why the extensively studied species like the Red Deer or Soay Sheep and other well-studied temperate mammals did not make it into the list?*

We specified in the abstract and at the end of the introduction that the species studied in the metaanalysis are mainly Holarctic species. We have also added a map showing all the study sites used in the meta-analysis. Finally, we've noted in the methods and added a "study

limitation" section at the end of the discussion an explanation for those species that were not studied in the meta-analysis and the consequences for the interpretation of results

The hypotheses developed in this article are based on the survival benefits of seasonal dormancy thanks to a period of complete inactivity lasting several months. The Red Deer or Soay Sheep remain active above ground throughout the year.

The effect of photoperiod on phenology is one of the mechanisms that has evolved to match an activity with the favorable condition. In this study, we are not interested in the mechanisms but in the evolutionary pressures that explain the observed phenology. Interspecific variation in the effect of photoperiod results from different evolutionary pressures, which we are trying to highlight. It is therefore not necessary to review mechanisms and effects of photoperiod, themselves requiring a lengthy review.

We also tested the “physiological constraint hypothesis” on several variables. Temperature and precipitation are factors correlated with sex differences in phenology of hibernation. These factors allow consideration of the geographical differences that influence hibernation phenology.

> *(3) Isn't the term 'energy limitation hypothesis' which is used throughout the manuscript a bit endotherm-centric? Especially if the goal is to draw generalities across ectotherms and endotherms. Moreover, climate (e.g. interaction of photoperiod and temperature in temperatures) most often induces or terminates diapause/dormancy in ectotherms so I am not sure if saying 'energy limitation hypothesis' is general enough.*

We renamed this hypothesis the "physiological constraint hypothesis" and we have made appropriate changes in the text so as not to focus physiological constraints solely on energy aspects.

> *(4) Since for some species, the data is averaged across studies to get species-level trait estimates, is there a scope to examine within population differences (e.g. across latitudes)? This may further strengthen the evidence and rule out the possibility of the environment, especially the length of the breeding season, affecting the timing of emergence and immergence.*

For a given species, data on hibernation phenology are averaged for different populations, but also for the same population when measurements are taken over several years. To test these hypotheses on a population scale, precise data on reproductive effort would be needed for each population tested, but this concerns very few species (less than 5).

Testing the effects of temperature and precipitation allows us to take into account the effects of climate on phenology.

> *(5) Although the authors are looking at the broader patterns, I felt like the overall ecology of the species (habitat, tropical or temperate, number of broods, etc.) is overlooked and could act as confounding factors.*

Yes, that's why we also tested the physiological constraints hypothesis, including the effect of temperature and precipitation. For the life-history hypothesis, we also tested reproductive effort, which takes into account the number of offspring per year.

> *(6) I strongly think the data analysis part needs more clarity. As of now, it is difficult for me to visualize all the fitted models (despite Table 1), and the large number of life-history traits adds to this complexity. I would recommend explicitly writing down all the models in the text. Also, the Table doesn't make it clear whether interaction was allowed between*

> *the predictors or not. More information on how PGLS were fitted needs to be provided in the main text which is in the supplementary right now. I kept wondering if the authors have fit multiple models, for example, with different correlation structures or by choosing different values of lambda parameter. And, in addition to PGLS, authors are also fitting linear regressions. Can you explain clearly in the text why was this done?*

To simplify the results, we reduced the number of models to just three: one for emergence and two for immergence. In place of Table 1, we have written the structure of the models used. We have added a sentence to the statistics section: “each PGLS model produces a λ parameter representing the effect of phylogeny ranging between 0 (no phylogeny effect) and 1 (covariance entirely explained by co-ancestry)”. We have tested only three PGLS models and the estimated lambda value for these models is 0.

> *(7) Figure 2 is unclear, and I do not understand how these three regression lines were computed. Please provide more details.*

We tested new models and modified existing figures.

> ***Reviewer #2 (Public Review):***
>
> *Summary:*
>
> *An article with lots of interesting ideas and questions regarding the evolution of timing of dormancy, emphasizing mammalian hibernation but also including ectotherms. The authors compare selective forces of constraints due to energy availability versus predator avoidance and requirements and consequences of reproduction in a review of between and within species (sex) differences in the seasonal timing of entry and exit from dormancy.*
>
> *Strengths:*
>
> *The multispecies approach including endotherms and ectotherms is ambitious. This review is rich with ideas if not in convincing conclusions.*
>
> *Weaknesses:*
>
> *The differences between physiological requirements for gameatogenesis between sexes that affect the timing of heterothermy and the need for euthermy during mammalian hibernator are significant issues that underlie but are under-discussed, in this contrast of selective pressures that determine seasonal timing of dormancy. Some additional discussion of the effects of rapid climate change on between and within species phenologies of dormancy would have been interesting.*
>
> ***Reviewer #2 (Recommendations For The Authors):***
>
> *This review provides a very interesting and ambitious among and within-species comparison of the seasonal timing of entry and exit from dormancy, emphasizing literature from hibernating mammals (sans bats and bears) and with attention to ectotherms. The authors test hypotheses related to the timing of food availability (energy) versus life history considerations (requirements for reproduction, avoiding predation) while acknowledging that these are not mutually exclusive. I offer advice for clarifications and description of the limitations of the data (accuracy of emergence and immergence times), but mainly seek more emphasis for small mammalian hibernators on the contrast for requirements for significant periods of euthermy prior to the emergence in males versus females, a contrast that has energetic and timing consequences in both the active and hibernation seasons.*

> *A consideration alluded to but not fully explained or discussed is the differences in mammals between species and sexes in the timing of what can be called ecological hibernation, which is the seasonal duration that an animal remains sequestered in its burrow or den, and heterothermic hibernation, between the beginning and end of the use of torpor. The two are not synonymous. When "emergence" is the first appearance above ground, there is a significant missing observation key to the energetic contrasts discussed in this review, that of this costly pre-emergence behavior.*

To explain the difference between heterothermic hibernation and ecological hibernation, we've added a section in review Criteria from materials and methods :

“In this study, we addressed what can be called ecological hibernation, i.e. the seasonal duration that an animal remains sequestered in its burrow or den, which is assumed to be directly linked to the reduced risk of predation. In contrast, we did not consider heterothermic hibernation, which corresponds to the time between the beginning and end of the use of torpor. So when we mention hibernation, emergence or immergence, the specific reference is to ecological hibernation.”

> *In arctic and other ground squirrel species, males remain at high body temperatures after immerging and remaining in their burrows in the fall for several days to a week, and more consistently and importantly, males that will attempt to breed in the spring end torpor but remain constantly in their burrows for as much as one month at great expense whilst undergoing testicular growth, spermatogenesis, spemiation, and sperm capacitation, processes that require continuous euthermy. Female arctic ground squirrels and non-breeding males do not and typically enter their first torpor bout 1-2 days after immergence and first appear above ground 1-3 days after their last arousal in spring.*
>
> *The weeks spent euthermic in a cold burrow in spring by males while undergoing reproductive maturation require a significant energetic investment (can equate to the cost of the previous heterothermic period) that contrasts profoundly with the pre-mating energetic investment by females.*
>
> *Males cache food in their hibernacula and extend their active season in late summer/fall in order to do so and feed from these caches in spring after resuming euthermy, often emerging at body weights similar to that at immergence. Similar between-sex differences in the timing of hibernation and heterothermy occur in golden-mantled and Columbian ground squirrels and likely most other Urocitellus spp., though less well described in other species. These differences are related to life histories and requirements for male vs. female gameatogenesis and, at the same time, energetic considerations in the costs to males for remaining euthermic while undergoing spermatogenesis and the cost related to whether males undergo gonadal development being dependent on individual body mass and cache size. These issues should be better discussed in this review.*
>
> *It is the time required to complete spermatogenesis, spermiation, and maturation of sperm not the time for growth of different sizes of testes that drives the preparation time for males. This is relatively constant among rodents. I challenge the assumption that larger testes take longer to grow than smaller ones.*

We took this comment into account. As we found little evidence of an increase in testicular maturation time with relative testicular size (apart from table 4 in Kenagy and Trombulak, 1986), we no longer tested the effect of relative testicular size on protandry.

We examined whether the ability to store food before hibernation might reduce protandry. Although food storage in the burrow may be favored for overcoming harsh environments or

predation, 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, protandry : 20 day, 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).

We developed these aspects in the discussion

> *While it is admirable to include ectotherms in such a broad review and modelling, I can't tell what data from how many ectothermic species contributed to the models and summary data included in the figures.*

Too few data on ectotherms were available to include ectotherms in the meta-analysis

> *Some consideration should be made to the limitations of the data extracted from the literature of the accuracy of emergence and immergence dates when derived from only observations or trapping data. The most accurate results come from the use of telemetry for location and data logging reporting below vs. above ground positioning and body temperature.*

We added a "study limits" section to the discussion to address all the limits in this commentary.

> *L64 "favor reproduction", better to say "allow reproduction", since there is strong evolutionary pressure to initiate reproduction early, often anticipating favorable conditions for reproduction, to maximize the time available for young to grow and prepare for overwintering themselves.*
>
> *Also, generally, it is not how "harsh" an environment is but rather how short the growing season is.*

We took this comment into account.

> *L80 More simply, individuals that have amassed sufficient energy reserves as fat and caches to survive through winter may opt to initiate dormancy. This may decrease but not obviate predation, since hibernating animals are dug from their burrows and eaten by predators such as bears and ermine.*

In this sentence, we indicated a gap between dormancy phenology and the growing season, which suggests survival benefits of dormancy other than from a physiological point of view. We've changed the sentence to make it clearer : “However, some animals immerge in dormancy while environnemental conditions would allow them (from a physiological point of view) to continue their activity, suggesting other survival benefits than coping with a short growing season”

> *L88 other physiological or ecological factors.... (gameatogenesis).*

In this study, we examine possible evolutionary pressures and therefore the environmental factors that may influence hibernation phenology. We focus on reproductive effort because, assuming predation pressure, we would expect a trade-off between survival and reproduction.

> *L113 beginning early to afford long active seasons to offspring while not compromising the survival of parents.*

We added to the sentence:

“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) or beginning early to afford long active seasons to offspring while not compromising the survival of parents.”

> *L117 based on adequate preparation for overwintering and enter dormancy….*

We modified the sentence as follows :

recovering from reproduction, and after acquiring adequate energy stores for overwintering”

> *L123 given that males outwardly invest the least time in reproduction yet generally have shorter hibernation seasons would seem to reject this hypothesis. This changes if you overtly include the time and energy that males expend while remaining euthermic preparing for hibernation, a cost that can be similar to energy expended during heterothermy.*

Males invest a lot of time in reproduction before females emerge (whether for competition or physiological maturation) and some males seem to be subject to long-term negative effects linked to reproductive stress (see Millesi, E., Huber, S., Dittami, J., Hoffmann, I., & Daan, S. (1998). Parameters of mating effort and success in male European ground squirrels, Spermophilus citellus. Ethology, 104(4), 298-313). Both processes may contribute to reducing the duration of male hibernation.

> *L125 again, costs to support euthermy in males undergoing reproductive development is an investment in reproduction.*

You're right, but it's difficult to quantify. We tested a model that takes into account the reproductive effort during reproduction and prior to reproduction. We also considered the hypothesis that species living in a cold climate might have a low protandry while having a high reproductive effort due to their ability to feed in the burrow (interaction effect between reproductive effort and temperature). We think these changes answer your comment.

> *L134 It isn't growing large testes that takes time, but instead completing spermatogenesis and maturation of sperm in the epdidymides.*

We removed this part.

> *L140 Later immergence in male ground squirrels is related to accumulation and defense of cached food, activities that are related to reproduction the next spring. An experimental analysis that would be revealing is to compare immergence times in females that completed lactation to the independence of their litters vs. females that did not breed or lost their litters. Who immerges first?*
>
> *Body mass variation from emergence to the end of mating in males seems to explain the delayed immergence of males in species that don't hide food in their burrows for hibernation. For example, in spermophilus citellus, males immege on average more than 3 weeks after females, yet they do not hide food in their burrows for the winter.*

Such a study already exists and shows that non-breeding females immerge earlier than breeding females. We refer to it

L386: “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).”

> *L164 So you examined literature from 152 species but included data from only 29 species? Did you include data from social hibernators (marmots) that mate before emergence?*

With current models, we have 28 different species. We have few species because very few have data on both sex difference data and information on reproductive effort data (especially for males).

Data on sex differences in hibernation were not available for social hibernating species.

> *L169 Were these data from trapping or observation results? How reliable are these versus the use of information from implanted data loggers or collars that definitively document when euthermy is resumed and/or when immergence and first emergence occurs (through light loggers)?*

We did not focus heterothermic hibernation, but in ecological hibernation. We have no idea of the margin of error for these types of data, but we have discussed these limitations in the "Study limitations" section.

> *L180, again, it is the time required to complete spermatogenesis and spermiation not the time for the growth of different sizes of testes that drives the preparation time for males. This is relatively constant among rodents. I challenge the assumption that larger testes take longer to grow than smaller ones.*

We removed this part.

> *L200 Males that accumulate caches in fall and then feed from those during the spring pre-emergence euthermic interval and after will often be at their seasonal maximum in body mass. Declining from that peak may not be stressful.*

It has been suggested that reproductive effort in Spermophilus citellus might induce long-term negative effects that delay male immergence.

Millesi, E., Huber, S., Dittami, J., Hoffmann, I., & Daan, S. (1998). Parameters of mating effort and success in male European ground squirrels, Spermophilus citellus. Ethology, 104(4), 298-313.

> *L210 How about altitude, which affects the length of the growing season at similar latitudes?*

We extracted the location of each study site to determine the temperature and precipitation at that precise location (based on interpolated climate surface). We therefore take into account differences in growing season (based on temperature) in altitude between sites.

> *L267 How did whether males cache food or not figure into these comparisons? Refeeding before mating occurs during the pre-emergence euthermic interval.*

We removed this part.

> *L332, 344 not a "proxy" but functionally related to advantages in mating systems with multiple mating males.*

We removed this part.

> *L353 The need for a pre-emergence euthermic interval in male ground squirrels requires costs in the previous active season in accumulating and defending a cache and the proximal costs in spring while remaining at high body temperatures prior to emergence with resulting loss in body mass or devouring of the cache.*

You're right, but in this section, we quickly explain the benefits of food catching compared with other species that don't do so.

> *L385 This review should discuss why females are not known to cache and contrast as "income breeders" from "capital breeder" males. What advantages of caches are females indifferent to (no need for a prolonged pre-emergence period) and what costs of accumulating caches do they avoid (prolonged activity period and defense of caches).*

We clarified the case of female emergence.

L321 : “Thus, an early emergence of males may have evolved in response to sexual selection to accumulate energy reserve in anticipation of reproductive effort. Females, on the contrary, are not subject to intraspecific competition for reproduction and may have sufficient time before (generally one week after emergence) and during the breeding period to improve their body condition.”

> *L388 I don't understand the logic of the conclusion that "did not …adequately explain the late male immergence" in this section. The greater mass loss in males over the mating period is afforded by the presence of a cache that requires later immergence.*

We removed this part.

> *L412 Not just congeners that invest less in reproduction, but within species individuals that do not attempt to breed in one or more years and thus have no reproductive costs should be an interesting comparison for differences in phenology from individuals that do breed. Non-breeders are often yearlings but can be a significant overall proportion of males that fail to fatten or cache enough to afford a pre-emergence euthermic period.*

L385: “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).”

The sentence refers to individuals who reproduce little or not at all.

> *L445 Males that gain weight between emergence and mating may do so by feeding from a cache regardless of how "harsh" an environment is.*

We observe this phenomenon even in species that are not known to hoard food

“Gains in body mass observed for some individuals, even in species not known to hoard food, may indicate that the environment allows a positive energy balance for other individuals with comparable energy demands.”

> *L492 Some insects retreat to refugia in mid-summer to avoid parasitism (Gynaephora).*

Escape from parasites is also a benefit of dormancy.

> *Fig 1 - It is difficult to see the differences in black and green colors, esp if color blind. Maternal effort is front-loaded within the active season (line for "optimal period" shown in midseason).*
>
> *Add "energy" underneath c) Prediction (H1) and "reproduction" underneath d) "Prediction (H2). Explain the orange vs black, green colors of triangles.*

We made the necessary changes

> *Fig 2 - I don't buy the regression lines as significant in this figure. The red line, cannot have a regression with two sample points and without the left-hand most dot, nothing is significant.*

We deleted this graph.

> *Fig 3 - females only?*

We deleted this graph.