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Latitude, life history and sexual size dimorphism correlate with reproductive seasonality in rodents

Heldstab, Sandra A

Abstract: Rodents show an immense variation in reproductive seasonality, spanning the whole spectrum from strictly seasonal to continuous reproduction throughout the year. However, the factors causing this variation have so far mostly been investigated in single-species studies that could not address phylogenetic constraints. By applying both a categorical description and a quantitative measure, the present study characterises the degree of reproductive seasonality in the wild of 272 rodent species. Using a comparative approach, the relationships of 12 variables, comprising five life-history variables, three abiotic variables, two niche variables and two allometric variables, with reproductive seasonality in rodents, were tested. The majority of rodents reproduced non-seasonally and had particularly high intraspecific variation in reproductive seasonality compared to other mammalian groups. Their opportunistic breeding strategies, their large geographic ranges with wide latitude and elevation ranges, and their ability to live in human-made environments may be related to this broad intraspecific variation of birth season length in rodents. The most important variables associated with rodent reproductive seasonality were mid-latitude of the species' geographical range, temperature, litters per year, weaning age, age at sexual maturity and sexual size dimorphism. Birth seasons become shorter with increasing latitude and colder temperatures, corresponding to the decreasing length of the favourable season. Species with more pronounced birth seasonality have fewer litters, which are weaned earlier and reach sexual maturity later, corresponding to the shorter period of optimal environmental conditions for reproduction. Sexual size dimorphism was weakly associated with birth seasonality, with more seasonal species having a higher degree of male-biased sexual dimorphism, potentially because male-male competition and female monopolisation are more likely to evolve in species with short mating seasons. In conclusion, habitat seasonality and life-history adaptations are most strongly associated with reproductive seasonality in rodents, which has important implications for zoo husbandry and for the effects of climate change on rodents.

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Latitude, life history, and sexual size dimorphism correlate with reproductive seasonality in rodents

Sandra A. HELDSTAB Department of Anthropology, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland, and Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland. Email: sandra.heldstab@uzh.ch

ABSTRACT

1. Rodents show an immense variation in reproductive seasonality, spanning the whole spectrum from strictly seasonal to continuous reproduction throughout the year. However, the factors causing this variation have so far mostly been investigated in single-species studies that could not address phylogenetic constraints.
2. By applying both a categorical description and a quantitative measure, the present study characterises the degree of reproductive seasonality in the wild of 272 rodent species.
3. Using a comparative approach, the relationships of 12 variables, comprising five life-history variables, three abiotic variables, two niche variables, and two allometric variables, with reproductive seasonality in rodents were tested.
4. The majority of rodents reproduced non-seasonally and had particularly high intraspecific variation in reproductive seasonality compared to other mammalian groups. Their opportunistic breeding strategies, their large geographic ranges with wide latitude and elevation ranges, and their ability to live in human-made environments may be related to this broad intraspecific variation of birth season length in rodents.
5. The most important variables associated with rodent reproductive seasonality were mid-latitude of the species' geographical range, temperature, litters per year, weaning age, age at sexual maturity, and sexual size dimorphism. Birth seasons become shorter with increasing latitude

and colder temperatures, corresponding to the decreasing length of the favourable season. Species with more pronounced birth seasonality have fewer litters, which are weaned earlier and reach sexual maturity later corresponding to the shorter period of optimal environmental conditions for reproduction. Sexual size dimorphism was weakly associated with birth seasonality, with more seasonal species having a higher degree of male-biased sexual dimorphism, potentially because male-male competition and female monopolisation are more likely to evolve in species with short mating seasons.

6. In conclusion, habitat seasonality and life-history adaptations are most strongly associated with reproductive seasonality in rodents, which has important implications for zoo husbandry and for the effects of climate change on rodents.

Keywords: birth seasonality, gestation, litter size, reproduction, Rodentia, sexual dimorphism, weaning age

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INTRODUCTION

Reproduction is energetically very expensive, particularly for small mammals such as rodents. In many rodent species, females must more than double their food intake during lactation to nourish themselves and their large litters, even under laboratory conditions with excess food and optimal temperatures (Myrcha et al. 1969, Randolph et al. 1977, Studier 1979, Merson & Kirkpatrick 1983). Moreover, females need to spend enough time with their offspring to keep them warm in colder regions (Collins & Smith 1976, Harland & Millar 1980, Johnson & Cabanac 1982), or restrict foraging activities to night-

time to prevent overheating at high ambient temperatures (Bozinovic et al. 2000). As food shortage in combination with temperatures even mildly deviating from the optimum makes reproduction energetically very challenging, the timing of birth is crucial for maximising reproductive success.

Rodents are characterised by extensive seasonal variation in reproduction. This variation ranges from continuous non-seasonal reproduction during the whole year at one extreme (e.g., Anderson et al. 1983, Dubost & Henry 2017, Begall et al. 2018), to a strongly seasonal reproduction restricted to a short breeding season of less than one month at the other (e.g., Hoogland 1995). Several ecological, physiological, and social factors have been proposed to explain this broad spectrum of reproductive seasonality, summarised by Sadleir (1969), Bronson (1989), and Steinlechner and Puchalski (2003). Knowledge of rodent reproduction is mostly derived from single-species studies (e.g., Pidduck & Falls 1973, Begall et al. 1999, Rensburg et al. 2002, Feoktistova & Meschersky 2005, Muteka et al. 2006) or from published work covering relatively few species (e.g., Lord 1960, Waterman 1996, Monadjem 1999, Tkadlec 2000, Özkurt et al. 2005, Dubost & Henry 2017, but see Hayssen 2008). Although such studies are tremendously valuable for understanding the root cause of reproductive seasonality, they do not allow phylogenetic constraints to be addressed.

The first objective of this paper is therefore to collate and summarise data on birth seasonality in the wild from many rodent species, and compare the data interspecifically. The second objective is to assess the influence on reproductive seasonality of 12 variables that have been suggested in previous studies to play a significant role in birth seasonality. These variables comprise three abiotic variables (mid-latitude of a species' geographical range, temperature, and precipitation), two allometric variables (adult body mass and sexual size dimorphism), five life-history variables (litter size, litters per year, gestation length, weaning age, and age at sexual maturity), and two niche variables (home range size and diet breadth). Detailed predictions on how these 12 variables are expected to influence reproductive seasonality are given in Table 1.

Lastly, the third objective is to compare reproductive seasonality of rodents with that of other mammalian orders published in the literature. In contrast to many other mammals, most rodents are rather small and short-lived (Howard 1949, de Magalhães & Costa 2009, Jones et al. 2009) and thus

80 must always gamble to some degree with their reproduction. Long-lived mammals that live for several
81 years can afford to be more selective and, for instance, breed only in a particular season with optimal
82 conditions or even suspend breeding in a bad year. In contrast, short-lived mammals such as many rodent
83 species living just a few weeks or months are expected to be much less seasonal and more opportunistic
84 in their reproduction, by, for example, responding to a sudden increase in food abundance after rainfall
85 (Newsome & Corbett 1975, Bronson 1988, Bronson & Heideman 1994, Prendergast et al. 2002, Wube
86 et al. 2008). Nevertheless, it is expected that at least some rodent species breed seasonally in predictably
87 harsh environments, because especially smaller mammals must economise their energy requirements
88 for both reproduction and thermoregulation, as they have higher metabolic rates, higher costs of
89 thermoregulation and lower body fat stores than bigger mammals (Rubner 1883, Kleiber 1961, Kenagy
90 & Bartholomew 1985, White & Seymour 2003, Glazier 2005).

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Table 1. Predictions about how birth seasonality in rodents is expected to be related to the 12 variables investigated in the current study.

Variables	Predictions	References	Prediction upheld?
<i>Abiotic variables</i>			
Latitude	Rodents occurring at higher latitudes have a shorter birth season because species living in high latitude must fit the whole reproductive cycle into a shorter time window of optimal environmental conditions.	Bronson (1989) Bilenca et al. (1994) Tkadlec (2000) Whorley and Kenagy (2007) Hayssen (2008) Zerbe et al. (2012) Heldstab et al. (2018) Heldstab et al. (2020)	Yes, very strong
Temperature	Warmer habitats result in less seasonal reproduction because warmer mean annual temperatures are associated with longer periods of favourable conditions for mating and birthing.	Bronson and Pryor (1983) Tkadlec (2000) Heldstab et al. (2020)	Yes, moderate
Precipitation	Precipitation influences water and food availability (via plant productivity). Species living in habitats with a higher amount of precipitation are therefore expected to reproduce less seasonally.	Perrin and Swanepoel (1987) Bronson (1989) Leirs et al. (1994) Brown and Ernest (2002) Letnic and Dickman (2005) Muteka et al. (2006) Andino et al. (2016) Heldstab et al. (2020)	No
<i>Allometric variables</i>			
Adult body mass	Previous studies suggested that body mass should have an effect on reproductive seasonality due to its correlation with life history variables. Authors argued that large species are unable to fit the whole reproductive cycle into a single year, so that their energetic expenditure is spread over a longer period that will, by necessity, include a time with less favourable environmental conditions; therefore a strict reproductive seasonality would not be beneficial.	Bronson (1989) Janson and Verdolin (2005) van Noordwijk et al. (2013)	No
Sexual size dimorphism	Species with a higher degree of male-biased sexual size dimorphism have shorter birth seasons because male-male competition and female monopolisation are more likely to evolve in species with short mating seasons.	Zerbe et al. (2012)	Yes, weak
<i>Life history variables</i>			
Litters per year	Shorter breeding seasons result in fewer litters per year, because the conditions suitable for breeding are constrained to a shorter reproductive period.	Spencer and Steinhoff (1968) Tökölyi et al. (2014)	Yes, strong
Litter size	Shorter breeding seasons at higher latitudes, possibly accompanied by reduction in potential longevity, promote selection for larger litter sizes to sustain an	Lord (1960) Moore (1961) Smith and McGinnis (1968) Spencer and Steinhoff (1968) Swihart (1984) Bronson (1989)	No, but deserves future studies

	equal level of reproduction within a shorter period of time.	Innes and Millar (1995) Whorley and Kenagy (2007) Hayssen (2008) Tökölyi et al. (2014)	
Weaning age	Seasonally reproducing species are weaned earlier due to a shorter time window of optimal environmental conditions to raise offspring.	Trillmich (1990) Gentry and Kooyman (2014)	Yes, strong
Gestation length	Reproductive seasonality is associated with shorter gestation length, to ensure birthing and mating take place at beneficial times of the year for species living in seasonal habitats.	Kiltie (1988) Zerbe et al. (2012) Tökölyi et al. (2014) Heldstab et al. (2018) Heldstab et al. (2020)	No
Age at sexual maturity	Species living in seasonal habitats (with short breeding seasons) attain sexual maturity at an older age. Due to the limited time windows of optimal conditions for reproduction and shorter activity periods (e.g. due to hibernation) in seasonal habitats, many species are expected to postpone their first breeding event to the next year.	Lackey (1978) Swihart (1984) Symonds (1999) Amat and Meiri (2018)	Yes, moderate
<i>Niche variables</i>			
Home range size	Solitary species with large home ranges do not often encounter potential mates. Therefore, females in species with larger home ranges should have a longer oestrous period in order to alleviate the uncertainty of finding a mate, which might result in a less seasonal birthing pattern.	Innes and Millar (1995) Spady et al. (2007)	No
Diet breadth	Omnivorous species with greater diet breadth have a more relaxed birthing pattern than species that rely upon highly specialised foods. Species with a generalist feeding strategy can shift easily from one food source to another, thereby buffering seasonal change in the availability of specific foods.	Bronson (1988) Bronson (1989) Di Bitetti and Janson (2000) Janson and Verdolin (2005) Stevenson et al. (2009) Heldstab et al. (2020)	No

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METHODS

Data

To investigate which factors influence reproductive seasonality in the natural habitat of different rodents, a broad dataset on birth seasonality covering 272 rodent species was compiled from the literature. Birth seasonality was described both in a categorical and a quantitative way (Appendix S1). As a continuous measure, birth season length in months was used. A more precise measure of birth seasonality in days would have been desirable, but was unfortunately not available for most species. For the categorical measure, each species was assigned to one of five birth seasonality categories based on its birthing pattern (following Zerbe et al. 2012, Heldstab et al. 2018, 2020): category 1: narrow peak (less than approximately two months), no births for the rest of the year; category 2: expanded peak (> two months) or double peak, no births for the rest of the year; category 3: peak(s) accompanied by a small number of births throughout the year; category 4: births throughout the year, undulating pattern (preferred seasons possible); category 5: constant births throughout the year without a clear preferred season. If several sources of data were available for one species, preference was given to the study with the highest number of births, the longest study period or the birth season most often mentioned in the literature.

Data on all 12 explanatory variables, namely the five life-history variables (gestation length, weaning age, age at sexual maturity, litter size, and litters per year), the two niche variables (home range size, and diet breadth expressed as the number of food types in the diet), the three abiotic variables (absolute mid-latitude of the species' geographical range, mean precipitation per year at the mid-latitude of geographical range, and mean annual temperature at the mid-latitude of geographical range), and the two allometric variables (mean adult body mass averaged for both sexes, and sexual size dimorphism expressed as the ratio of male versus female body mass), were also retrieved from the published literature (detailed references are given in Appendix S1). Ideally, these variables (with the exception of sexual size dimorphism) would all have been from reproductive females. However, for many species this information was not available. Results for analyses including female body mass instead of mean body mass averaged for both sexes are, however, largely identical to our results, and female body mass was also unrelated to birth seasonality (Appendix S2). Furthermore, although mid-latitude of the species'

geographical range is a standard measure, it is problematic for species with a wide or disjunct distribution. Therefore, additional analyses including the latitudinal range of a species' distribution were performed.

Statistical analyses

Statistical analyses were performed in JMP 13.0 (SAS Institute 1989-2016) and in R 3.4.1 (R Core Team 2017). All analyses were controlled for phylogenetic non-independence using phylogenetic generalised least-squares regressions (PGLS; Martins & Hansen 1997) using the 'caper' package (Orme 2013) in R. Caper estimates PGLS model parameters in maximum likelihood and the parameter lambda (λ), which quantifies the magnitude of the phylogenetic signal in the model residuals (Freckleton et al. 2002). The phylogeny was based on a composite supertree including branch length estimations from Fritz et al. (2009). Results for analyses using a more recently updated phylogenetic tree from Upham et al. (2019) with a lower species coverage remained largely similar (Appendix S3).

To determine the most important explanatory variables of birth seasonality measured in categories or in numbers of months, all twelve explanatory variables mentioned above were included in the statistical analyses. To compare coefficients, all continuous predictors were centred (around the mean) and scaled (by the standard deviation) before incorporation in the models (Schielzeth 2010), but raw data were presented in the figures. Model assumptions of normality and homogeneity of residuals were checked by visually inspecting histograms and qq-plots of the residuals, as well as by plotting residuals against fitted values. To assess potential multicollinearity between these different explanatory variables, variance inflation factors (VIF) were generated using non-phylogenetic generalised linear models and the function 'vif' in the 'car' package (Fox & Weisberg 2018) in R. The VIF for mean annual temperature was >5 , indicating a problematic amount of covariance among predictors (Rogerson 2001). To solve this, temperature was excluded from the full models and its influence on reproductive seasonality was tested separately. All remaining variables had VIFs <5 (Appendix S4).

To determine the most important predictors of birth seasonality, an information-theoretic model selection based on minimisation of the AICc (Akaike Information Criterion corrected for small sample sizes; Hurvich & Tsai 1989) was performed. The model selection was run across all possible models built with the 11 explanatory variables mentioned above (the effect of temperature on birth seasonality was tested separately), including those rodent species having complete variable records ($n = 98$). As the AICc did not conclusively differentiate the most highly ranked model for each of the two candidate model sets, multi-model averaging was used to account for uncertainty in the models (Grueber et al. 2011) including models with $\Delta\text{AICc} < 2$ (Burnham et al. 2011). For both sets of candidate models, ΔAICc was calculated as the difference in AICc between the focal model and the AICc of the best-fitting model in the candidate model set, which has a ΔAICc of 0. Estimates of each variable were averaged across the candidate models (means were weighted by the Akaike weight of a given model). The relative importance of a predictor variable was obtained by summing the Akaike weights of the models in the candidate model set including the focal predictor, following the method described by Symonds and Moussalli (2011).

RESULTS

A significant positive correlation between the five ordinal birth season categories and the continuous variable, the birth season length in months, was found (PGLS: $p < 0.001$, $n = 270$, $\lambda = 0.339$, $\beta = 2.672$, $\text{SE} = 0.125$, $t = 21.297$), indicating that the quantitative and the categorical approaches yielded comparable results. The ordinal birth seasonality categories showed a normal distribution (Fig. 1A). The birth season length ranged from one to 12 months, but its distribution was highly left skewed; 27% of species had a birth season length of 12 months (Fig. 1B). These results suggest that, although more than one-fourth of the rodent species included in the analysis reproduce throughout the year, the majority of species exhibit undulating patterns with preferred seasons for reproductive activity. Furthermore, rodents show a large degree of intraspecific variation in birth season length. As evident in Appendix S1,

for many rodent species, various birth season lengths have been described in the literature, ranging in the most extreme case of the field vole *Microtus agrestis* from one to 12 months.

The birth season categories and the birth season length in months across the rodent phylogeny are given in Fig. 2A and B. The genera containing the most strictly seasonally reproducing species with a birth season length of one month or less were *Callospermophilus*, *Ictidomys*, *Marmota*, *Poliocitellus*, *Spermophilus*, and *Uroditellus* (named *Spermophilus* and *Marmota* in Fig. 2A and B according to the old nomenclature of Fritz et al. 2009).

Model selection and averaging showed that the most important variables associated with the degree of birth seasonality in rodents were mid-latitude of a species' geographical range, litters per year, weaning age, age at sexual maturity, and sexual size dimorphism (relative importance ≥ 0.37 ; Tables 2 and 3, Appendix S5). Birth seasonality, measured in either months or categories, was negatively correlated to the mid-latitude of a species' geographical range (Tables 2 and 3, Fig. 3). Results integrating latitudinal range of a species' distribution are strikingly similar (Appendix S6). Species with a wider latitudinal distribution had longer birth seasons (Appendix S6). However, this association was always much weaker than the association with mid-latitude of a species' geographical range. Weaning age and litters per year were positively correlated with birth seasonality (whether measured in categories or in months), indicating that species with a more pronounced birth seasonality do have fewer litters per year which are weaned earlier (Tables 2 and 3, Fig. 3). In contrast, age at sexual maturity was negatively correlated with birth seasonality (measured in months or categories), suggesting that species with a longer birth season became sexually mature at a younger age (Tables 2 and 3, Fig. 3). Sexual size dimorphism was negatively linked to birth seasonality, but only when seasonality was measured in categories: more seasonal species had a higher degree of male-biased sexual size dimorphism (Tables 2 and 3, Fig. 3). Adult body mass, gestation length, litter size, precipitation, diet breadth, and home range size were unrelated to reproductive seasonality in rodents (Tables 2 and 3). Mean annual temperature, which had to be analysed separately due to the high multicollinearity with latitude, was positively correlated with reproductive seasonality, indicating that warmer habitats were associated with less seasonal reproduction (PGLS birth seasonality length in months: $p < 0.001$, $\lambda = 0.599$, $\beta = 0.142$, $SE =$

0.026, $t = 5.422$, PGLS birth seasonality categories: $p < 0.001$, $\lambda = 0.510$, $\beta = 0.042$, $SE = 0.008$, $t = 5.403$).

Table 2. Averaged predictor variable estimates and their relative explanatory importance for reproductive seasonality in rodents (birth season length in months, $n = 98$ species). Numbers in bold indicate predictor variables for which confidence intervals of effect sizes do not overlap with zero. Model averaging estimates were based on eight models with $\Delta AICc$ ($AICc$ focal model – $AICc$ best model) < 2 , since the best $AICc$ model is not strongly weighted (weight = 0.20; Symonds & Moussalli 2011). Reference levels of categorical variables have an estimate of 0; CI = confidence interval. A full list of models is given in Appendix S5.

Predictor variables	Relative importance of predictors	Model averaging estimates	95% CI
Intercept		-0.020	(-0.304, -0.009)
Latitude	1.000	-0.311	(-0.325, -0.296)
Precipitation	0.255	0.020	(-0.009, 0.049)
Adult body mass	0	0	0
Sexual size dimorphism	0	0	0
Litter size	0	0	0
Litters per year	0.588	0.089	(0.034, 0.143)
Gestation length	0	0	0
Weaning age	1.000	0.213	(0.201, 0.226)
Age at sexual maturity	0.481	-0.074	(-0.133, -0.014)
Home range size	0.081	-0.004	(-0.017, 0.009)
Diet breadth	0	0	0

Table 3. Averaged predictor variable estimates and their relative explanatory importance for reproductive seasonality in rodents (measured in birth seasonality categories, $n = 98$ species). Numbers in bold indicate predictor variables for which confidence intervals of effect sizes do not overlap with zero. Model averaging estimates are based on 13 models with ΔAICc (AICc focal model – AICc best model) < 2 , since the best AICc model is not strongly weighted (weight = 0.14; Symonds & Moussalli 2011). Reference levels of categorical variables have an estimate of 0; CI = confidence interval. A full list of models is given in Appendix S5.

Predictor variables	Relative importance of predictors	Model averaging estimates	95% CI
Intercept		-0.026	(-0.035, -0.016)
Latitude	1.000	-0.379	(-0.393, -0.365)
Precipitation	0.054	0.004	(-0.007, 0.016)
Adult body mass	0	0	(0.000, 0.000)
Sexual size dimorphism	0.415	-0.038	(-0.064, -0.012)
Litter size	0	0	(0.000, 0.000)
Litters per year	0.735	0.117	(0.076, 0.158)
Gestation length	0	0	(0.000, 0.000)
Weaning age	0.810	0.140	(0.098, 0.182)
Age at sexual maturity	0.366	-0.050	(-0.088, -0.011)
Home range size	0.142	-0.012	(-0.029, 0.005)
Diet breadth	0	0	(0.000, 0.000)

DISCUSSION

By applying both a categorical description (birth season categories 1-5) and a quantitative measure (birth season length in months), this study characterises the degree of reproductive seasonality of 272 rodent species in the wild, and tests the influence of twelve variables that were previously suggested to play a role in birth seasonality. I show that rodents have a high degree of intraspecific variation in birth season length: more than one quarter of all species I investigated reproduce throughout the year. Factors that might explain this broad variation of birth season length within species, such as an opportunistic breeding strategy, a large geographical range across wide latitude and elevation ranges, and the ability to live in human-made environments, are discussed below. The most important variables associated with the degree of birth seasonality were mid-latitude and mean annual temperature of a species' geographical range, litters per year, weaning age, and age at sexual maturity. Sexual size dimorphism had a weaker relationship with birth seasonality. This signifies that abiotic variables of the natural habitat and life-history adaptations are most strongly associated with reproductive seasonality in rodents.

Characterisation of rodent birth seasonality

Consistent with previous work (Sadleir 1974, Bronson 1985), the present study found large intraspecific variation in rodent birth seasonality. Rodents thriving in human habitats, such as house mice *Mus musculus* and brown rats *Rattus norvegicus*, might have high intraspecific variation in reproductive seasonality because individuals living in human-created environments with constant food availability and warm shelters have larger time windows for birth than their conspecifics living in natural habitats (Venables & Leslie 1942, Laurie 1946, Leslie et al. 1952, Pelikan 1974). In other species such as the Eurasian harvest mouse *Micromys minutus* and the hazel dormouse *Muscardinus avellanarius*, the large within-species variation might be due to their large geographic ranges (Hutterer et al. 2016, Kryštufek et al. 2019). Rodent populations of several species are known to adjust the length of their birthing season to their geographical location (Lynch et al. 1981, Bronson 1985, Bilenca et al. 1994, Whorley & Kenagy 2007). In species with a more limited geographic range, intraspecific variation in birth seasonality might

occur because rodents are known to reproduce very opportunistically with high year-to-year variability, depending on various factors such as weather (Liu et al. 2007, Stevenson et al. 2009, Andino et al. 2016), food availability (Taylor & Green 1976, Cittadino et al. 1994) and population density (Batzli et al. 1977, Smith et al. 2006).

The genera with the most strictly seasonally reproducing species were *Callospermophilus*, *Ictidomys*, *Marmota*, *Poliocitellus*, *Spermophilus*, and *Uroditellus*. Many species of these genera live at northern latitudes and/or high elevations of up to 4000 m above sea level, which might explain their seasonal birthing pattern (Myers et al. 2006, Batbold et al. 2016, Cassola 2016a, 2016b, Roach 2017). In addition, many of these species are known to have short activity periods, sometimes of less than 80 days per year as in the little ground squirrel *Spermophilus pygmaeus* (Cassola 2017), or to reproduce shortly after emergence from hibernation (Müller-Using 1956, Sun et al. 2012, Batbold et al. 2016), which might result in the very pronounced birth seasons in these genera.

Variables associated with seasonal reproduction in rodents

ABIOTIC VARIABLES: LATITUDE, TEMPERATURE, AND PRECIPITATION

Overall, this study shows that the variable most closely related to reproductive seasonality in rodents is the mid-latitude of a species' geographical range. Previous intra- and interspecific studies in rodents similarly confirmed a strong relationship between latitude and birth seasonality (Conaway 1971, Bronson 1988, Bilenca et al. 1994, Tkadlec 2000, Whorley & Kenagy 2007). As expected, birth time windows became narrower with increasing latitude of the natural habitat, because spring starts later and winter starts earlier in the year, resulting in a decline of the length of the favourable season at higher latitudes (Sparks & Menzel 2002). Since reproduction requires significant energy investments, the optimal timing of parturition to avoid hostile conditions when offspring are unlikely to survive exerts a strong selective pressure on short birthing periods at high latitudes (Prendergast et al. 2002).

Many environmental factors are associated with latitude, including temperature, precipitation, and primary productivity (MacArthur 1972). The result of this study, that latitude had the strongest

relationship with seasonal reproduction, but that mean annual temperature showed an additional relationship with reproductive seasonality, supports the concept that it is not latitude *per se* that is the decisive factor relating to reproductive seasonality, but rather the ecosystem in which rodent species reside, as already proposed by Bronson (1998). As shown here and in previous studies (Bronson & Pryor 1983, Tkadlec 2000), habitats that were, for their latitude, warmer were associated with less seasonal reproduction.

ALLOMETRIC VARIABLES: ADULT BODY MASS AND SEXUAL SIZE DIMORPHISM

As shown by Dubost and Henry (2017) for five rodent species, adult body mass was not related to reproductive seasonality in rodents in the present study, which includes a much higher number of species and corrects for phylogeny. Investigating another allometric variable, namely sexual size dimorphism, I found a negative relationship with birth season length in rodents, suggesting that species with a more seasonal reproduction have a higher degree of male-biased sexual size dimorphism. Male-biased sexual size dimorphism is predominantly attributed to intense intrasexual competition in males for mates, where male body size determines efficiency in defeating same-sex rivals and consequently reproductive success (Heske & Ostfeld 1990, Andersson 1994, Fairbairn et al. 2007, Lindenfors et al. 2007, García-Navas et al. 2016). Therefore, as proposed by Zerbe et al. (2012) for ruminants, one explanation for the negative association between birth seasonality and sexual size dimorphism in rodents could be that, in species with seasonal reproduction and hence synchronised mating with most females in oestrus at the same time, male-based sexual size dimorphism to monopolise females is more beneficial and hence more likely to evolve (but see Isaac 2005).

LIFE HISTORY VARIABLES: LITTER SIZE, LITTERS PER YEAR, GESTATION LENGTH, WEANING AGE, AND AGE AT SEXUAL MATURITY

One way in which mammals ensure that mating, birthing and raising offspring occur at a beneficial time of the year in seasonal habitats is to shorten their reproductive cycle (Kiltie 1984, Kiltie 1988).

Consistent with this prediction (see also Table 1), seasonally reproducing rodent species living in habitats with short time windows of optimal environmental conditions for breeding do have fewer litters which are weaned earlier. Furthermore, due to the decreasing length of the favourable season, late-born individuals in several seasonal species are known to postpone their first breeding event to the next year (Cockburn 1987, Gliwicz 1990, Tkadlec & Zejda 1998, Wilson et al. 2017). This might explain why seasonally reproducing rodents attain sexual maturity at an older age.

Unlike a previous study in rodents, which found that species in environments with more distinct temperature seasonality have shorter gestation periods (Tökölyi et al. 2014), a higher degree of reproductive seasonality was not linked to a shorter gestation length in the present study. Similarly, in sciurids, latitude, as a proxy for birth season length, had little influence on gestation length (Hayssen 2008). Rodents generally have short gestation periods, enabling them to fit the whole reproductive cycle in a very short time window (Conaway 1971, Perrin 1989, Wilson et al. 2017). Furthermore, many rodent species experience a postpartum oestrus, so that they can simultaneously suckle one litter while carrying another in the uterus with only a small increase in the duration of pregnancy (Dewsbury et al. 1979, Connor & Davis 1980, Pérez 1992). These characteristics might be the reason for the absence of a correlation between gestation and birth season length in rodents.

Contrary to what was expected (Table 1), average litter size was not negatively correlated with reproductive seasonality. Few direct comparisons between birth season length and litter size exist in rodents. Studies using latitude as proxy for birth season length generally found positive correlations between latitude and litter size (Lord 1960, Moore 1961, Smith & McGinnis 1968, Spencer & Steinhoff 1968, Sadleir 1969, Waterman 1996, Whorley & Kenagy 2007, Hayssen 2008). However, the percentage of variation in litter size explained by latitude is generally very small if the analysis is corrected for phylogenetic non-independence of taxa. Furthermore, several exceptions to this positive trend between litter size and latitude were noted (e.g., Lord 1960, Smith & McGinnis 1968, Innes 1978, Millar et al. 1979, Bilenca et al. 1994, Hayssen 2008, Viñals et al. 2012) suggesting that the relationship between litter size and either birth season length or latitude deserves future study.

NICHE VARIABLES: HOME RANGE SIZE AND DIET BREADTH

Solitary species with large home ranges do not often encounter potential mates (Llewellyn & Enders 1954, Greenwald 1956). Females of such species are therefore expected to have long oestrous periods to alleviate the uncertainty of finding a male (Larivière & Ferguson 2003). This should lead to less seasonal birthing patterns (see also Table 1). The present study was, however, unable to detect a relationship between home range size and seasonality of reproduction.

Food availability is a major driver of reproductive activity in small mammals such as rodents (Bronson & Heideman 1994, Dubost & Henry 2017). Even in larger mammals such as primates, reproductive seasonality is tightly linked to seasonal food fluctuations. For instance, highly folivorous primate species are known to exhibit long birth seasons, because mature leaves are more uniformly available through time than fruits and insects (Di Bitetti & Janson 2000, Janson & Verdolin 2005, Heldstab et al. 2020). Along these lines, the expectation in rodents (Bronson 1988) is that omnivorous species with a higher diet diversity would have a more relaxed birthing pattern than species that rely upon highly specialised foods. Species that evolved a generalist feeding strategy can shift easily from one food source to another, thereby buffering seasonal change in the availability of specific foods (Prendergast et al. 2002, Andino et al. 2016). In the current study, diet breadth was not related to reproductive seasonality in rodents. However, diet breadth is a relatively crude measure for diet diversity. Additionally, a reduced diet breadth with a focus on a limited range of food does not automatically imply that this food source is subject to seasonal fluctuations. Furthermore, diet breadth and home range size data were not derived from reproductive females, which might confound the present analyses. Further work is therefore needed to substantiate that niche variables have no influence on birth seasonality.

Comparison of reproductive seasonality in rodents with other mammalian groups

Rodents are among the smallest terrestrial mammals, which has important implications for the comparison of their reproductive seasonality to that of other taxonomic groups. More importantly, the

lineage diversification of rodents is also very different. Rodents' small size, short dispersal distances, heavy mortality, and high reproductive output lead to more reproductive isolation, greater genetic diversity, and thus more lineage splitting in this order (e.g., Harrison et al. 2003, Spradling et al. 2004, Belfiore et al. 2008, Castiglia et al. 2012, Leite et al. 2014, Wilson et al. 2017). Selective pressures related to reproductive seasonality in rodents are therefore different to those in larger-bodied mammalian groups, making it interesting to compare rodent birth seasonality with that of other mammalian orders.

Rodents show the largest degree of intraspecific variation in birth season length of the taxonomic groups investigated so far, such as ruminants, carnivores, and primates (Zerbe et al. 2012, Heldstab et al. 2018, Heldstab et al. 2020). A possible explanation for this difference is that rodents have a faster reproductive cycle than these other three orders, allowing them to breed much more opportunistically and adjust birth season length according to environmental conditions (e.g., Taylor & Green 1976, Liu et al. 2007) or high food abundance in human-created environments (e.g., Leslie et al. 1952). Furthermore, a particular feature of the reproductive physiology of many rodent species is that two different phenotypes may exist within a population: 1) one phenotype whose reproductive function is under photoperiodic control, which will result in a latitude-dependent reproductive seasonality; and 2) another phenotype without photoperiodic control, which may therefore take advantage of beneficial short-term situations that are out of synch with the 'average' annual cycle (Bronson 1989, Bronson 2009). The existence of these two phenotypes and the fact that many rodent species have much larger geographic ranges than, for instance, primates, which are mostly confined to the tropics (Heldstab et al. 2020), is also expected to contribute to the high intraspecific variation in birth seasonality in rodents (Bronson 1989).

The most important variable relating to rodent reproductive seasonality was mid-latitude of the species' geographical range. Previous studies in Lagomorpha (Bronson 1989), Ruminantia (Zerbe et al. 2012), Carnivora (Heldstab et al. 2018), Primates (Di Bitetti & Janson 2000, Janson & Verdolin 2005, Heldstab et al. 2020), Eulipotyphla (Hoole et al. 2016), and Macroscelidea (Neal 1995) found similar relationships of breeding seasonality with latitude: individuals or species living at higher latitudes have shorter breeding seasons. As found in ruminants (Zerbe et al. 2012), but in contrast to carnivores

(Heldstab et al. 2018), primates (Heldstab et al. 2020), and brushtail possums *Trichosurus vulpecula* (Isaac & Johnson 2003), sexual size dimorphism in rodents was negatively correlated with birth seasonality: more seasonal species had a higher degree of male-biased sexual size dimorphism. However, as in ruminants (Zerbe et al. 2012), sexual size dimorphism was also only marginally negatively associated with birth season length in rodents.

Unlike to what has been reported in primates (Heldstab et al. 2020), carnivores (Tökölyi et al. 2014, Heldstab et al. 2018), and ruminants (Zerbe et al. 2012, Tökölyi et al. 2014), a higher degree of reproductive seasonality was not linked to a shorter gestation length in rodents in the present study. One reason for the difference between rodents and the other mammalian groups that have been investigated is the small body size of rodents. Large animals in seasonal environments need to reduce the length of their reproductive cycle to squeeze it into a single year, so that they do not lose out on reproductive opportunity in the next year (Kiltie 1984, 1988). Small mammals such as rodents exhibit extremely rapid foetal and neonatal growth rates, and thus already have very short gestation periods (Conaway 1971, Perrin 1989, Wilson et al. 2017), enabling them to fit the whole reproductive cycle in a very short time window. Furthermore, many rodent species experience a postpartum oestrus, allowing them to gestate and lactate simultaneously (Dewsbury et al. 1979, Connor & Davis 1980, Pérez 1992), which further shortens the length of the reproductive cycle. Although rodents do not adjust gestation length, they still seem to adapt life history to seasonal habitats with short favourable time periods, as seasonal species do have fewer litters per year, which are weaned earlier and reach sexual maturity later. Selection in highly seasonal environments has also favoured fewer litters in lagomorphs (Swihart 1984), bats (Tökölyi et al. 2014), elephant shrews (Neal 1995), and Eulipotyphla (Symonds 1999), shorter lactation periods in seals (Trillmich 1990, Gentry & Kooyman 2014) and older age at sexual maturity in lagomorphs (Swihart 1984) and Eulipotyphla (Symonds 1999).

CONCLUSIONS

Among the mammalian orders investigated so far, rodents show a particular non-seasonal birthing pattern with a high intraspecific variation, suggesting that the majority of species follows an opportunistic breeding strategy with a higher reproductive output under optimal environmental conditions. Therefore, I expect that many rodent species should even broaden their birthing time windows under constant resource provisioning in zoos.

Besides life history and sexual size dimorphism, the most important variables associated with variation in rodent birth seasonality are mid-latitude of the species' geographical range and mean annual temperature of the natural habitat. The importance of these abiotic variables in relation to reproductive seasonality in rodents may also have important implications for the reproductive success of a given species due to warmer climate. Especially in seasonal breeders, the strong connection between latitude, temperature and reproductive seasonality may result in a temporal mismatch between the seasonal peak in births and the peak of optimal foraging conditions due to changing climate. For instance, the yellow-bellied marmots *Marmota flaviventris* of the Rocky Mountains, North America, have one short breeding season per year, which occurs as soon as the females emerge from hibernation (Frase & Hoffmann 1980). In response to warmer spring air temperatures, these marmots are now emerging 38 days earlier than 23 years ago, while the snow is too deep to forage for herbs successfully (Inouye et al. 2000), resulting in a considerable reduction of litter size and pregnancy rates (van Vuren & Armitage 1991).

Several main factors associated with birth season length in rodents differ substantially from other mammalian orders investigated so far, in particular life history variables. This cautions against making generalisations, and calls for future order-based studies on birth seasonality in mammals.

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FIGURES

Fig. 1. The distribution of rodent species according to their reproductive seasonality, characterised by (A) the birth season categories and (B) the birth season length in months.

Fig. 2. The phylogenetic tree used in the present study from Fritz et al. (2009), with an indication of how (A) the birth season categories and (B) the birth season length in months are distributed across the tree, ranging from very short birth season (a highly seasonal reproductive pattern) to very long birth season (a non-seasonal reproductive pattern).

Fig. 3. Relationship between either the birth season length in months or the birth season categories and (A and B) the mid-latitude of a species' geographical range, (C and D) litters per year, (E and F) age at sexual maturity, (G and H) weaning age, (I and J) mean annual temperature, and (K and L) sexual size dimorphism. Sexual size dimorphism did not correlate with birth season length in months. OLS regression lines (solid) and corresponding 95% confidence intervals (grey shading) are shown, as well as PGLS regression lines (dashed). For statistics, see Tables 2, 3, and Appendix S5.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. List of rodent species and data used for this study

Appendix S2. Results of analyses including female body mass instead of mean body mass averaged across both sexes.

Appendix S3. Results of analyses using a more recently updated phylogenetic tree from Upham et al. (2019), but with lower species coverage.

Appendix S4. Results of testing for collinearity among predictor variables. Variation inflation factors (VIF) for both full models and reduced models after multicollinearity are presented.

Appendix S5. Model set obtained after model selection based on $\Delta AICc < 2$. Best-supported models and multiple-model parameter estimates for birth season length in months and for birth season categories.

Appendix S6. Results including latitudinal range of a species' distribution.