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# Habitat characteristics and life history explain reproductive seasonality in lagomorphs

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## Abstract

Lagomorphs show extensive seasonal variation in their reproduction. However, the factors causing this large variation have so far mostly been investigated intraspecifically and therefore provide only some exemplary comparisons of lagomorph reproductive seasonality. The present study applies both a categorical description (birth season categories 1–5) and a quantitative measure (birth season length in months) to summarize the degree of birth seasonality in the wild of 69 lagomorph species. Using a comparative approach, I tested the influence of 13 factors, comprising six habitat, five life history and two allometric variables on birth season length in lagomorphs. Leporids mainly show non-seasonal birthing patterns with high intraspecific variation. Their opportunistic breeding strategy with high reproductive output and their large distribution areas across wide latitude and elevation ranges might be the reasons for this finding. Ochotonids reproduce strictly seasonally, likely because they live at northern latitudes, are high-altitude specialists, and occur in limited distribution areas. The most important factors associated with variation in lagomorph birth seasonality are mid-latitude, mean annual temperature and precipitation of a species' geographical range and life history adaptations including fewer but larger litters in seasonal habitats. Birth seasons become shorter with increasing latitude, colder temperatures, and less precipitation, corresponding to the decreasing length of optimal environmental conditions. Leporid species with shorter breeding seasons force maternal resources into few large litters to maximise reproductive output while circumstances are favourable. Since allometric variables were only weakly associated with reproductive seasonality, life history adaptations and habitat characteristics determine birth seasonality in Lagomorpha.

**Keywords** Lagomorpha · Reproduction · Latitude · Temperature · Litter size · Gestation length

## Introduction

Reproduction is energetically very expensive for most organisms. This is particularly true for placental mammals, where females bear the metabolic costs of pregnancy and lactation (McNab 2006; Speakman 2008; Heldstab et al. 2017). For mammals living in seasonal habitats with frequent periods of food scarcity, it is therefore essential that birth and lactation

occur during the most favourable time of the year to increase their reproductive success (e.g., Lancaster and Lee 1965; Soto et al. 2004).

Lagomorphs show extensive seasonal variation in their reproduction. In some species, such as many pikas (Ochotonidae), all breeding activity takes place during a very restricted part of the year of only around one to two months (e.g., Chapman and Flux 1990; Smith et al. 2018). Other lagomorph species are capable of reproducing during a broader time window (e.g., Barkalow 1962; Newson 1964; Franken and Hik 2004; Rioja et al. 2011) or throughout the year but show seasonal birth peaks (e.g., Prakash and Taneja 1969; Stubbe et al. 1991; Vázquez et al. 2007). Lastly, in a fourth group of species, reproduction is entirely non-seasonal (Haysen et al. 1993; Wilson et al. 2016).

Several ecological, physiological, and social factors have been proposed to explain this broad spectrum of reproductive seasonality in Lagomorpha (e.g., Barkalow 1962;

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Conaway et al. 1974; Swihart 1984; Boyd 1985; Ben Saad and Maurel 2002; Alves and Rocha 2003; Franken and Hik 2004; Portales et al. 2004; Rödel et al. 2005; Virgos et al. 2006; Tablado et al. 2009; Rioja et al. 2011; Schai-Braun et al. 2017). However, this knowledge derives almost exclusively from single-species studies and therefore provides only some exemplary comparisons of seasonality in reproduction between different lagomorph species. Furthermore, future studies enhancing our understanding of reproductive behaviour in the order Lagomorpha, with approximately one-fifth of species being threatened with extinction (Smith 2018), are also fundamental to captive-breeding programs and conservation management (Côté 2003). The importance of lagomorphs both as a pest of agricultural significance and as a key prey species and major human food resource additionally emphasizes the need to understand what controls their reproductive activity (Cowan and Bell 1986; Tablado et al. 2009; Delibes-Mateos et al. 2011; Lumpkin and Seidensticker 2011; Smith et al. 2019).

The first aim of this paper is therefore to collate and summarize data on birth seasonality from the wild of the majority of lagomorph species and compare them interspecifically. The second objective is to assess the influence of 13 factors on reproductive seasonality in lagomorphs that have been suggested in previous studies to play a role in birth seasonality: namely, six habitat characteristics (mid-latitude and latitude range of a species' geographical distribution (Sadleir 1969; Conaway et al. 1974; Bronson 1988), altitude (Conaway et al. 1974; Schai-Braun et al. 2017), temperature (Portales et al. 2004; Rödel et al. 2005; Vázquez et al. 2007; Tablado et al. 2009; Portales-Betancourt et al. 2012; Wells et al. 2016), precipitation (Wood 1980; Franken and Hik 2004; Portales et al. 2004; Vázquez et al. 2007; Rioja et al. 2011; Portales-Betancourt et al. 2012), and home range size (Innes and Millar 1995; Spady et al. 2007)), two allometric variables (sexual size dimorphism (Valdespino 2007; Zerbe et al. 2012; Heldstab 2021) and body mass (Janson and Verdolin 2005; Rödel et al. 2005; Tökölyi et al. 2014)), and five life history traits (litter size, litters per year, gestation length, weaning age, and age at sexual maturity (Lord 1960; Conaway et al. 1974; Chapman 1984; Swihart 1984; Bronson 1989; Tablado et al. 2009; Tökölyi et al. 2014)). The influence of these 13 factors on birth seasonality will be tested across the whole order Lagomorpha and for each of the distinct four ecotypes (hares and jackrabbits, rabbits, rock- and talus-dwelling pikas, and burrowing pikas) separately. For a more detailed description of how these factors may influence birth seasonality, see Heldstab (2021) and supplementary material of Heldstab et al. (2018).

Lastly, the third aim is to compare reproductive seasonality of Lagomorpha with other mammalian orders. Relative to most other mammals, lagomorphs are characterised by extremely rapid foetal and neonatal growth rates (Case

1978; Eisenberg 1981; Swihart 1984) including post-partum oestrus (females can simultaneously suckle one litter while carrying another in the uterus) and superfetation in the genus *Lepus* (female hares are able to carry a second fertilized ovum in their uterus already containing a pregnancy) (Flux 1967). These characteristics allow lagomorphs to accomplish a reproductive cycle and maximize litter production within a very short time period but impose high energetic demands on females (Flux 1981; Keith 1981; Swihart 1984). Lagomorph species are therefore expected to breed only during optimal environmental conditions in seasonal habitats resulting in a pronounced birth season for species living at high latitudes and/or elevations. On the other hand, the fast reproductive cycle allows lagomorph species to breed opportunistically, e.g., responding to a sudden increase in food availability after rainfall, which may result in a non-seasonal birthing pattern with high intraspecific variation for those species living in regions with large variations in temperature and/or precipitation.

## Materials and methods

To investigate which factors influence reproductive seasonality in the natural habitat of different lagomorphs, a broad dataset on birth seasonality covering 69 species was compiled from the literature. Birth seasonality was described both in a quantitative and a categorical way (Table 1). As a continuous measure, birth season length in months was used as in Heldstab (2021). 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, 2021; Heldstab 2021): Category 1: narrow peak (less than approximately 60 days), no births for the rest of the year; category 2: expanded peak (> 60 days) 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 explanatory variables, namely, the habitat characteristics (mid-altitude, latitude range, mean altitude, mean annual temperature and precipitation of the species' geographical distribution, and home range size), allometric variables (adult body mass and sexual size dimorphism expressed as the ratio of male vs. female body mass), and life-history traits (gestation length, litters per year, litter size, weaning age, and age at sexual maturity) were compiled from the published literature. Although litter size is a

**Table 1** Birth seasonality and biological characteristics of 69 lagomorph species

Species	Allometric variables				Life history traits				Habitat characteristics				Birth seasonality			
	Adult body mass (g)	Sexual size dimorphism	Gestation length (d)	Litter size	Litters per year	Weaning age (d)	Age at sexual maturity (d)	Distinct ecotypes	Home range size (km <sup>2</sup> )	Mid-latitude (°)	Latitude range (°)	Mean altitude (m)	Mean temperature (°C)	Mean precipitation (mm)	Birth season length (months)	Birth season categories
<i>Brachylagus idahoensis</i>	502	0.90	24 <sup>a</sup>	4.0 <sup>a</sup>	3.0 <sup>a</sup>	NA	329.0	2	0.0038	42.6	10.45	1337 <sup>a</sup>	6.9	842.7	4(2,3,5) <sup>a,b,c,d,e,f,g</sup>	3(1,2)
<i>Bunolagus monticulus</i>	1650	0.83 <sup>a</sup>	36 <sup>b</sup>	1.2	1.5 <sup>a</sup>	NA	NA	2	0.1400	-31.6	1.76	1100	15.6	939.5	10(9) <sup>a,d,e</sup>	3(2)
<i>Caprolagus hispidus</i>	2510	0.89 <sup>b</sup>	40	2.5 <sup>a</sup>	2.8	NA	NA	2	0.0042	27.7	3.18	175	23.6	1234.6	2(3,5) <sup>e,f,h,i,j</sup>	2(1)
<i>Lepus alleni</i>	3450	1.02	42	1.9 <sup>a</sup>	3.5	NA	178.0 <sup>a</sup>	1	4.5800	27.6	11.45	750	19.9	1274.8	9(10) <sup>a,d,e,f,g,k,l</sup>	3(2)
<i>Lepus americanus</i>	1850	0.92	36 <sup>b</sup>	3.6	2.5	25.7	365.0 <sup>a</sup>	1	0.0400	52.0	33.12	2896 <sup>b</sup>	-1.3	444.4	5(2,3,4,5,6,7,8) <sup>a,c,d,f,g,m,n,o,p,q</sup>	2(3)
<i>Lepus arcticus</i>	4650	1.02	53 <sup>b</sup>	5.1	1.5	59.5 <sup>a</sup>	329.0	1	2.2600	65.6	36.09	450	-13.2	145.0	2(3,4,5) <sup>a,d,e,g,r,s,t</sup>	1(2)
<i>Lepus brachyurus</i>	2350	NA	45 <sup>b</sup>	1.5 <sup>a</sup>	2.5	30.0 <sup>a</sup>	305.0 <sup>b</sup>	1	0.2000 <sup>a</sup>	36.3	10.56	1350	10.6	830.2	5(7,12) <sup>a,d,e,u</sup>	4(3,5)
<i>Lepus californicus</i>	2450	0.88	44 <sup>b</sup>	3.2 <sup>a</sup>	4.1	18.5	228.1	1	0.5700	33.7	28.53	1875	13.4	1035.5	9(4,7,8,10,12) <sup>a,d,e,f,g,v,w,x,y,z,aa,ab</sup>	3(2)
<i>Lepus callotis</i>	2350	0.62 <sup>c</sup>	42 <sup>c</sup>	2.2	3.0	NA	NA	1	NA	24.6	15.58	1650 <sup>c</sup>	16.8	1359.9	4(5,7) <sup>d,e,i,ac,ad,ae</sup>	2(3)
<i>Lepus capensis</i>	2100	0.97 <sup>d</sup>	42	1.5 <sup>a</sup>	7.0 <sup>a</sup>	26.8	148.1	1	0.4100	1.3	72.17	900	23.5	1409.0	7(3,5,6,8,9,12) <sup>a,c,e,f,af</sup>	4(3)
<i>Lepus comus</i>	2020 <sup>a</sup>	NA	NA	2.4	2.5 <sup>a</sup>	NA	NA	1	NA	25.5	7.70	2250 <sup>d</sup>	12.7	1147.4	6(2,3,5) <sup>d,e,ag</sup>	2
<i>Lepus coreanus</i>	2350 <sup>b</sup>	NA	45 <sup>b</sup>	2.5 <sup>a</sup>	2.5 <sup>a</sup>	NA	NA	1	0.1500 <sup>b</sup>	38.4	8.25	500 <sup>e</sup>	5.9	818.3	6 <sup>a,c</sup>	2
<i>Lepus corsicanus</i>	4250	1.07 <sup>e</sup>	41 <sup>d</sup>	1.5 <sup>a</sup>	3.0 <sup>a</sup>	NA	NA	1	0.9237 <sup>c</sup>	39.6	5.69	1200	14.7	1034.3	12(10) <sup>d,e,ah</sup>	4
<i>Lepus europaeus</i>	4250	0.88 <sup>k</sup>	42	2.2	4.4	31.5 <sup>a</sup>	187.3	1	0.3200	50.0	30.09	1200	5.5	588.0	8(7,9,12) <sup>a,d,e,g,ai,ak,al</sup>	3(2)
<i>Lepus flavigularis</i>	2300	NA	32 <sup>c</sup>	2.0 <sup>b</sup>	2.0 <sup>b</sup>	12.0 <sup>b</sup>	213.5 <sup>c</sup>	1	0.5500 <sup>d</sup>	16.3	0.96	250 <sup>f</sup>	24.4	1627.4	8(5,6,7,10) <sup>e,am,an,ao,ap</sup>	3
<i>Lepus granatensis</i>	2481	NA	42 <sup>a</sup>	1.5	3.5	NA	NA	1	0.3000 <sup>e</sup>	39.9	7.78	950	13.1	965.7	12 <sup>d,e,aq,ar</sup>	4
<i>Lepus insularis</i>	2800	NA	42 <sup>f</sup>	4.0 <sup>b</sup>	3.0 <sup>b</sup>	NA	NA	1	NA	24.5	0.14	150 <sup>g</sup>	22.5	NA	7(5,6,8) <sup>ei</sup>	3
<i>Lepus mandshuricus</i>	1840 <sup>a</sup>	NA	NA	2.4	2.5 <sup>c</sup>	NA	NA	1	NA	45.6	11.47	600 <sup>h</sup>	0.2	565.3	5 <sup>d,e,al</sup>	2
<i>Lepus nigricollis</i>	2700	0.88	36	1.8	7.2	17.0 <sup>e</sup>	182.5	1	0.0100	20.8	29.71	2275 <sup>i</sup>	21.1	1368.1	12(6,11) <sup>c,d,e,f,gu,as</sup>	4
<i>Lepus oiosotus</i>	2875	0.90 <sup>f</sup>	NA	1.5 <sup>a</sup>	2.0	NA	NA	1	NA	33.9	14.26	3950	-3.6	809.4	3(2) <sup>d,e,ag,atau</sup>	2
<i>Lepus othus</i>	5350	0.99	46	6.3 <sup>a</sup>	1.0	49.0	NA	1	NA	61.2	12.91	330 <sup>h</sup>	-4.3	214.9	2(1,3) <sup>a,d,e,g,aw</sup>	1(2)
<i>Lepus saxatilis</i>	3600	0.99 <sup>d</sup>	38	1.5	5.4	NA	365.0 <sup>a</sup>	1	NA	-29.4	10.92	1525 <sup>e</sup>	16.3	1093.3	5(3,10) <sup>a,e,f,aw</sup>	3
<i>Lepus sinensis</i>	1481	NA	NA	3.0 <sup>c</sup>	NA	21.0	NA	1	NA	26.2	12.02	2500 <sup>j</sup>	16.7	1120.3	4 <sup>d,e</sup>	2
<i>Lepus timidus</i>	1481 <sup>a</sup>	0.93	50	3.2	3.0	23.2 <sup>d</sup>	228.5	1	0.8600	59.1	37.22	1850	-5.2	331.8	7(1,2,3,4,6,8,9) <sup>a,d,f,g,at,ax,ay,az</sup>	2
<i>Lepus tolai</i>	1590 <sup>a</sup>	NA	46 <sup>g</sup>	5.0 <sup>a</sup>	2.5 <sup>a</sup>	12.5 <sup>e</sup>	NA	1	0.0210 <sup>f</sup>	40.5	17.03	750 <sup>j</sup>	2.0	753.3	4(5,6) <sup>e,g,al</sup>	2
<i>Lepus townsendii</i>	3290	0.89	39 <sup>b</sup>	4.5	2.0 <sup>a</sup>	27.5	262.2	1	2.5000 <sup>g</sup>	45.4	18.62	2175 <sup>k</sup>	5.3	707.0	5(2,3,4,6) <sup>a,c,d,e,f,g,ii,ba,bb</sup>	2

Table 1 (continued)

Species	Allometric variables			Life history traits			Habitat characteristics					Birth seasonality				
	Adult body mass (g)	Sexual dimorphism	Gestation length (d)	Litter size	Litters per year	Weaning age (d)	Age at sexual maturity (d)	Distinct ecotypes	Home range size (km <sup>2</sup> )	Mid-latitude (°)	Latitude range (°)	Mean altitude (m)	Mean temperature (°C)	Mean precipitation (mm)	Birth season (months)	Birth season categories
<i>Lepus victoriatæ</i>	2250	NA	NA	1.6	7.0 <sup>e</sup>	30.0 <sup>f</sup>	244.0 <sup>d</sup>	1	0.0750 <sup>e</sup>	-1.3	62.43	NA	23.8	1529.4	12(10) <sup>e,e,u</sup>	5(4)
<i>Lepus yarkandensis</i>	1470 <sup>a</sup>	NA	NA	3.9	2.5	NA	NA	1	NA	39.3	5.01	1050 <sup>l</sup>	9.9	719.7	6(7) <sup>d,e,g,b,c</sup>	2
<i>Ochotona alpina</i>	326	NA	30 <sup>b</sup>	3.7 <sup>a</sup>	2.0	21.0	329.0	3	0.0090 <sup>h</sup>	46.3	16.53	1450 <sup>l</sup>	-6.2	489.1	4(2,3) <sup>e,f,i,j</sup>	2
<i>Ochotona cansus</i>	75	NA	20 <sup>b</sup>	3.7	2.3	18.0	348.4	3	0.0006	34.4	10.28	3250 <sup>l</sup>	-1.9	806.9	5(4) <sup>d,e,u,b,b,c</sup>	2
<i>Ochotona collaris</i>	95	1.00 <sup>g</sup>	30 <sup>h</sup>	3.4	2.0	24.0 <sup>g</sup>	321.5	3	0.0010	64.4	10.17	1844 <sup>e</sup>	-9.4	238.5	1(2,3,4) <sup>a,d,e,f,b,f,b,g</sup>	1(2)
<i>Ochotona coreana</i>	163	NA	NA	4.5 <sup>a</sup>	2.0 <sup>a</sup>	NA	NA	4	NA	41.4 <sup>a</sup>	2.22	1750	NA	NA	3 <sup>e</sup>	2
<i>Ochotona curzoniae</i>	163	NA	22	4.4	3.5	21.0 <sup>f</sup>	365.0 <sup>e</sup>	4	0.0011	34.1	13.07	4000	-4.8	786.8	4(2,5) <sup>d,e,f</sup>	2
<i>Ochotona dauurica</i>	195	NA	30	5.9	2.3	28.0 <sup>f</sup>	82.2	4	0.0014 <sup>e</sup>	42.8	19.41	2200	-0.2	598.8	4(2,3,5) <sup>a,d,e,f,i,j,h</sup>	2
<i>Ochotona erythrotis</i>	268	NA	NA	5.0 <sup>d</sup>	2.0 <sup>f</sup>	NA	NA	3	NA	36.3	7.72	3000	-4.9	759.4	3 <sup>d,e,g</sup>	2(3)
<i>Ochotona gloveri</i>	205	NA	NA	3.0 <sup>a</sup>	NA	NA	NA	3	NA	30.1	7.37	2950 <sup>l</sup>	-1.6	925.5	3(2,5) <sup>d,e</sup>	2
<i>Ochotona hoffmanni</i>	285 <sup>c</sup>	NA	30 <sup>i</sup>	NA	NA	NA	NA	3	NA	48.6 <sup>g</sup>	1.77	1500 <sup>a</sup>	NA	NA	3 <sup>d,e</sup>	2
<i>Ochotona hyperborea</i>	109	NA	28	4.1	1.5 <sup>g</sup>	14.0 <sup>h</sup>	NA	3	0.0022	56.9	35.72	1200 <sup>h</sup>	-9.2	320.3	3(2,4) <sup>d,e,a,l</sup>	2
<i>Ochotona ladacensis</i>	255	NA	NA	NA	NA	NA	NA	4	0.0004 <sup>e</sup>	36.0	7.26	4925 <sup>j</sup>	-6.1	749.1	1(2) <sup>d,e,u</sup>	1
<i>Ochotona macrotis</i>	215	NA	30 <sup>j</sup>	4.1	2.0	31.0 <sup>f</sup>	323.2	3	0.0016 <sup>e</sup>	34.7	18.88	4215	-1.6	882.0	4(3) <sup>a,d,e,f,i,j</sup>	2
<i>Ochotona manchurica</i>	185	NA	NA	4.0 <sup>a</sup>	1.0 <sup>a</sup>	NA	NA	4	NA	49.9 <sup>a</sup>	6.73 <sup>a</sup>	850	NA	NA	2 <sup>e</sup>	2
<i>Ochotona opaca</i>	137 <sup>a</sup>	NA	26 <sup>a</sup>	7.5 <sup>c</sup>	2.5 <sup>e</sup>	NA	206.0 <sup>d</sup>	4	0.0028 <sup>e</sup>	47.7 <sup>a</sup>	3.61	700 <sup>l</sup>	NA	NA	2 <sup>d</sup>	2
<i>Ochotona pallasi</i>	220	0.90 <sup>h</sup>	25	7.0	2.5	19.4	308.5	4	0.0018	45.2	12.07	4450	-0.5	570.5	5(2,3,4) <sup>d,i,j</sup>	2
<i>Ochotona princeps</i>	149	1.08	30	2.9	2.0	26.5	326.1	3	0.0011	44.9	19.32	3338	4.4	769.1	3(2,4) <sup>d,e,g,b,j</sup>	2(1)
<i>Ochotona pusilla</i>	186	0.78 <sup>h</sup>	22	8.5	3.5	20.0 <sup>a</sup>	27.9	4	0.0002 <sup>e</sup>	50.5	8.18	280 <sup>a</sup>	2.7	526.0	3(2,4) <sup>d,e,f,i,j</sup>	2
<i>Ochotona roylei</i>	157	NA	30 <sup>k</sup>	2.5 <sup>a</sup>	1.0 <sup>a</sup>	21.0	293.8	3	0.0001 <sup>b</sup>	32.3	9.85	3800	-3.6	959.5	3(2,4) <sup>a,d,e,f</sup>	2
<i>Ochotona rufescens</i>	198	NA	26	6.2 <sup>a</sup>	4.0	18.0 <sup>a</sup>	53.1	4	0.0163 <sup>e</sup>	32.2	12.90	1850	13.9	1209.5	5(3,4,6) <sup>d,e,f,i,j</sup>	2
<i>Ochotona rutula</i>	270 <sup>d</sup>	0.99 <sup>h</sup>	30 <sup>a</sup>	4.1	2.5	20.0	329.0	3	0.0006 <sup>e</sup>	41.0	6.17	2500 <sup>m</sup>	1.3	798.0	4(1,3,5) <sup>d,e,f,i,j</sup>	2
<i>Ochotona thibetana</i>	104	NA	NA	2.9	3.0 <sup>h</sup>	NA	NA	4	NA	30.4	10.76	3250	3.9	932.9	3(4) <sup>e,b,k</sup>	2
<i>Ochotona turuchanensis</i>	142 <sup>c</sup>	NA	NA	3.4 <sup>e</sup>	1.0 <sup>e</sup>	NA	NA	3	0.0029 <sup>e</sup>	66.1 <sup>a</sup>	14.89	600 <sup>l</sup>	NA	NA	3(2) <sup>d,e</sup>	2
<i>Oryctolagus cuniculus</i>	1590 <sup>a</sup>	1.03	30	5.0	4.5	26.0	161.6	2	0.0400	44.2	27.07	750 <sup>n</sup>	10.4	716.7	7(4,5,6,8,9,12) <sup>a,d,e,f,g,h,i,j,m</sup>	4(2,3)
<i>Pentalagus furnessi</i>	2400	1.14 <sup>i</sup>	NA	1.0 <sup>a</sup>	2.5 <sup>a</sup>	107.0 <sup>j</sup>	NA	2	0.0115 <sup>i</sup>	28.1	0.86	347 <sup>o</sup>	NA	NA	6(5) <sup>d,e,b,n</sup>	3(2)
<i>Poelagus marjorita</i>	2715	NA	35	1.2	NA	NA	91.5 <sup>b</sup>	2	0.0001 <sup>g</sup>	-1.4	25.14	1030 <sup>e</sup>	24.0	1593.4	12 <sup>a,d,e,f,u</sup>	4(5)

Table 1 (continued)

Species	Allometric variables				Life history traits				Habitat characteristics				Birth seasonality			
	Adult body mass (g)	Sexual size dimorphism	Gestation length (d)	Litter size	Litters per year	Weaning age (d)	Age at sexual maturity (d)	Distinct ecotypes	Home range size (km <sup>2</sup> )	Mid-latitude (°)	Latitude range (°)	Mean altitude (m)	Mean temperature (°C)	Mean precipitation (mm)	Birth season length (months)	Birth season categories
<i>Pronolagus crassicaudatus</i>	2725	NA	35 <sup>1</sup>	1.5	NA	NA	NA	2	NA	-29.4	7.06	775 <sup>p</sup>	16.4	1193.6	12 <sup>d,e,u</sup>	4(5)
<i>Pronolagus randensis</i>	2385	NA	NA	1.1	NA	NA	NA	2	NA	-20.3	14.52	1250 <sup>a</sup>	18.5	1319.2	12 <sup>e,u</sup>	5
<i>Pronolagus rupestrus</i>	1700	1.08 <sup>d</sup>	38 <sup>b</sup>	1.5 <sup>a</sup>	3.5 <sup>i</sup>	NA	NA	2	NA	-16.8	36.12	1170 <sup>a</sup>	17.6	1255.9	5 <sup>d,e,bo,bp</sup>	2
<i>Romerolagus diazi</i>	494	1.05	39	2.0	4.5 <sup>h</sup>	27.7	185.1	2	0.0188 <sup>e</sup>	19.1	0.13	3252 <sup>e</sup>	13.8	1211.0	12(3,5,8) <sup>a,d,e,fbq</sup>	4
<i>Sylvilagus aquaticus</i>	2150	1.01	37	3.0	2.9	21.0	149.0	2	0.0100	33.1	9.65	130 <sup>a</sup>	17.8	1116.6	6(5,7,8,11,12) <sup>a,d,e,fg</sup>	3(4)
<i>Sylvilagus auduboni</i>	1003	0.94	28	3.1 <sup>a</sup>	8.0 <sup>d</sup>	24.5	76.6	2	0.0300	33.6	29.70	900 <sup>q</sup>	13.1	1042.8	7(6,8,12) <sup>a,d,e,fg,br</sup>	3(4)
<i>Sylvilagus bachmani</i>	714	0.97	27	3.4	5.5 <sup>a</sup>	16.7	137.3 <sup>b</sup>	2	0.0023 <sup>j</sup>	34.5	23.32	1035 <sup>r</sup>	12.9	1008.3	6(5,7) <sup>d,e,fg,ubs</sup>	2
<i>Sylvilagus cunicularius</i>	2078	0.97 <sup>d</sup>	30	3.7	NA	12.0	NA	2	0.0368	19.8	8.35	2150	19.5	1512.3	12 <sup>d,e,bl,bu</sup>	4
<i>Sylvilagus dicei</i>	1100 <sup>a</sup>	NA	30	4.5	NA	31.1	NA	2	NA	9.6	1.92	1800 <sup>s</sup>	24.8	1748.7	8(12) <sup>e</sup>	3(4)
<i>Sylvilagus floridanus</i>	1150	0.95	28 <sup>b</sup>	4.6	4.8	23.4	89.9	2	0.0100	28.2	48.02	460 <sup>a</sup>	15.3	1097.3	7(6,8,12) <sup>a,e,fg,ibv,bw,bx</sup>	3
<i>Sylvilagus mansuetus</i>	960	NA	NA	2.0 <sup>c</sup>	NA	NA	NA	2	NA	25.0	0.22	5	20.6	NA	6 <sup>c,by</sup>	2
<i>Sylvilagus nuttallii</i>	865	0.91	29 <sup>b</sup>	4.8	3.5	30.9	85.9	2	0.0001 <sup>k</sup>	42.2	17.00	1840	6.1	811.8	4(2,3,5) <sup>a,d,e,fg,ubz</sup>	2
<i>Sylvilagus obscurus</i>	897	0.97 <sup>d</sup>	28 <sup>a</sup>	4.0 <sup>c</sup>	3.0 <sup>h</sup>	16.0 <sup>a</sup>	75.0 <sup>e</sup>	2	0.0738 <sup>e</sup>	36.9 <sup>a</sup>	7.43	683 <sup>l</sup>	NA	NA	6(7) <sup>a,d,e</sup>	2
<i>Sylvilagus palustris</i>	1125	0.95	34	4.0 <sup>a</sup>	6.0	13.5 <sup>f</sup>	152.1	2	0.0300	31.1	12.26	76 <sup>c</sup>	19.3	1200.2	12(7,8,10) <sup>a,d,e,ga,ca,cb</sup>	5(4)
<i>Sylvilagus transitionalis</i>	897	0.95	28	4.2 <sup>a</sup>	2.5	15.9	NA	2	0.0043	42.9	3.81	280 <sup>a</sup>	7.7	704.4	5(3,4,6,8) <sup>a,d,e,fg,u,cc</sup>	3(2)
<i>Sylvilagus varynaensis</i>	1671	0.92 <sup>j</sup>	35 <sup>a</sup>	2.6 <sup>c</sup>	NA	NA	NA	2	NA	7.6 <sup>a</sup>	0.53	161 <sup>t</sup>	NA	NA	8 <sup>d,e</sup>	3(2)

**Table 1** (continued)

Adult body mass from Smith et al. (2018) unless otherwise noted: a Jones et al. (2009), b (Myers et al. 2006), c (Wilson et al. 2016), d (Smith et al. 2016)

Sexual size dimorphism: ratio between body mass of males and females taken from Swihart (1984) unless otherwise noted: a (Duthie 1989), b (Chapman and Flux 1990), c (Best and Henry 1993b), d (Davis and Roth 2008), e (Scarselli et al. 2018), f (Cai and Feng 1982), g (Franken and Hik 2004), h (Sokolov et al. 2009), i (Myers et al. 2006), j (Durant and Guevara 2000), k (Flux 1967). Note: The value for *Lepus corsicanus* is only based on 2 males and 2 females

Gestation length from Jones et al. (2009) unless otherwise noted: a (Wilson et al. 2016), b (Smith et al. 2018), c (Córdova Izquierdo and Ruiz Lang 1994), d (Mengoni 2011), e (Rioja et al. 2011), f (Nowak 1999), g (Swihart 1984), h (MacDonald and Jones 1990), i (Chapman and Flux 1990), j (Smith and Lissovsky 2016), k (Myers et al. 2006), l (Virgos et al. 2006)

Litter size from Jones et al. (2009) unless otherwise noted: a (Smith et al. 2011), c (Wilson et al. 2016), d (Happold 2013), e (Lissovsky 2004)

Litters per year from Jones et al. (2009) unless otherwise noted: a (Smith et al. 2011), c (Sokolov et al. 2009), d (Swihart 1984), e (Wilson et al. 2016), f (Smith et al. 2010), g (Revin 1968), h (Myers et al. 2006), i (Child et al. 2019)

Weaning age from Jones et al. (2009) unless otherwise noted: a (Smith et al. 2011), c (Prakash and Taneja 1969), d (Isler and van Schaik 2012), e (Sokolov et al. 2009), f (Myers et al. 2006), g (Franken and Hik 2004), h (Wilson et al. 2016), i (Yamada and Cervantes 2005)

Age at sexual maturity from Jones et al. (2009) unless otherwise noted: a (Smith et al. 2018), b (Myers et al. 2006), c (Fariás et al. 2018), d (Smith et al. 2018), e (Wilson et al. 2016)

Distinct ecotypes from Smith et al. (2018), species were placed in one of four categories based on their main ecotype, as follows: 1: hares and jackrabbits, 2: rabbits, 3: rock- and talus-dwelling pikas; 4: burrowing pikas

Home range size from Jones et al. (2009) unless otherwise noted: a (Enari and Sakamaki 2012), b (Smith et al. 2018), c (Scarselli et al. 2018), d (Fariás et al. 2018), e (Wilson et al. 2016), f (Sokolov et al. 2009), g (Myers et al. 2006), h (Caravaggi 2018), i (Yamada et al. 2000), j (Álvarez et al. 2013), k (Skalski 1976)

Mid-latitude: centre of the latitude range that a species inhabits from Jones et al. (2009) unless otherwise noted: a (IUCN 2020)

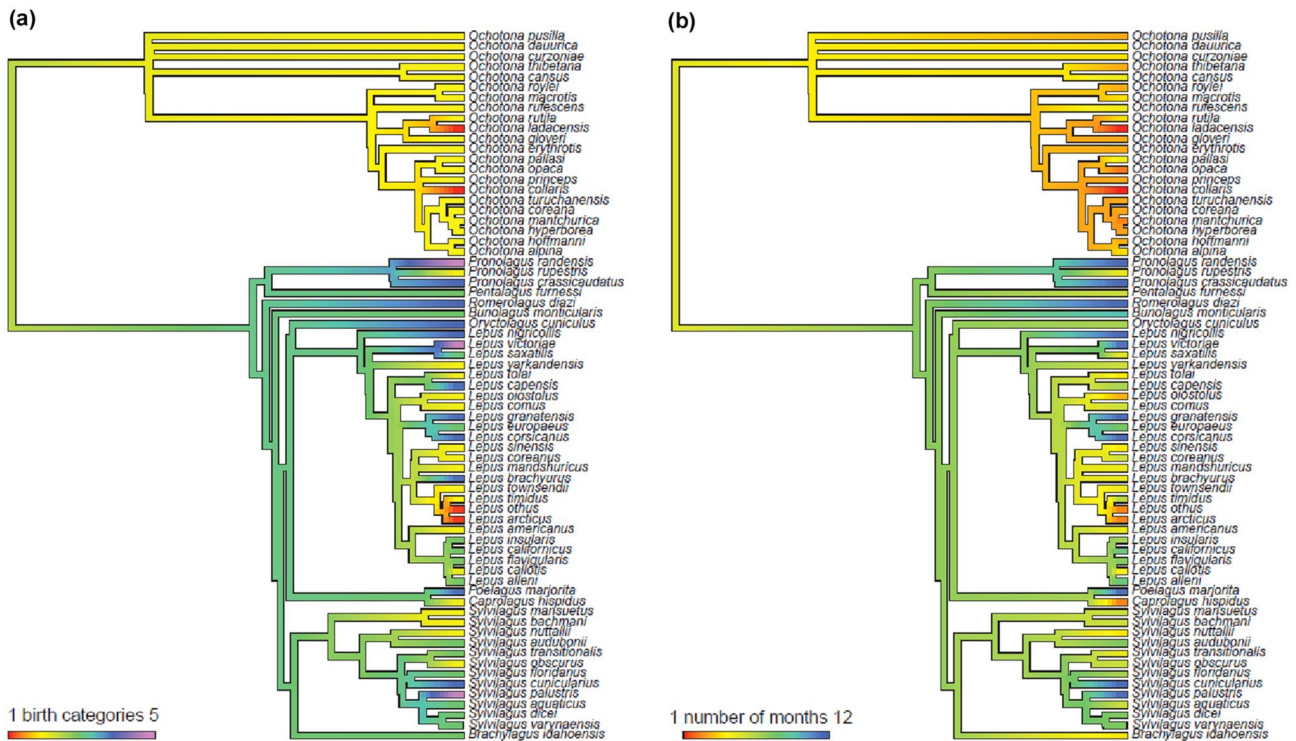
Latitude range from Jones et al. (2009) unless otherwise noted: a (IUCN 2020)

Altitude from IUCN (2020) unless otherwise noted: a (Leach et al. 2015), b (Bailey 1936), c (Best and Henry 1993b), d (Wang et al. 1985), e (Myers et al. 2006), f (Lorenzo et al. 2006), g (Nelson 2009), h (Chapman and Flux 1990), i (Molur et al. 2005), j (Smith et al. 2010), k (Lim 1987), l (Wilson et al. 2016), m (Corbet 1978), n (Cubas et al. 2018), o (Yamada and Cervantes 2005), p (Duthie 1989), q (Vargas Cuenca and Cervantes 2005), r (Chapman 1974), s (Wilson and Mittermeier 2009), t (Smith et al. 2018)

Mean annual temperature from Jones et al. (2009)

Mean annual precipitation from Jones et al. (2009)

Seasonality of reproduction: the reported categories not in parentheses were used, which were considered most typical for the species; categories in parentheses represent other patterns described for the species in the literature: a (Myers et al. 2006), b (Green and Flinders 1980), c (Feldhamer et al. 2003), d (Wilson et al. 2016), e (Smith et al. 2018), f (Hayssen et al. 1993), g (Swihart 1984), h (Ghose 1978), i (Nowak 1999), j (Oliver 1980), k (Lorenzo and Brown 2019), l (Best and Henry 1993a), m (Newson 1964), n (Keith et al. 1966), o (Maser et al. 1981), p (Schmidt and Goutley 1992), q (Zimova et al. 2018), r (Hearn et al. 1987), s (Parker 1977), t (Best and Henry 1994a), u (Chapman and Flux 1990), v (Lechleitner 1959), w (Gross et al. 1974), x (Tiemeier and Plener 1964), y (Vorhies and Taylor 1933), z (Portales-Betancourt et al. 2012), aa (Portales et al. 2004), ab (Best 1996), ac (Best and Henry 1993b), ad (Bednarz 1977), ae (Bogan and Jones 1975), af (Flux and Jarvis 1970), ag (Smith et al. 2010), ah (Mengoni 2011), ai (Holly 2001), aj (Lincoln 1974), ak (Schai-Braun et al. 2020), al (Sokolov et al. 2009), am (Rioja et al. 2011), an (Rioja et al. 2008), ao (Cervantes 1993), ap (Fariás et al. 2006), aq (Alves and Rocha 2003), ar (Alves et al. 2002), as (Prakash and Taneja 1969), at (Feng et al. 1986), au (Lu 2010), av (Best and Henry 1994b), aw (Happold 2013), ax (Naumov and Shatalova 1974), ay (Angerbjörn and Flux 1995), az (Schai-Braun et al. 2017), ba (Rogowitz 1992), bb (Lim 1987), bc (Smith and Johnston 2016), bd (Smith 1990), be (Jiang and Wang 1991), bf (Franken and Hik 2004), bg (MacDonald and Jones 1987), bh (Smith and Cook 2016), bi (Smith and Lissovsky 2016), bj (Smith and Weston 1990), bk (Smith and Liu 2016), bl (Lockley 1976), bm (Stubbe et al. 1991), bn (Yamada and Smith 2016), bo (Child et al. 2019), bp (Skinner and Chimimba 2005), bq (Cervantes et al. 1990), br (Chapman and Willner 1978), bs (Chapman 1974), bt (Vázquez et al. 2007), bu (Cervantes et al. 1992), bv (Barkalow 1962), bw (Conaway et al. 1974), bx (Chapman et al. 1980), by (Lorenzo et al. 2011), bz (Chapman 1975), ca (Forys 1995), cb (Chapman and Willner 1981), cc (Litvaitis and Lanier 2019)



**Fig. 1** The phylogenetic tree used in the present study from Fritz et al. (2009), with an indication how **a** the birth season categories and **b** the birth season length in months are distributed across the

tree, ranging from very short (a highly seasonal reproductive pattern, red) to very long (a non-seasonal reproductive pattern, dark blue)

standard measure, it is unfortunately rarely clearly defined in the literature as either number of embryos conceived, number of healthy embryos close to parturition (after accounting for the resorption of embryos) or the number of young at parturition. Furthermore, the number and size of litters have been shown to vary intraspecifically within lagomorphs according to latitude, elevation, snowmelt, the probability of survival of young, and due to metapopulation dynamics (e.g., Keith et al. 1966; Millar 1973; Conaway et al. 1974; Hewson and Taylor 1975; Smith 1978; Tablado et al. 2009). In the present study, preference was given to litter size values deriving from the number of young at parturition and litter size and litters per year values most commonly mentioned in the literature. Detailed sources of data for the whole dataset are given in Table 1.

Statistical analyses were performed in JMP™ 13.0 (SAS Institute Inc 1989–2016) and in R 4.0.4 (R Core Team 2021). All analyses were controlled for phylogenetic non-independence using phylogenetic generalized least-squares regressions (PGLS: Martins and Hansen 1997) using the “caper” package (Orme et al. 2013) in R. PGLS is a modification of generalised least squares using the knowledge of phylogenetic relationships to produce an estimate of expected covariance in cross-species data (Symonds and Blomberg 2014). Closely related species are assumed to have more similar

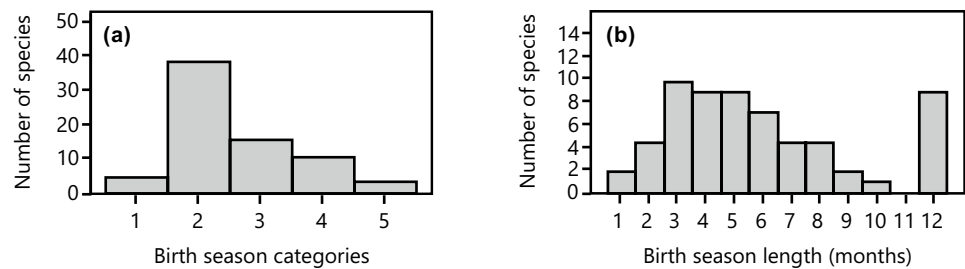
traits because of their shared ancestry and hence produce more similar residuals from the least-squares regression line. By taking into account the expected covariance structure of these residuals, modified slope and intercept estimates are generated that can account for interspecific autocorrelation due to phylogeny. Caper estimates PGLS model parameters in maximum likelihood (Orme et al. 2013) and the parameter lambda ( $\lambda$ ), which quantifies the magnitude of the phylogenetic signal in the model residuals (Freckleton et al. 2002). The value of  $\lambda$  can vary between 0, indicating no phylogenetic signal, and 1, indicating that the observed pattern fits a Brownian motion model of trait evolution along the branches of the phylogeny such that similarity between species is directly proportional to relatedness.

The lagomorph phylogeny was extracted from the composite mammalian supertree including branch length estimations provided by Fritz et al. (2009) and is given in Fig. 1. Seven species (*Lepus victorae*, *Ochotona coreana*, *Ochotona hoffmanni*, *Ochotona manchurica*, *Ochotona opaca*, *Sylvilagus obscurus*, and *Sylvilagus varynaensis*) were not part of this supertree and therefore added manually in Mesquite (Maddison and Maddison 2001) following the latest IUCN taxonomy (IUCN 2020).

To determine the most important explanatory variables of birth seasonality either measured in categories or number of



**Fig. 2** The distribution of lagomorph species according to their reproductive seasonality characterized by **a** the birth season categories and **b** the birth season length in months



months, all thirteen explanatory variables mentioned above were tested in univariate PGLS analyses. Unfortunately, performing multivariate regressions or multi-model averaging was impossible because each explanatory variable had a different sample size (due to missing values for several understudied species) and there was problematic high multicollinearity between predictors (Rogerson 2001) (Online Resource 1). The critical level of significance ( $P = 0.050$ ) was adjusted by Bonferroni correction for multiple testing to ( $P = 0.004$ ). 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. The values of home range size, adult body mass, gestation length, weaning age, and age at sexual maturity were log-transformed before analysis to reduce the skew of their distribution. Additionally, to investigate the effect of habitat characteristics, allometric variables and life-history traits on birth seasonality in more detail, the four distinct ecotypes of lagomorphs (hares and jackrabbits, rabbits, rock- and talus-dwelling pikas, and burrowing pikas) were each analysed separately.

## 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:  $p < 0.001$ ,  $n = 69$ ,  $\lambda < 0.001$ ,  $\beta = 1.055$ ,  $SE = 0.019$ ,  $t = 14.000$ ), indicating that the quantitative and the categorical approach yielded a comparable ranking of species. The ordinal birth seasonality categories showed a right-skewed distribution with the highest number of species in category 2, indicating that the majority of lagomorphs reproduce during an expanded but determined time window of more than 2 months with no births for the rest of the year (Fig. 2a). The birth season length in months ranged from 1 to 12 months and its distribution was also right skewed but showed a second peak at birth season length of 12 months with 14.5% of species reproducing year-round (Fig. 2b). Lagomorphs show a high degree of intraspecific variation in birth season length. As evident in Table 1, for many species, various birth season lengths have been described in the literature ranging in the

most extreme cases of volcano rabbits (*Romerolagus diazi*) and cape hares (*Lepus capensis*) from 3 to 12 months and of mountain hares (*Lepus timidus*) from 1 to 9 months.

The phylogenetic patterns of reproductive seasonality are given in Fig. 1a and b. The most strictly seasonally reproducing group were the pikas (Ochotonidae) with an average birth season length of 3.23 months and the most seasonal species, the collared pika (*Ochotona collaris*) and the Ladak pika (*Ochotona ladacensis*) followed by hares with an average birth season length of 6.60 months, and the rabbits with an average birth season length of 7.73 months.

The most important factors influencing the degree of birth seasonality in lagomorphs were mid-latitude, mean annual temperature and precipitation of a species' geographical distribution, litter size, and litters per year (Tables 2 and 3). Birth seasonality either measured in months or categories was negatively correlated to the mid-latitude of a species' geographical distribution (Fig. 3a and b) showing that reproductive periods became shorter with increasing latitude. Mean annual temperature (Fig. 3c and d) and precipitation (Fig. 3e and f) were positively correlated with reproductive seasonality, indicating that lagomorph species living in warmer habitats with more precipitation exhibit an expanded birth season. Litters per year was positively (Fig. 3g and h) and litter size negatively (Fig. 3i and j) correlated with birth season length, suggesting that species with a more pronounced birth seasonality have larger but fewer litters per year than species which have a more expanded birthing pattern. Adult body mass was positively linked to birth seasonality but only if measured in months (Fig. 3k and l), where heavier species are less likely to be seasonal breeders. Latitude range, mean altitude of a species' geographical distribution, home range size, gestation length, weaning age, age at sexual maturity, and sexual size dimorphism had no influence on reproductive seasonality in lagomorphs (Tables 2 and 3).

Investigating each of the four distinct ecotypes separately, I found that for hares and jackrabbits, the most important factors influencing birth seasonality were litter size, litters per year and mean annual temperature (Online Resources 2 and 3). Mean annual temperature and litters per year were positively and litter size negatively correlated with birth seasonality either measured in the number of

**Table 2** Results from phylogenetic generalized least squares regression models testing for the effect of various predictor variables on birth season length in months

Predictor variables	Estimate	Std. error	t-value	P-value	N	$\lambda$	Adj. R <sup>2</sup>
<i>Habitat characteristics</i>							
<b>Mid-latitude</b>	<b>-0.093</b>	<b>0.023</b>	<b>-4.104</b>	<b>&lt; 0.001</b>	<b>69</b>	<b>0.235</b>	<b>0.189</b>
Latitude range	0.017	0.023	0.726	0.470	69	0.427	-0.007
Mean altitude	<0.001	<0.001	0.328	0.744	68	0.457	-0.014
<b>Mean annual temperature</b>	<b>0.208</b>	<b>0.030</b>	<b>6.874</b>	<b>&lt; 0.001</b>	<b>61</b>	<b>0.000</b>	<b>0.435</b>
<b>Mean annual precipitation</b>	<b>0.005</b>	<b>&lt; 0.001</b>	<b>4.789</b>	<b>&lt; 0.001</b>	<b>59</b>	<b>0.160</b>	<b>0.274</b>
log(home range size)	0.187	0.182	1.030	0.309	48	0.264	0.001
<i>Life history traits</i>							
log(gestation length)	0.238	2.469	0.096	0.924	53	0.295	-0.019
<b>Litter size</b>	<b>-0.687</b>	<b>0.220</b>	<b>-3.119</b>	<b>0.003</b>	<b>67</b>	<b>0.252</b>	<b>0.117</b>
<b>Litters per year</b>	<b>1.080</b>	<b>0.211</b>	<b>5.117</b>	<b>&lt; 0.001</b>	<b>58</b>	<b>0.201</b>	<b>0.306</b>
log(weaning age)	-2.065	0.956	-2.162	0.037	39	0.572	0.086
log(age at sexual maturity)	-0.788	0.757	-1.040	0.305	37	0.402	0.002
<i>Allometric variables</i>							
<b>log(mean adult body mass)</b>	<b>1.372</b>	<b>0.271</b>	<b>5.067</b>	<b>&lt; 0.001</b>	<b>69</b>	<b>0.000</b>	<b>0.266</b>
Sexual size dimorphism	5.479	4.175	0.753	0.457	36	0.219	-0.013

Significant effects after Bonferroni correction ( $P=0.004$ ) are highlighted in bold

**Table 3** Results from phylogenetic generalized least squares regression models testing for the effect of various predictor variables on reproductive seasonality characterized by five birth season categories

Predictor variables	Estimate	Std. error	t-value	P-value	N	$\lambda$	Adj. R <sup>2</sup>
<i>Habitat characteristics</i>							
<b>Mid-latitude</b>	<b>-0.032</b>	<b>0.007</b>	<b>-4.603</b>	<b>&lt; 0.001</b>	<b>69</b>	<b>0.161</b>	<b>0.229</b>
Latitude range	0.010	0.007	1.365	0.177	69	0.505	0.013
Mean altitude	<0.001	<0.001	-0.523	0.603	68	0.435	-0.011
<b>Mean annual temperature</b>	<b>0.065</b>	<b>0.009</b>	<b>7.068</b>	<b>&lt; 0.001</b>	<b>61</b>	<b>0.000</b>	<b>0.449</b>
<b>Mean annual precipitation</b>	<b>0.002</b>	<b>&lt; 0.001</b>	<b>5.135</b>	<b>&lt; 0.001</b>	<b>59</b>	<b>0.121</b>	<b>0.304</b>
log(home range size)	0.023	0.057	0.409	0.685	48	0.249	-0.018
<i>Life history traits</i>							
log(gestation length)	-0.255	0.733	-0.348	0.729	53	0.301	-0.017
<b>Litter size</b>	<b>-0.218</b>	<b>0.069</b>	<b>-3.157</b>	<b>0.002</b>	<b>67</b>	<b>0.277</b>	<b>0.120</b>
<b>Litters per year</b>	<b>0.423</b>	<b>0.059</b>	<b>7.141</b>	<b>&lt; 0.001</b>	<b>58</b>	<b>0.000</b>	<b>0.467</b>
log(weaning age)	-0.436	0.351	-1.244	0.221	40	0.363	0.014
log(age at sexual maturity)	-0.091	0.258	-0.353	0.726	37	0.322	-0.025
<i>Allometric variables</i>							
log(mean adult body mass)	0.263	0.174	1.511	0.136	69	0.305	0.019
Sexual size dimorphism	1.554	1.647	0.944	0.352	36	0.343	-0.003

Significant effects after Bonferroni correction ( $P=0.004$ ) are highlighted in bold

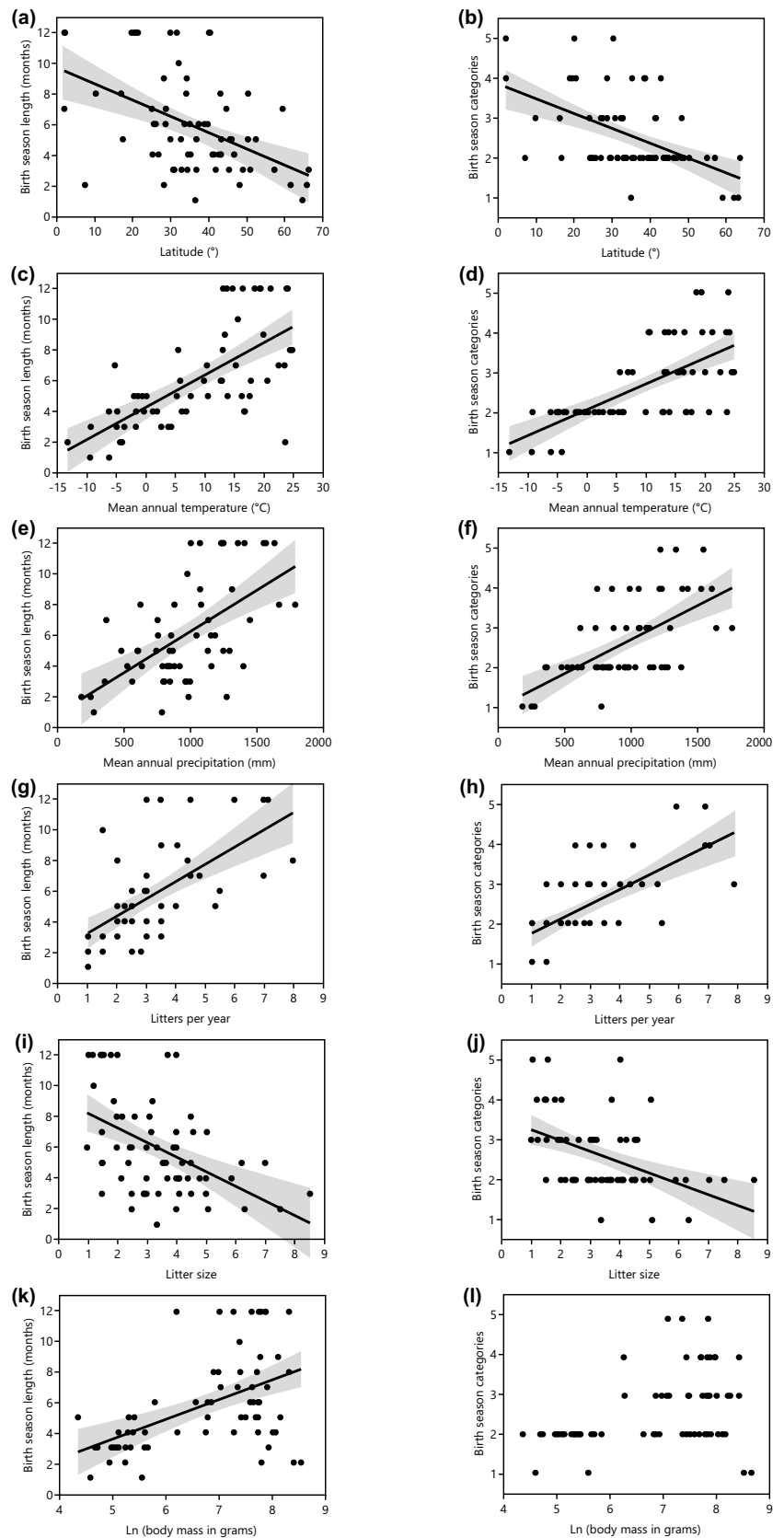
months or categories. Additionally, mean annual precipitation showed a positive and mid-latitude negative relationship with reproductive seasonality in hares and jackrabbits but only if birth seasonality was measured in categories (Online Resources 2 and 3). For the other three ecotypes (rabbits, rock-and talus-dwelling pikas, and burrowing pikas), none of the 13 tested factors had a significant influence on birth seasonality after Bonferroni correction for multiple testing (Online Resources 4–9). The only factor close to significance was litters per year in rabbits showing

a positive trend on birth season length measured in months (Online Resources 4).

## Discussion

Lagomorphs occur worldwide (except in Antarctica) across a wide range of habitats spanning altitudes from sea level to more than 5000 m and latitudes from the equator up to 80°N (Wilson et al. 2016; Smith et al. 2018). Not surprisingly, lagomorphs are important for maintaining the equilibrium

**Fig. 3** Relationship between either the birth season length in months or the birth season categories and (a and b) the latitude of a species' geographical distribution, (c and d) mean annual temperature, (e and f) mean annual precipitation, (g and h) litters per year, (i and j) litter size, and (k and l) adult body mass. Body mass did not correlate with birth season categories. OLS regression lines (solid) and corresponding 95% confidence intervals (grey shading) are shown. For statistics, see Tables 2 and 3



of many different ecosystems given that they are primary consumers and key prey species for a large array of predators (e.g., Tablado et al. 2009; Vaughan et al. 2013; Badingqiuying et al. 2016). This emphasizes the need to understand what controls population dynamics in Lagomorpha including their reproductive behaviour.

By applying both a categorical description (birth season categories 1–5) and a quantitative measure (birth season length in months), this study characterizes the degree of reproductive seasonality in the wild of 69 lagomorph species and tests the influence of 13 variables that were previously suggested to play a role in birth seasonality. I found that many lagomorph species exhibit a high degree of intraspecific variation in birth season length with the majority of species reproducing for an expanded but determined period of more than two months. I further show that the most important factors influencing the degree of birth seasonality were mid-latitude, mean annual temperature, and precipitation in a species' geographical range, litter size and litters per year. Although less strongly, body mass was also correlated with birth season length. These results signify that environmental conditions of the natural habitats, as well as life history adaptations, determine birth seasonality in the order Lagomorpha.

### Characterization of birth seasonality in Lagomorpha

Consistent with previous studies (e.g., Conaway et al. 1974; Smith 1978; Wood 1980; Gibb et al. 1985; Franken and Hik 2004; Tablado et al. 2009), lagomorphs show a large intraspecific variation in birth seasonality. This is especially true for Leporidae (rabbits, jackrabbits and hares) with wide geographical ranges (Schai-Braun and Hackländer 2016) and some very successful invasive species that have been introduced in numerous countries (Flux and Fullagar 1992; Montuire 2001; Chapman and Flux 2008). Since populations of several leporid species are known to adjust the length of their birthing season to their geographical location (Conaway et al. 1974; Bronson 1989; Tablado et al. 2009), large within-species variation might be a consequence of their extensive distribution. In species with a more limited geographic range, intraspecific variation in birth seasonality might occur because lagomorphs are known to reproduce very opportunistically with high year-to-year variability, depending on various factors such as weather and snow cover (Flux 1970; Franken and Hik 2004; Portales et al. 2004; Rödel et al. 2005; Morrison and Hik 2007), food availability (Flux 1970; Millar 1972; Smith 1978) and predation risk influencing population density (Wood 1980; Boonstra et al. 1998).

In contrast to leporids, most pikas (Ochotonidae) reproduce strictly seasonally. Many species of this family live at northern latitudes (Smith et al. 2018; Thapa et al. 2018), are

high-altitude specialists (Smith 1974) and occur in limited distribution areas (Leach et al. 2015). These characteristics might explain their seasonal birthing pattern because the period of optimal environmental conditions for parturition and subsequent conception is short in northern alpine environments (Sparks and Menzel 2002), particularly for mammalian herbivores. The snow-free season is often shorter than two months and young must therefore be born late enough to avoid snow or low-quality food resources and early enough to allow growth and accumulation of body fat stores to survive the subsequent winter (O'Donoghue and Boutin 1995; Franken and Hik 2004). Thus, there is great selective pressure for early births, and short birthing periods for northern mountain-dwelling mammals such as many pika species (Smith 1978) (see below for the influence of latitude and altitude on birth seasonality).

### Factors associated with seasonal reproduction in Lagomorpha

#### Habitat characteristics: latitude, latitude range, altitude, temperature, precipitation and home range size

Overall, this study shows that mid-latitude, mean annual temperature and precipitation of a species' habitat have a significant influence on reproductive seasonality in lagomorphs. Previous intraspecific studies in lagomorphs similarly confirmed a strong relationship between latitude and birth seasonality (Barkalow 1962; Conaway et al. 1974; Flux 1981; Gibb et al. 1985; Bronson 1989; Chapman and Flux 2008; Tablado et al. 2009). Birth 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 and 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 for short birthing periods at high latitudes (Prendergast et al. 2002). Latitudinal range, however, had no influence on reproductive seasonality in lagomorphs. In comparable studies across rodent, primate and Carnivora species, I found that species with a wider latitudinal range had longer birth seasons (Heldstab et al. 2018, 2021; Heldstab 2021). However, the effect of latitudinal range was always much smaller than the effect of mid-latitude.

Another factor that is supposed to have similar effects as latitude on the reproductive strategy of lagomorphs is the mean altitude of species distribution. As for increasing latitude, the favourable season becomes shorter with increasing altitude (Mooney and Billings 1961; Sadleir 1969; Körner

2007). I therefore expected that the birth season would be more pronounced for species living in high-altitudinal habitats. However, unlike previous studies in the Eastern cottontail (*Sylvilagus floridanus*) and Alpine mountain hares (*L. timidus varronis*), which found an effect of altitude on the onset of reproduction (Conaway et al. 1974) or on litter size (Schai-Braun et al. 2017), I found no influence of altitude on reproductive seasonality across Lagomorpha.

As shown here and in previous single-species studies, habitats or years that were warmer (Hewson and Taylor 1975; Frylestam 1980; Myrberget 1983; Angerbjörn 1986; Tablado et al. 2009) and had a higher amount of precipitation (Vorhies and Taylor 1933; Bothma and Teer 1977; McKay and Verts 1978; Wilde 1979; Wood 1980) were associated with less seasonal reproduction. Low temperatures and low amounts of precipitation are associated with reduced food availability (e.g., reduced vegetation growth) (Boutin and Larsen 1993; Tablado et al. 2009) and with increased thermal stress (Gilbert et al. 1987; Rödel et al. 2004), resulting in poor body condition and a temporary cessation of breeding (Flux 1970; Andersson et al. 1981; Bell and Webb 1991; Rödel et al. 2005) consequently leading to a more seasonal reproduction.

### Life history traits: gestation length, litter size, litters per year, weaning age and age at sexual maturity

Highly seasonal habitats provide shorter time windows of optimal conditions for breeding. Female mammals living in such environments are therefore expected to force maternal resources into a few large litters to maximise reproductive output while circumstances are favourable. Consistent with this prediction, I found that the majority of lagomorph species (with the possible exception of Ochotonidae, see below for the results of the four distinct ecotypes) with shorter birth seasons do have larger but fewer litters per year than species which a more expanded birthing pattern. A smaller comparative study across 22 lagomorph species also found that the number of litters decreases and the litter size augments with shorter breeding seasons (Swihart 1984). Studies using proxies for birth season length, such as latitude or temperature, similarly confirm the negative relationship between breeding season length and litter size intraspecifically in European hares (*Lepus europaeus*) (Hewson and Taylor 1975), Eastern cottontails (*S. floridanus*) (Conaway et al. 1974) and snowshoe hares (*Lepus americanus*) (Keith et al. 1966) and interspecifically in the genus *Lepus* (Flux 1981) and *Sylvilagus* (Lord 1960) and the family Leporidae (Virgos et al. 2006). Another study in European rabbits (*Oryctolagus cuniculus*) supports the present finding that the number of litters per year increased with the length of the breeding season (Tablado et al. 2009). In sum, there is ample evidence for Leporidae that litter size and the number

of litters per year are adjusted according to their birth season length (see discussion of results for Ochotonidae below).

Other ways in which mammals gain selective advantages in seasonal habitats is by shortening gestation length and/or accelerating foetal and neonatal growth to ensure that mating, birthing and raising offspring occur at a beneficial time of the year (Kiltie 1988; Zerbe et al. 2012; Heldstab et al. 2018, 2021; Heldstab 2021). Across eight New World rabbits, Chapman (1984) showed that species living at northern latitudes with shorter breeding seasons had a shorter gestation length. However, a higher degree of reproductive seasonality was not linked to a shorter gestation length in the present study, correcting for phylogenetic non-independence of taxa and covering a much higher number of species. In support, a study across 17 leporids was also not able to find a relationship between the variation of monthly average temperatures and gestation times (Virgos et al. 2006). Relative to other eutherian mammals, lagomorphs exhibit very short gestation periods (Swihart 1984; Wilson et al. 2016). Furthermore, females of many lagomorph species experience 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 (Millar 1973, 1974; Flux 1981; Keith 1981). In the genus *Lepus*, females are also known to superfetate, carrying a second fertilized ovum in their uterus during an already ongoing pregnancy (Flux 1967). These characteristics might be the reason for the absence of a correlation between gestation and birth season length in lagomorphs.

Concerning offspring growth in lagomorphs, Swihart (1984) found a correlation between the length of the breeding season and the age of first reproduction, but weaning age and age at sexual maturity had no influence on reproductive seasonality in the current study. These contrasting results suggest that the link between birth seasonality and ontogenetic development deserves future study in lagomorphs.

### Allometric variables: adult body mass and sexual size dimorphism

Sexual size dimorphism had no influence on reproductive seasonality in lagomorphs. Another allometric variable, namely adult body mass, had no effect on birth seasonality measured in categories but correlated positively with birth season length measured in months. To my knowledge, there are no published studies investigating the relationship between breeding season length and either body mass or sexual size dimorphism in the order Lagomorpha. Analysing the breeding season length data of Swihart (1984) with a smaller sample size but a more precise measure of birth seasonality in days, the relationship between birth season length and both body mass (PGLS:  $p = 0.326$ ,  $n = 20$ ,  $\lambda < 0.001$ ,  $\beta = 24.195$ ,  $SE = 23.953$ ,  $t = 1.010$ ) as well as between birth

season length and sexual size dimorphism (PGLS:  $p=0.387$ ,  $n=19$ ,  $\lambda < 0.001$ ,  $\beta = -327.990$ ,  $SE = 369.580$ ,  $t = -0.887$ ) were not significant either. In Swihart's study, environmental conditions also had a stronger influence than body mass on several other reproductive traits. Davis and Roth (2008) found little evidence for a correlation between sexual size dimorphism and various fecundity-related traits in comparisons among cottontail rabbits.

### Factors associated with seasonal reproduction within the four distinct ecotypes

As shown for the whole order of Lagomorpha, habitats that were warmer, had a higher amount of precipitation and were located at lower latitudes were also associated with less seasonal reproduction in hares and jackrabbits. These findings are consistent with single-species studies in this ecotype, e.g., in European hares (*L. europaeus*) (Hewson and Taylor 1975; Frylestam 1980), mountain hares (*L. timidus*) (Myrberget 1983; Angerbjörn 1986), antelope jackrabbits (*Lepus alleni*) (Vorhies and Taylor 1933), and black-tailed jackrabbits (*Lepus californicus*) (Vorhies and Taylor 1933).

Again consistent with the results across the whole Lagomorpha dataset, I also found that hares and jackrabbits with shorter birth seasons do have larger but fewer litters per year than species which a more expanded birthing pattern. Similarly, in rabbits, there was a tendency for species with a more seasonal reproduction to have fewer litters per year. Previous studies in hares and jackrabbits likewise confirm that litter size is inversely related to the duration of the reproductive season (Keith et al. 1966; Hewson and Taylor 1975; Flux 1981). Earlier published work, for instance in mountain hares (*L. timidus*) (Flux 1970; Kauhala et al. 2005), Eastern cottontails (*S. floridanus*) (Conaway et al. 1974) and European rabbits (*O. cuniculus*) (Tablado et al. 2009), supports the positive relationship between the number of litters per year and the length of the breeding season found in the present study within rabbits and within hares and jackrabbits.

Within the two ecotypes burrowing pikas and rock- and talus-dwelling pikas, none of the 13 factors had a significant influence on birth seasonality. However, the datasets comprising in most of the analyses less than 10 species are very small and problematic for phylogenetic comparative analyses (Münkemüller et al. 2012). It is therefore difficult to draw any firm conclusion from these analyses of the two ecotypes of pikas. As for many lagomorph species too, additional data for pikas are needed to solve the lack of knowledge concerning their reproductive seasonality and life history to make phylogenetic comparisons such as the present one possible.

### Comparison of reproductive seasonality in lagomorphs with other mammalian groups

Similarly to rodents (Heldstab 2021) but unlike Carnivora (Heldstab et al. 2018), ruminants (Zerbe et al. 2012) and primates (Heldstab et al. 2021), many lagomorph species also show a large degree of intraspecific variation in birth season length. A possible explanation for this high within-species variation is that rodents and lagomorphs have a faster reproductive cycle than the other three orders (Case 1978; Eisenberg 1981; Swihart 1984) including a post-partum oestrus (Dewsbury et al. 1979) and superfetation in the genus *Lepus* (Flux 1967). This allows them to breed much more opportunistically and adjust birth season length according to predation risk (Wood 1980; Boonstra et al. 1998), weather (Bronson 1988; Franken and Hik 2004) or food abundance (Leslie et al. 1952; Millar 1972; Smith 1978; Wube et al. 2008). What is additionally expected to contribute to the high intraspecific variation in birth season length in rodents and lagomorphs is their occurrence across a much larger geographical range (Schai-Braun and Hackländer 2016; Wilson et al. 2016; Smith et al. 2018) than, for instance, primates, which are mostly confined to the tropics (Heldstab et al. 2021).

Mid-latitude of the species' geographical range, as well as mean annual temperature and precipitation had strong effects on reproductive seasonality in lagomorphs. Previous studies in Rodentia (Heldstab 2021), Ruminantia (Zerbe et al. 2012), Carnivora (Heldstab et al. 2018), Primates (Di Bitetti and Janson 2000; Janson and Verdolin 2005; Heldstab et al. 2021) and Macroscelidea (Neal 1995) also found that species living at higher latitudes have shorter breeding seasons.

In the present study across lagomorphs, habitats that were warmer and had a higher amount of precipitation were associated with longer seasonal reproduction. Comparative studies in rodents (Tkadlec 2000; Heldstab 2021) and primates (Heldstab et al. 2018) also showed a positive effect of temperature on the length of the breeding season. Mean annual precipitation in a species' habitat did not, however, translate into a less seasonal birthing pattern in these two orders. The strictly herbivorous diet of the large majority of lagomorphs might be responsible for the stronger influence of precipitation on their birth seasonality. Diets of rodents and primates are much more variable including also fruits, seeds, nuts, meat, or insects in significant proportions not observed in lagomorphs (Wilman et al. 2014). The broader diet range in these two orders likely makes food availability and ultimately reproductive seasonality less dependent on precipitation; in contrast, the lagomorph diet is mostly forbs, herbs and grasses. In addition, since many lagomorphs, in particular, pikas, live at high altitudes (Smith et al. 2018), snow might also elicit a stronger influence of precipitation on reproductive

seasonality in comparison to the other two orders inhabiting mostly low-altitudinal habitats.

Solitary species with large home ranges do not often encounter potential mates (Llewellyn and 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 and Ferguson 2003). This should lead to less seasonal birthing patterns. A study in ursids supports this prediction, although the observed effect of home range size was small (Spady et al. 2007). The present study, a study with a larger sample of Carnivora species (Heldstab et al. 2018), as well as comparative studies in rodents (Heldstab 2021) and primates (Heldstab et al. 2021) were all unable to detect an influence of home range size on seasonal reproduction.

Contrasting what has been reported in primates (Heldstab et al. 2021), carnivores (Tökölyi et al. 2014; Heldstab et al. 2018) and ruminants (Zerbe et al. 2012; Tökölyi et al. 2014) but as found in rodents (Heldstab 2021), a higher degree of reproductive seasonality was not linked to a shorter gestation length in lagomorphs in the present study. I suggest two reasons for the difference between rodents and lagomorphs in comparison to the other mammalian orders: their small body size and their post-partum oestrus allowing them to gestate again immediately following the birth of the young. 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 the reproductive opportunity in the next year (Kiltie 1988). Small mammals such as rodents and lagomorphs exhibit extremely rapid foetal and neonatal growth rates and thus already have very short gestation periods (Swihart 1984; Wilson et al. 2016). The post-partum oestrus shortens the time between lactation and the next pregnancy, enabling rodents and lagomorphs to fit the complete reproductive cycle in an even shorter time window. Although lagomorphs do not adjust gestation length, they still seem to adapt life history to seasonal habitats with short favourable time windows, as seasonal Leporid species do have fewer but larger litters. Selection in highly seasonal environments has also favoured fewer litters in rodents (Heldstab 2021), bats (Tökölyi et al. 2014), elephant shrews (Neal 1995), and Eulipotyphla (Symonds 1999), larger litter sizes in primates (Heldstab et al. 2021), earlier weaning age in rodents (Heldstab 2021) and seals (Gentry and Kooyman 2014), and older age at sexual maturity in Eulipotyphla (Symonds 1999) and Rodentia (Heldstab 2021).

As found in primates (Heldstab et al. 2021) and carnivores (Heldstab et al. 2018), but unlike in ruminants (Zerbe et al. 2012) and rodents (Heldstab 2021), sexual size dimorphism in lagomorphs was not related to birth season length. Even in ruminants and rodents, sexual size dimorphism was also only marginally negatively associated with birth season length. The other allometric variable, body mass, also only

had a small influence on lagomorph birth seasonality, as it was only correlated with birth season length measured in months but not in categories. Studies in primates (Plavcan et al. 2005; Heldstab et al. 2021), Carnivora (Heldstab et al. 2018), rodents (Heldstab 2021) and ruminants (Zerbe et al. 2012) demonstrate a similar weak impact of body mass on reproductive seasonality. In sum, habitat and life history characteristics seem to be much more important for lagomorph reproductive traits than allometric variables, as already suggested by Swihart (1984).

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## Declarations

**Conflict of interest** The author declares that she does not have any conflict of interest.

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