

High survival during hibernation affects onset and timing of reproduction

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Abstract The timing of reproduction is one of the most crucial life history traits, with enormous consequences for the fitness of an individual. We investigated the effects of season and timing of birth on local survival probability in a small mammalian hibernator, the common dormouse (*Muscardinus avellanarius*). Local monthly survival probability was lowest in the early active season (May–August, $\phi_{\text{adult}} = 0.75\text{--}0.88$, $\phi_{\text{juvenile}} = 0.61\text{--}0.68$), increased during the late active season (August–October), and highest during hibernation (October–May, $\phi_{\text{adult}} = 0.96\text{--}0.98$, $\phi_{\text{juvenile}} = 0.81\text{--}0.94$). Consequently, dormice had an extremely high winter survival probability. We observed two peaks in the timing of reproduction (June and August/September, respectively), with the majority of juveniles born late in the active season. Although early investment in reproduction seems the better life history tactic [survival probability until onset of reproduction: $\phi_{\text{born early}} = 0.46$, 95% confidence interval (CI) 0.28–0.64; $\phi_{\text{born late}} = 0.19$, 95% CI = 0.09–0.28], only females with a good body condition (significantly higher body mass) invest in reproduction early in the

year. We suggest the high over-winter survival in dormice allows for a unique life history pattern (i.e., combining slow and fast life history tactics), which leads to a bimodal seasonal birth pattern: (1) give birth as early as possible to allow even the young to breed before hibernating, and/or (2) give birth as late as possible (leaving just enough time for these young to fatten) and enter directly into a period associated with the highest survival rates (hibernation) until maturity.

Keywords Gliridae · Life history · Predation · Program MARK · Small mammal

Introduction

Timing of reproduction is one of the most crucial life history traits, with enormous consequences for the production of viable offspring and hence fitness (Dobson and Oli 2008; Gaillard et al. 1989; Oli 2004; Varpe et al. 2007). One complication in optimising the timing of reproduction (and thus life history strategies) is that many species live in seasonal environments with fluctuating climatic conditions and food availability. Investment in reproduction should be adjusted to an optimal time frame coincidental with favourable environmental conditions (Johansson and Rowe 1999; Lambin and Yoccoz 2001). Thus, under harsh winter conditions, even small mammalian species with “fast” life histories (early onset of reproduction, high annual output, low survival rates; e.g. Gaillard et al. 1989) typically cease reproduction and instead maximise their investment in maintenance and survival.

One of the most extreme adaptations to periods of cold and food shortage is hibernation, which is widespread among mammalian orders (Geiser and Ruf 1995). Hibernation

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is typically accompanied by retreat into caves or underground burrows. Hibernators undergo gonadal involution, which renders them incapable of reproducing for periods of approximately 6–9 months. In large hibernators, such as marmots (which are among the largest mammals undergoing deep torpor; Geiser and Ruf 1995), juvenile growth and prehibernation fattening takes several months. Therefore, in marmots and other large hibernators, this strategy of seasonal adaptation inevitably results in restricting reproduction to a single litter per year. However, this low annual reproductive output is compensated by the relatively high longevity of adults (Arnold 1993) due to body size (which lowers extrinsic mortality during the summer) and evasion of predators during underground hibernation. Extremely “slow” life histories, i.e. high longevity combined with low annual reproduction, also occur in many small-sized hibernating bats, which has been attributed to their flight capability, which additionally minimises predation risk (Brunet-Rossini and Austad 2004; Wilkinson and South 2002).

It is not easy to predict the optimal life history tactics of small—i.e. mouse-sized—non-volant hibernators. A prime example of such a species is the common dormouse (*Muscardinus avellanarius*), a north-temperate zone hibernator that weighs approximately 25 g. Depending on the area inhabited, dormice may have one or two litters in their 5-month breeding season. This intermediate level of annual reproductive output, which is generally lower than that of similar-sized non-hibernating rodents (e.g. Getz et al. 2005; Lambin and Yoccoz 2001), may result from ambivalent selection pressures. In general, survival rates in a mammal of this size can be expected to be low—mainly due to high predation risk—which should favour an early onset and multivoltine reproduction (e.g. Lambin and Yoccoz 2001). This may be true, however, only as long as the animals are active and foraging. A recent meta-analysis has shown that most hibernators have higher monthly survival rates during the winter than during the active season (Turbill et al. 2011). The authors argue that the decreased predation risk, associated with hibernation in protected burrows, and the absence of foraging may explain this phenomenon. Hence, seasonally lowered extrinsic mortality may select for a delayed onset of maturity and reduced reproductive rate. The common dormouse, therefore, may provide unique insights into the evolution of life history tactics in general, yet surprisingly little is known about the seasonal or annual survival rates in this or—for that matter—other small hibernators (but see Meaney et al. 2003; Schorr et al. 2009).

We used data from a 6-year capture–recapture study to determine differences in seasonal survival rates in the common dormouse. The data were collected from a population in Lithuania that was characterised by two birth peaks per breeding season, one in June and one in August (Juškaitis 2008; Fig. 1). This breeding pattern is unusual since small

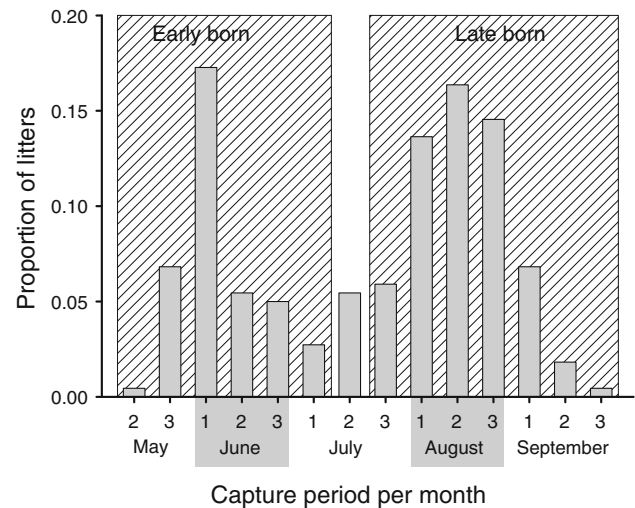


Fig. 1 Annual distribution of birth dates based on data collected from dormice (*Muscardinus avellanarius*) litters ($n = 579$). This figure is modified from Juškaitis (2008). Shown are data collected between 1981 and 2007 at two study sites in Lithuania. Note: data from the present study are only a part of the data shown in this figure. Shaded areas Classification of early and late-born juveniles for the present study

mammals, unless reproduction is restricted by extremely unfavourable environmental conditions, generally show a unimodal birth distribution within the reproduction season (Bronson 1989). The common dormouse is therefore a good model species for studies addressing questions concerning the optimal timing of reproduction within a limited breeding season. It has long been recognised that optimal timing of birth may differ between the parent’s and offspring’s perspective and that time constraints for growth or changing food resources during the breeding season may lead to profound differences in the quality of young born at different times (Ejsmond et al. 2010; Varpe et al. 2007). Hence, we examined whether juvenile dormice born either early or late in the breeding season (and thus facing the first hibernation season at a different age) differ in (1) their probability to survive to the adult stage, (2) their survival rate as adults, (3) their lifetime reproductive success and, implicitly, their reproductive value (females). The aim of our study was to gain some insight not only into the optimal timing of reproduction in small hibernators but also into possible long-lasting consequences of the date of birth.

Materials and methods

Study species, study area and nest-box controls

The common dormouse is a small rodent of the family Gliridae (weight 17–30 g; Juškaitis 2008) distributed mainly across Europe (Morris 1999). Dormice occur in deciduous

Table 1 Descriptive statistics of the common dormouse (*Muscardinus avellanarius*) population in Lithuania 2001–2006

Descriptive variables	Study year					
	2001	2002	2003	2004	2005	2006
Number of captured adult males	38	34	36	46	41	54
Number of captured adult females	30	27	37	50	33	29
Number of captured juveniles	114	128	202	121	218	231
Number of captured adults in May	40	39	43	60	47	46
Calculated abundance in May ^a	45 ± 3	39 ± 4	52 ± 3	63 ± 2	52 ± 2	85 ± 25
Population density (ind./ha in May)	0.75	0.65	0.87	1.05	0.87	1.42
Number of litters	23	35	46	47	43	43
Average litter size	4.13	4.05	4.21	3.74	3.90	4.26

^a Abundance [shown as the number (n) ± standard error of the mean (SEM)] was calculated using closed population models implemented in the program MARK 6.0 (White and Burnham 1999)

or mixed forests with a well-developed understorey (Bright and Morris 1990, 1992; Juškaitis 2008). They are nocturnal and forage in shrubs and bushes for flowers, fruits, seeds and insects (Richards et al. 1984).

Dormice hibernate during winter, and also exhibit short torpor bouts during their active season (Juškaitis 2008; Vogel 1997; Vogel and Frey 1995). At our study, site hibernation lasts from late September/October to April/May. They do not store food, and during hibernation they rely solely on their body fat reserves. Males emerge from hibernation before females, and mating occurs from April until September. Females can raise two litters per year, with a minimum interval of 30 days between the birth days (Juškaitis 2008).

The study site was located in the Šakiai district of Lithuania (55°03'N, 23°04'E) and covered 60 ha of mixed, middle-aged (approx. 60 years old) forest. Within the study site, the major tree species were birch (*Betula pendula* and *B. pubescens*) and Norway spruce (*Picea abies*). Hazel (*Corylus avellana*), an energy-rich food resource for dormice, was also widespread at the study site. However, we did not observe strong fluctuations (e.g., a hazel masting event) during the study period. Juškaitis (2008) provides a detailed description of the study site.

We evaluated data collected during the period 2001–2006 since the capture effort was very similar during this period. A total of 359 wooden nest-boxes (internal size 12 × 12 × 23 cm, entrance hole 35 mm in diameter) were monitored. The nest-boxes were placed in a grid system, with an inter-nest-box distance of 25–50 m (for detailed description, see Juškaitis 2008), and mounted to trees at a height of 3–4 m. Dormice were captured from the nest-boxes which they use as sleeping sites during the daytime. The nest-boxes thus provided were occupied exclusively during the active season. In contrast, hibernacula were self-built nests and situated in dense leaf litter or belowground (just below the surface; Juškaitis 2008). One capture period

involved the monitoring of all 359 nest-boxes, and the analysed data comprised data collected during 11 capture periods per year (one each in April, July and September; two each in May, June, August and October). Newly captured dormice were marked individually using a numbered ring around the hind leg and then sexed. Body mass was recorded during each capture using a spring balance (Pesola, Baar, Switzerland). When a female was found with her young, litter-size as well as the sex and body mass of juveniles were recorded. Females with visible nipples were also classified as lactating. In the case that females were found to be pregnant or lactating several times within an active season, only captures that occurred at least 40 days after the last breeding event were counted as a new breeding event (unless recently born, small juveniles were present). We classified the age of the animals as either juvenile (prior to first hibernation) or adult (after first hibernation).

Estimation of abundance

Animal abundance was estimated using closed population models (Otis et al. 1978) implemented in the program MARK 6.0 (White and Burnham 1999). Abundances were modelled for each year using only the two capture periods in May. Since we never encountered any weaned juveniles at the study site in May, these estimates were considered to reflect the number of adult animals present after hibernation as a comparable measure. Densities were calculated based on the modelled animal abundance in May per hectare of the study site (Table 1).

Estimation of local survival and recapture probability

We used Cormack–Jolly–Seber models as implemented in the program MARK 6.0 (White and Burnham 1999) to estimate local survival probability (ϕ ; i.e. the combined effects of mortality and emigration), and recapture probabilities

(p) in the dormouse population (Lebreton et al. 1992). Data were collected, models were developed and the results were retrieved using the RMark library (ver. 2.9.1; Laake 2009; Laake and Rextad 2009) within the statistical package R (ver. 2.10.1; R Development Core Team 2009).

All animals first captured as juveniles were classified as either “early-born” or “late-born” juveniles (dataset “Birth”, $n = 605$; compare Fig. 1). The marking of juveniles started at an age of 4 weeks. All juveniles marked in June and July (and hence mostly born in May–June) were considered to be early-born; dormice first captured at the beginning of August with a body mass of >15 g were also considered as early-born. Dormice first captured in August with a body mass of <11 g or those captured in September and October with a body mass of <16 g were classified as late-born (based on known growth curves; Juškaitis 2008). This conservative classification excluded all animals that could not be reliably identified as early- or late-born juveniles. It should be noted that this classification differs slightly from that used in a previous evaluation of the same data set with another focus (Juškaitis 2008).

Captures were pooled per month (with one exception: capture data in April and May were pooled due to very few captures in April), resulting in 6 monthly capture periods per year (May–October). Since our data were too sparse to run a fully time-dependent model, we used a reduced model for our analysis. Replacing the parameter “time” by the parameter “season”, we assumed that monthly survival was constant within each of the “seasons”, i.e. the early active season (May–August), the late active season (August–October) and the winter season (hibernation, October–May). This classification allowed us to compare survival rates for animals born at different times in the year. Additionally, a pre-evaluation of survival probabilities in adult dormice revealed that this time classification was the best fitting model among all possible variations [Electronic Supplementary Material (ESM) 1].

We first tested our general model [$\phi(\text{age}*\text{birth}*\text{season}*\text{sex})$ $p(\text{age}*\text{birth}*\text{season}*\text{sex})$] for overdispersion using the bootstrap goodness-of-fit approach implemented in the program MARK. Based on 1,000 bootstrap replicates, this test indicated that our global model fitted the data adequately ($P = 0.99$). We used the median \hat{c} -approach as implemented in program MARK to conservatively correct for a possible slight overdispersion.

Starting from the general model we fixed the survival estimates to those of the fully parameterised model and created all possible models for recapture probability (ESM 2). In a second step, we used the configurations for p from the most likely models (see below for model selection procedure) and constructed models with all possible factor combinations for ϕ , using an R function designed to generate all possible additive and multiplicative combinations of param-

eters. It was necessary to choose this stepwise approach since calculating all possible model combinations (of p and ϕ) exceeded the available computer capacity. Emanating from the general model, we selected more parsimonious models based on minimising the Akaike information criterion corrected for quasi-likelihood ($\hat{c} = 1.19$) and small sample size (QAIC_c) (Akaike 1973; Burnham and Anderson 2002). The lowest QAIC_c identified the model that represented the data adequately with a minimum number of parameters. All models within a difference of $\Delta\text{QAIC}_c < 2$ from the best model were considered, as these have a substantial level of empirical support (Burnham and Anderson 2002). Since p was restricted to the four most likely parameter combinations (ESM 2), we calculated 4×51 possible combinations for survival probabilities (i.e. a total of 204 models). The final local survival estimates were computed using model averaging (program RMark) considering all likely models ($\Delta\text{QAIC}_c < 2$). The presence of interactions between the parameters is noted with an asterisk (*) and additive effects are noted with an addition sign (+). Survival probability is always given with upper and lower 95% confidence interval (CI). We used the Delta Method (Oehlert 2010) to calculate confidence intervals for the mean local survival probability per year (annual survival) and until first reproduction (survival until maturity). Confidence intervals were used to interpret the effect of factors on survival estimates, with non-overlapping confidence intervals considered to be significantly different. Survival probabilities for time periods (e.g. hibernation) were calculated from monthly survival probability (ϕ_m), and the number of month spent in hibernation as: $\phi_{\text{hibernation}} = (\phi_m)^n$.

Additional statistical analysis

Due to the different birth dates of juvenile dormice (late-born animals were not captured before August), we analysed body mass changes in juveniles and adults separately. Body mass data were log-transformed to achieve normality. To compare juveniles with different birth dates (early vs. late) we used a time scale denoted “month after weaning” with 1 = first month after weaning (June vs. August), 2 = second month after weaning (July vs. September) and 3 = third month after weaning (August vs. October). To test for the effects of sex, birth (early- vs. late-born), month (for juveniles: month after weaning) and year (entered as factors) on body mass, we computed linear mixed effects (LME) models using the R-library “nlme” package (Pinheiro et al. 2009). LME models were also computed to test for the effects of age, month, year, birth (all entered as factors) and body mass (entered as a covariate) on litter size, as well as the effects of body mass (prior to reproduction, month entered as a covariate) on reproductive decision in adult females (in these data sets, the data were not transformed

Table 2 Models^a of local survival probabilities in common dormice

No.	Survival parameters	Recapture parameters	QAIC _c	ΔQAIC _c	QAIC _c weight	npar	Dev.
1	$\phi(\text{age}*\text{birth} + t_s*\text{sex})$	$p(\text{age}*t_s*\text{sex})$	1,924.64	0.00	0.18	21	975.07
2	$\phi(\text{age}*\text{birth} + t_s*\text{sex})$	$p(\text{age}*t_s*\text{sex} + \text{birth})$	1,925.99	1.35	0.10	22	974.34
3	$\phi(\text{age}*\text{sex} + \text{birth}*t_s)$	$p(\text{age}*\text{birth}*t_s*\text{sex})$	1,926.31	1.67	0.08	33	951.54
4	$\phi(\text{age}*\text{sex} + \text{birth}*t_s)$	$p(\text{age}*t_s*\text{sex})$	1,926.52	1.87	0.07	21	976.95
5	$\phi(\text{age} + \text{birth} + t_s*\text{sex})$	$p(\text{age}*t_s*\text{sex})$	1,926.78	2.14	0.06	20	979.28
7	$\phi(\text{age}*\text{birth} + t_s)$	$p(\text{age}*t_s*\text{sex})$	1,927.14	2.50	0.05	18	983.79
83	$\phi(\text{age}*t_s)$	$p(\text{age}*t_s*\text{sex})$	1,957.02	32.38	<0.001	16	1,017.8
160	$\phi(\text{age})$	$p(\text{age}*t_s*\text{sex})$	1,981.91	57.27	<0.001	14	1,046.8
Full	$\phi(\text{age}*\text{birth}*t_s*\text{sex})$	$p(\text{age}*\text{birth}*t_s*\text{sex})$	1,948.95	24.31	<0.001	48	941.99

No., Model rank; QAIC_c, quasi-likelihood corrected Akaike information criterion (AIC) for small sample size; ΔQAIC_c, difference between model QAIC_c and minimum QAIC_c; QAIC_c weight, relative strength of evidence for a model within the set of models computed; npar, number of parameters; Dev., deviance (total deviation between the computed model and a saturated model of the data); φ, local survival probability; p, recapture probability; t_s, time interval “season” [estimates for early active season (May–August), late active season (August–October) and winter (hibernation, October–May)]

^a Models were ranked by QAIC_c. Models no. 7, 83, and 160 are the best models considering three, two, or a single parameter respectively

since residuals were normally distributed). To adjust for repeated measurements of the same individuals, subject ID was always entered as the random factor in these models (Pinheiro et al. 2009). The analysis of variance (ANOVA) from each model was computed using marginal sums of squares. Starting with a saturated model, we sequentially eliminated non-significant terms (not shown in ANOVA tables of final models). Unless stated otherwise, values are given as the mean ± standard error of the mean (SEM).

Results

Number of individuals

Neither the number of captured individuals nor the number of litters changed significantly over the study period (Table 1). In contrast, the modelled abundance (and density) showed a significant increase ($F_{1,4} = 8.1327, P = 0.046$); however, this effect was solely caused by the high abundance estimate in 2006 (the last study year).

In total, 117 (19.3%) early-born juveniles (i.e. May–June; females: $n = 59$, males: $n = 58$) and 488 (80.7%) late-born juveniles (i.e. August–September; females: $n = 251$, males: $n = 237$) were captured. Thus, there was a significantly higher proportion of juveniles born late in the active season ($\chi^2 = 452.56, df = 1, P < 0.0001$).

Local survival probability

All best fitting models included the parameters “age”, “birth”, “season” and “sex” (Table 2). The averaged

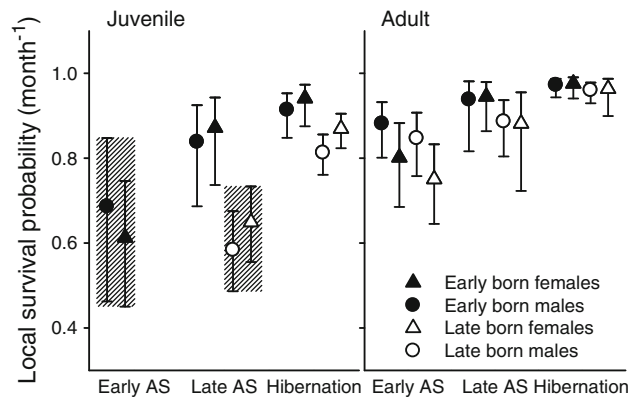


Fig. 2 Monthly local survival probability in early- and late-born dormice [averaged estimates from all models <2 ΔQAIC_c (quasi-likelihood corrected Akaike information criterion for small sample size), ranking 1–4 in Table 2]. Survival estimates are shown with 95% lower and upper confidence intervals (CI). *Early AS* Early active season (May–August), *Late AS* late active season (August–October), *Hibernation* winter season (October–May). *Shaded areas* Monthly local survival probability within the first and second month after weaning for early and late-born juveniles, respectively. Although born in different seasons, juvenile local survival did not significantly differ between the two groups in this time interval

survival estimates from models with a ΔQAIC_c < 2 (first four models Table 2) are shown in Fig. 2.

The lowest local monthly survival probabilities were estimated for juveniles within the first 2 months after weaning (early active season in early-borns and late active season in late-borns; Fig. 2). Neither sex nor date of birth significantly influenced monthly survival probabilities within this time frame (early-born: $\phi_{\text{males}} = 0.69, 95\% \text{ CI } 0.46\text{--}0.85; \phi_{\text{females}} = 0.61, 95\% \text{ CI } 0.45\text{--}0.75$; late-born: $\phi_{\text{males}} = 0.58, 95\% \text{ CI } 0.49\text{--}0.68; \phi_{\text{females}} = 0.65, 95\% \text{ CI } 0.56\text{--}0.73$). Compared

Table 3 Analysis of variance table of factors influencing body mass in adult and juvenile dormice

Factors	<i>df</i> (number)	<i>df</i> (density)	<i>F</i> value	<i>P</i> value
Adult dormice				
Intercept	1	276	59,528.16	<0.0001
Birth	1	85	31.62	<0.0001
Sex	1	85	1.16	0.2843
Month	6	276	142.38	<0.0001
Birth × month	6	276	2.51	0.0220
Sex × month	6	276	18.32	<0.0001
Juvenile dormice				
Intercept	1	589	1,765.27	<0.0001
Birth	1	589	1.78	0.1823
Month after weaning	2	383	98.89	<0.0001
Birth × month after weaning	2	383	7.02	0.0010

to these survival estimates after weaning, monthly survival probability of juvenile dormice increased significantly during the hibernation season (October–May; early-born: $\phi_{\text{males}} = 0.91$, 95% CI 0.85–0.95, $\phi_{\text{females}} = 0.94$, 95% CI 0.88–0.97; late-born: $\phi_{\text{males}} = 0.81$, 95% CI 0.76–0.86, $\phi_{\text{females}} = 0.87$, 95% CI 0.82–0.90; Fig. 2). Particularly in late-born juveniles, local survival probability switched directly from low values during the late active season into high winter values. Compared to early-borns, late-born juveniles showed somewhat lower local survival probabilities during hibernation. However, the largest differences were found between early-born females and late-born males—and not between similar sexes (Fig. 2). The probability of surviving to the onset of reproduction was significantly different and more than twofold higher in early-borns (to an age of 3 months, $\phi = 0.46$, 95% CI 0.28–0.64) than in late-borns (to an age of 10 months, $\phi = 0.19$, 95% CI 0.09–0.28).

The majority of adult dormice (>75%) in our data set were represented by animals born during the previous year. Thus, the survival estimates for adults in our analysis were based mainly on animals following their first hibernation season. The monthly survival probability among adults increased during the active season and reached its maximum during hibernation. Survival probability was significantly lower in the early active season (early-born: $\phi_{\text{males}} = 0.88$, 95% CI 0.80–0.93, $\phi_{\text{females}} = 0.80$, 95% CI 0.67–0.88; late-born: $\phi_{\text{males}} = 0.85$, 95% CI 0.76–0.91, $\phi_{\text{females}} = 0.75$, 95% CI 0.65–0.83) than in the hibernation season (early-born: $\phi_{\text{males}} = 0.97$, 95% CI 0.94–0.99, $\phi_{\text{females}} = 0.98$, 95% CI 0.94–0.99; late-born: $\phi_{\text{males}} = 0.96$, 95% CI 0.93–0.98, $\phi_{\text{females}} = 0.96$, CI = 0.90–0.99, Fig. 2). However, there were no significant effects of sex and timing of birth (early vs. late) on local survival probabilities in adult dormice. The calculated annual local survival probability in adults was not significantly different but tended to

be lower among late-born dormice ($\phi_{\text{late-born}} = 0.32$, 95% CI 0.12–0.54; $\phi_{\text{early-born}} = 0.48$, 95% CI 0.22–0.69).

Body mass

Seasonal changes in the body mass of adults differed between sexes, and between early- and late-born animals, as indicated by significant interactions between sex and month, as well as those between date of birth and month (Table 3). During the active season, adult males showed a slight decrease in body mass in the spring and a strong increase in body mass shortly before the onset of hibernation. In adult females, however, the increase in body mass during the active season was more constant and started immediately after emergence from hibernation, likely due to early pregnancies (Fig. 3). Adult male dormice tended to enter hibernation with a heavier body mass (on average +6.50 g, or 19%) than adult females (Fig. 3). The effects of date of birth were dependent on month and seemed to be most pronounced among females in the early active season (April, May, and July; Fig. 3).

Adult females reproducing in the early active season (only body weight data at least 1 month prior to parturition were analysed) showed a higher mean body mass (April: 19.25 ± 1.25 g, May: 17.51 ± 0.33 g, June: 20.03 ± 0.54 g) than non-reproductive females in the same time frame (April: 15.88 ± 1.08 g, May: 15.77 ± 0.24 g, June: 17.33 ± 0.55 g; $F_{1,79} = 34.29$, $P < 0.0001$).

There was a significant interaction between the effects of date of birth and month after weaning on the body mass of juveniles (Table 3). Late-born juveniles (both sexes) had a higher mean body mass in the second month after weaning (July vs. September), but early-borns showed a higher mean body mass in the first and third month after weaning (Fig. 3). In October, late-born juveniles showed a lower mean body mass than early-born juveniles (−7.3 g in females, −12.3 g

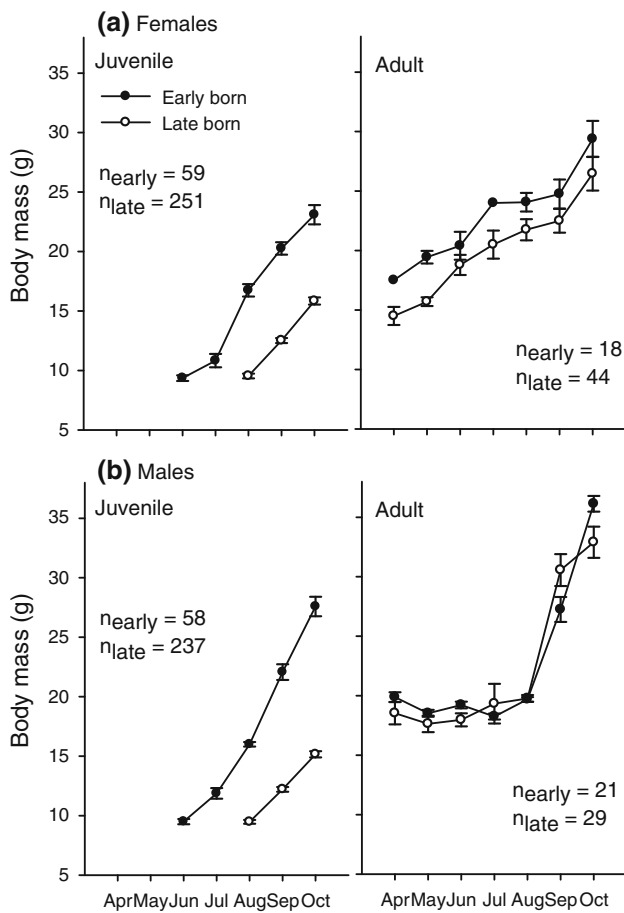


Fig. 3 Seasonal changes in body mass \pm standard error of the mean (SEM) as a function of age, sex and date of birth [early-born (May–June) vs. late-born (August–September) individuals]. It should be noted that the body masses shown for juveniles in October are biased by the inclusion of individuals with a below-average mass that did not survive hibernation (see “Results”)

in males; Fig. 3). Whereas early-born dormice showed a strong decrease in body mass during hibernation (–24% in females, –28% in males), this was not apparent from the average masses in late-born animals (Fig. 3). However, when only those late-born animals that survived hibernation were considered, we observed a slightly higher mean body mass in the previous October (as juveniles; males: 18.95 ± 1.15 g, females: 18.04 ± 0.82 g). Thus, it would appear that late-born animals with a low body mass did not survive hibernation but contributed to the bias in apparent body mass change during hibernation (Fig. 3). Still, body mass loss during hibernation seemed to be small [males: -0.42 g (–2.2%), females: -3.54 g (–19.6%)], suggesting that late-born dormice probably stayed active somewhat longer in the autumn.

Reproductive performance

Dormice showed two peaks of reproduction (June and August/September, respectively; Fig. 4, compare Fig. 1).

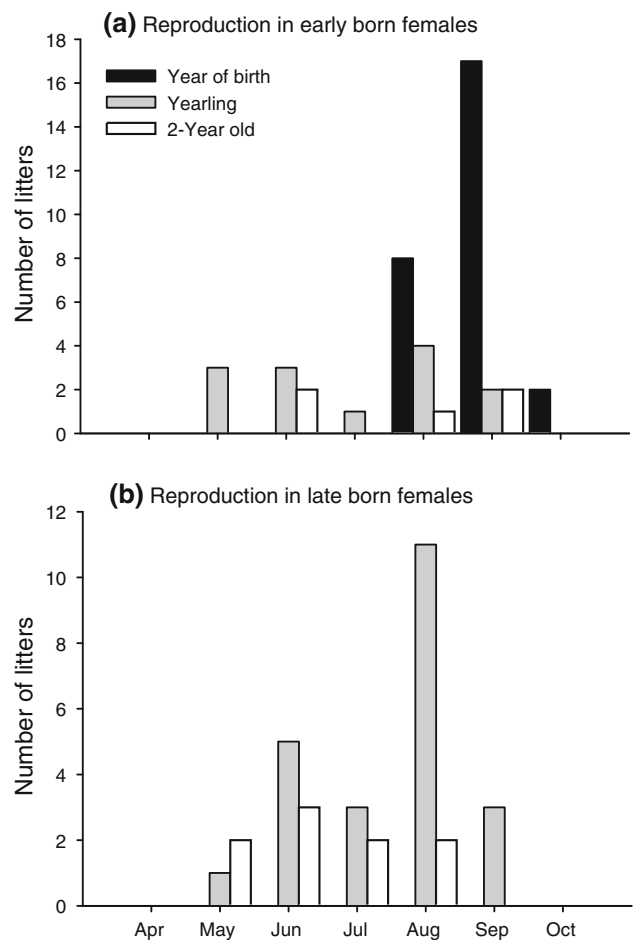


Fig. 4 Age-dependent differences in the onset and timing of reproduction in early- and late-born female dormice. Whereas early-born females started to reproduce prior to the first hibernation season, late-born females delayed the onset of reproduction until after the first hibernation season. The low number of litters born in July should be noted

The onset of reproduction (sexual maturity) in early-born females occurred in the active season of their year of birth. Only two individuals (3.4%) from the early-born juveniles in our data set had their first litter after their first hibernation season. In contrast, all late-born females started to reproduce after their first hibernation (Fig. 4). Thus, late-born dormice reached sexual maturity at a minimum age of 9–10 months, compared with 2–3 months in early-born females.

A significantly higher proportion of early-born females reproduced at least once at our study site (early-borns: 54.8%, late-borns: 7.2%; $\chi^2 = 74.79$, $df = 1$, $P < 0.001$). The majority of females had only one litter per life (early-born mothers: 71.0%, late-born mothers: 55.5%), and we observed a maximum of four litters per life in early- or late-born females. Late-born females showed a tendency to have more than one litter (2–4 litters) than early-borns (44.5 vs. 29%, non-significant difference). Mean litter size was

4.05 ± 0.16 juveniles/litter and was not significantly affected by age, weight, year or season of birth. Assuming a number of four juveniles per litter (since we observed some females only pregnant/lactating but not together with their juveniles), the calculated mean lifetime reproductive success for early-born females was 3.1 juveniles and for late-born females 0.51 juveniles. Calculating lifetime reproductive success for the small fraction of dormice that actually reached sexual maturity (survival probability until maturity not considered) showed that early-borns had a lifetime reproductive success of 5.8 juveniles and surviving late-born females produced 7.1 juveniles.

Discussion

Adult local survival probability

Analysing the seasonal variation in local survival probability of the common dormouse revealed that the early active season (May–August) carried the highest mortality risk for adult dormice. We suggest that three factors may be responsible for this phenomenon: (1) body fat reserves are likely to be depleted after hibernation; (2) food availability is low, and energy-rich seeds in particular are absent at this time of the year; (3) the onset of reproduction leads to high energy demands and increased predator exposure. By emerging from hibernation as early as April/May (males earlier than females), common dormice seem to trade-off an early onset of reproduction, which requires time for gonadal growth, against the increased risk of mortality owing to poor climatic conditions and low food resources. Both the availability and quality of food are higher in the late summer when ripe seeds and fruits are available. A comparable seasonal pattern of local survival (low survival in early summer and increased survival in late summer) was also observed in five edible dormice populations across Europe (Lebl et al. 2011). Since dormice during hibernation rely on their body fat reserves and do not cache food, we presume that less time spent foraging (and therefore decreased exposure to predators) led to the increased survival probability during the late active season at our study site. Juškaitis (2008) found that the tawny owl (*Strix aluco*) in particular can have a considerable impact on common dormouse populations, especially during the spring [5.7% of the population (inhabiting an area of 60 ha) was captured by a single tawny owl pair in the spring of 1986]. In Lithuania, the proportion of common dormice can reach up to 10% of all small mammals caught by owls during their breeding season (Balčiauskienė et al. 2005).

Adult males seemed to survive better than females, especially during the early active season. Although we did not observe significant differences in local survival probability

(overlapping 95% CIs) between sexes, adding the parameter “sex” still improved our model. Since males emerged from hibernation with a higher mean body mass than females, the higher body fat reserves in males could have contributed to this effect. Their greater increase in body mass during September and October (Fig. 3) suggests that males terminated investment into reproduction earlier in the active season than females—and therefore had more time to accumulate body fat reserves prior to hibernation. In edible dormice, for comparison, males start to hibernate as early as in late August, the time when females are still lactating (e.g. Bieber 1998).

Mean local survival was highest during hibernation, indicating that hibernation prolongs the lifespan of the common dormouse. In our population, the probability of surviving the 7 months of hibernation was, on average, 0.80 for adult dormice. In the non-hibernating (and similarly sized) yellow-necked wood mouse (*Apodemus flavicollis*) or the bank vole (*Myodes glareolus*), winter survival in the similarly harsh eastern Polish climate (Białowieża Primeval Forest) was only 0.14 and 0.23, respectively (Pucek et al. 1993). Based on our results, it would appear that high annual survival rates in small hibernators are mainly due to a low winter mortality. Our data therefore support the observation that hibernators have generally higher annual survival probabilities than non-hibernating species (Turbill et al. 2011). Indeed, monthly overwinter survival in adult dormice was 96–98% in our study. In the larger garden dormouse, *Eliomys quercinus* (Schaub and Vaterlaus-Schlegel 2001), and edible dormouse, *Glis glis* (Lebl et al. 2011), survival during hibernation was also estimated to be close to 100% (both studies used the program MARK for survival estimates). Our results, however, differ from the low winter survival probabilities reported for common dormice in earlier studies (reviewed in Juškaitis 2008). In Lithuania, for example, mortality during the winter (6–7 months) was estimated to be 63.5–72.4% (Juškaitis 2008). However, these previous estimates based on enumeration did not consider recapture probabilities. Hence, it seems likely that these lower estimates were caused by a number of animals that actually survived hibernation but were not recaptured in the following active season (e.g. died during the spring). Since hibernators vanish below ground or in well hidden nests for the entire winter season, it seems plausible to assume that the exposure to predators is minimised during this time frame, leading to an increased survival probability during hibernation. The positive effect of predator avoidance on survival during hibernation may be particularly beneficial for smaller mammals, which suffer in general from a higher predation pressure during the active season (see also Turbill et al. 2011). In comparison, larger hibernators have a relatively high survival probability in all seasons (Arnold 1993).

Dispersal and juvenile local survival probability

Cormack–Jolly–Seber models cannot distinguish between dispersal and mortality (Lebreton et al. 1992). It was possible to assess the potential effects of dispersal on local survival estimates, however, because the dispersal behaviour in our population of common dormice is very well studied (Juškaitis 2008). Juveniles may disperse after weaning (approx. 5 weeks of age) but then become sedentary at an age of approximately 2–3 months, when early-born females become sexually mature (Juškaitis 2008). Consequently, we are confident that our estimates of survival for all adults were largely uninfluenced by dispersal.

The lowest local survival estimates in our study were observed in juveniles, paralleled by the highest likelihood of dispersal (1–2 month after weaning). Thus, it is possible that actual survival probabilities were somewhat underestimated in both early-borns (during the early active season) and late-borns (during late active season and hibernation). However, there is no reason to assume different rates of dispersal between early- and late-born juveniles. Hence, a possible error in our survival estimates of juveniles would affect both groups and should have no bearing on the overall conclusions.

Timing of reproduction

Our results showed a fitness advantage for early-born juveniles. A significantly higher fraction of early-born females started to reproduce at the study site (54.8% in early-born females vs. 7.2% in late-born females). This was mainly caused by the much higher probability to survive until the onset of reproduction at an age of 2–3 months in early-born females ($\phi = 0.46$) rather than at an age of 9–10 months in late-born females ($\phi = 0.19$). Lifetime reproductive success was therefore much higher for early-born females than for late-borns (3.1 vs. 0.51 juveniles). Several studies have shown that in multivoltine species, early-born juveniles have significantly higher survival rates than late-born juveniles [e.g. guinea pigs (Kraus et al. 2005) or Townsend's voles, *Microtus townsendii* (Lambin and Yoccoz 1998; Lambin and Yoccoz 2001)]. Most rodents appear to reproduce as early as possible within the year, and investment in the first litter of the season is often higher than that in subsequent litters (e.g. Kraus et al. 2005). This is expected under the assumption that survival is generally low or environmental conditions decline toward the end of the breeding season (Lambin and Yoccoz 2001).

In dormice, however, the environmental conditions, namely food availability, show a different time course. Dormice consume fruits and seeds, which are more abundant in the summer and at the end of the active season. Moreover, these food resources are energy rich and allow rapid growth

and a fast accumulation of body fat reserves. Correspondingly, late-born juveniles gained more body mass in their second month after weaning than early-borns in their second month after weaning. However, the adaptation to energy-rich seeds in common dormice is much less pronounced than that in the edible dormice (as evidenced by the former's ability to reproduce early in each study year). In contrast, edible dormice always delay the birth of their single litter even until August, coincidentally with high seed availability (Bieber 1998). Life history tactics in common dormice thus seem to combine different strategies: while the first litters occurred as early as in May and showed high long-term survival opportunities (as expected in opportunistic breeders in a temperate climate), the majority of litters (80.7%; Fig. 4b) from animals analysed in our data set were born late in the active season, when energy-rich fruits and seeds are available. In the long-term study carried out by Juškaitis (2008; see Fig. 1), 34% of the litters were born in May–June, 14% in July and 52% in August–September. Thus, based on data collected on the population for >20 years, a high percentage of dormice reproduced late in the year.

For litters born late in the year, the exact timing of reproduction seems to be particularly important. Arguably, animals born as late as in late September are likely to suffer from time constraints compared with animals born only few weeks earlier in the season. For example, it has been shown that a mere 20-day difference in birth dates can significantly affect survival probabilities in juvenile hibernators (Rieger 1996). Slight disadvantages of a late birth are also supported by our observation that late-born juveniles entered hibernation with a lower mean body mass than early-born juveniles. We also observed within the population of late-borns that pre-hibernation body mass was higher (approx. 3 g) among animals that survived hibernation. These body mass differences may be responsible for the somewhat lower mean hibernation survival rates in late-born juveniles (Fig. 2). Still, low body mass loss over winter in late-born juveniles may also indicate that we did not record the final pre-hibernation body mass in this group. During the occasional nest-box controls in late October/early November, we found few late-born juveniles which had increased body mass in comparison to mid-October, indicating that some animals stayed active somewhat longer. However, these did not reach body masses as high as early-born juveniles before hibernation. Also, the majority of dormice had disappeared from the nest-boxes by the end of October, probably due to the onset of hypothermia (cf. Bieber and Ruf 2009).

It is clear that optimal timing of reproduction also involves maternal investments and costs. For adults, the early active season was the most unfavourable time of the year: body mass was at its lowest (due to depleted energy

reserves after hibernation and low food availability) and mortality at its highest. Actually, only the heaviest females were able to invest in early reproduction under these challenging conditions. On the other hand, the high availability of energy-rich food, as observed later in the active season, is likely to facilitate investment into reproduction. Thus, females in a poorer body condition apparently delay reproduction until environmental conditions have improved.

Still, the question remains why young-of-the-year females start to reproduce prior to the first hibernation at all. Alternatively, they could accumulate body fat reserves and delay reproduction until early the following year. However, given that early-born juveniles had only a 14% probability to survive from birth to the next spring, it is clear that early onset of reproduction (first litter in August/September) provides a selective advantage. A high predation risk during their “long” active season seems a disadvantage for early-born females. High mortality is known to lead to a significant advancement of sexual maturity (e.g. Servanty et al. 2009). Also, as demonstrated by Ejsmond et al. (2010), even if only a small fraction of late-born offspring reach adulthood, parents may improve their fitness by sacrificing offspring quality. In our data set, there was, however, no evidence for an impaired quality of late-born animals (i.e. the offspring of early-born females). Among the small fraction of late-born dormice that bred on the study site in subsequent years, lifetime reproductive success was no different (even somewhat higher: +1.3 juv./female) from that of early-born mothers. Thus, producing late-born offspring carries at least the chance to reach high lifetime reproductive success, especially since a larger proportion of this group is likely to produce more than one litter per life.

Bimodal birth peak

Taken together, the relatively high over-winter survival rates and the small body size in common dormice may have allowed for the combination of diverse life history tactics (slow and fast) that lead to a bimodal seasonal birth pattern (Figs. 1, 4). Because of the high survival probability during hibernation, the negative effect on fitness of delaying the onset of reproduction is much lower than that in non-hibernating small mammals. These mostly opportunistic breeders tend to reproduce whenever the environmental conditions are suitable (Bronson 1989). As reviewed by Bronson (1989), a bimodal birth peak occurs in small mammals mainly due to unsuitable environmental conditions within the reproductive season (e.g. drought, rainfall). The common dormice of our study population, however, showed a small investment in reproduction in the middle of the active season even though reproduction is not constrained by climatic conditions at this time of the year. Additionally, the minimum time needed between two

subsequent litters during the active season does not explain the pattern of a bimodal birth peak in the Lithuanian dormouse population. Actually, the shortest interval observed between the births of two litters within any one active season was 30–33 days in Lithuania (Juškaitis 2008). Thus, there is no temporal constraint that would explain the low number of juveniles born in midsummer (July). Hence, dormice seem to have two options to maximise fitness: (1) give birth as early as possible to allow these young to breed before hibernating and/or (2) give birth as late as possible (leaving just enough time for these young to fatten) and enter directly a period with highest survival rates (hibernation) until maturity.

The life history characteristics observed here—namely, the early onset of reproduction and its consequences for the timing of births and survival chances of young—apparently do not represent fixed traits in this species. Breeding by young-of-the-year-mothers has been observed in eight populations in six countries (reviewed in Juškaitis and Büchner 2010), and the frequency of occurrence may vary among populations. In Russia, for example, within a 7-year capture–mark–recapture study, only three breeding cases by young-of-the-year mothers were observed in a single year (Likhachev 1966). Accelerated or delayed onset of reproduction should largely depend on the level of extrinsic mortality (particularly predation pressure), and we would predict that in those populations with delayed reproduction mean survival rates during the active season are significantly higher than those at our Lithuanian study site. In fact, the percentage of common dormice in the diet of the tawny owl in parts of Lithuania (up to 10%; Balčiauskienė et al. 2005) is among the highest in Europe.

At the present time there seems to be a general consensus that mammal species can be ranked along a slow–fast continuum (Gaillard et al. 1989; Oli 2004; Promislow and Harvey 1990). Comparative studies in particular are based on the implicit assumption that certain speeds of life histories (as measured by, for example, generation time) are fixed, species-specific traits. Our present data show, however, that slow and fast life histories are not a fixed trait but that they can change within a species and even within a population. Only changes between fast and slow life histories, i.e. acceleration (early onset of reproduction) early in the active season and a slowing down (delayed onset of reproduction) late in the active season and hibernation, are likely to explain the bimodal birth peak observed at our study site. It appears that small mammals in particular, which can reach maturity rapidly, have the potential to show a high flexibility in adjusting their life history tactics to environmental conditions and predation pressure. Thus, small hibernators, such as the common dormouse, may be interesting models to further study the flexibility of mammalian life history tactics in general.

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