

Body mass dependent use of hibernation: why not prolong the active season, if they can?

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Summary

1. Hibernation is the most effective means for energy conservation during winter in mammals. The drawbacks of deep and prolonged torpor include reduced immunocompetence, and consequently, hibernators should be selected to minimize torpor expression when climatic conditions or energy availability (e.g. food or fat stores) permit. Therefore, it seems surprising that some hibernators employ extraordinary long hibernation seasons, lasting well beyond periods with unfavourable conditions.
2. Because of their extended use of torpor, edible dormice (*Glis glis*) provide an ideal model for scrutinizing interactions between energy reserves (i.e. body fat stores) and thermoregulatory patterns. We used a multimodel inference approach to analyse body temperature data (i.e. use of torpor) from 42 entire hibernation seasons over 4 years in females in relation to body mass.
3. Body mass prior to hibernation did not affect the duration of the hibernation season, but animals hibernated for *c.* 8 months, that is, 2 months longer than required by environmental conditions. Fatter individuals aroused significantly more often, had a higher mean minimum body temperature during torpor and remained euthermic for longer periods than leaner animals.
4. Surplus energy was therefore not used to shorten the hibernation season, but to rewarm more frequently, and to allow shallower torpor bouts. These adjustments apparently serve to avoid negative effects of torpor and, perhaps equally importantly, to minimize the time active above-ground. We argue that maintaining a short active season, despite surplus energy reserves, may be explained by known beneficial effects of hibernation on survival rates (via predator avoidance).
5. Our data provide quantitative evidence that hibernation is a flexible tool within life-history strategies. We conclude that, apart from energetic necessities due to harsh environmental conditions, predator avoidance may be an important factor influencing patterns of hibernation and torpor in mammals. Thus, our study indicates that climatic conditions alone are not a good predictor of hibernation patterns or survival in hibernating species during global climate change.

Key-words: body fat reserves, edible dormouse, hypothermia, life-history strategy, predation

Introduction

Mammalian hibernation has long been regarded as a crucial adaptation that permits reduced energy expenditure during unfavourable conditions, such as periods of low ambient temperatures (T_a), food shortages or drought (Hall 1832; Darwin 1839; Wyss 1932). The enormous

reduction of energy expenditure during this state of torpor to about 2–4% of the basal metabolic rate (BMR, Geiser 1988; Heldmaier & Ruf 1992) is generally viewed as a key to survive these life-challenging conditions. However, there seem to be several trade-offs connected to the state of hibernation, which are still under discussion.

In particular, there is evidence showing that the state of torpor itself, associated with low body temperatures (T_b), also appears to have negative physiological effects. These include a reduced immunocompetence (Burton & Reichman 1999; Prendergast *et al.* 2002), memory loss (Millesi

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et al. 2001; but see Clemens, Heldmaier & Exner 2009) and increased oxidative stress (Carey, Frank & Seifert 2000). Thus, individuals capable of doing so, that is, animals with larger energy reserves, should minimize the time in deep torpor, because they can afford to remain euthermic for much of the winter and thus largely avoid the negative side-effects of torpor (Humphries, Thomas & Kramer 2003b). Supporting evidence for this hypothesis comes from free-ranging chipmunks (*Tamias striatus*), which reduced torpor use in the presence of surplus food (Humphries, Kramer & Thomas 2003a). However, chipmunks store food to survive the hibernation season and fat-storing species might differ. Because mobility decreases with body mass gain (Trombulak 1989), an extremely high body mass can be a handicap, especially for arboreal species. Thus, fat-storing hibernators are more constrained by the size of their energy reserves (i.e. body fat) than food-storing hibernators.

The edible dormouse (*Glis glis*), henceforth 'dormouse', is a species that uses torpor extensively. The hibernation season in dormice, when they rely solely on fat accumulated prior to hibernation, is extremely long and lasts, on average, 8 months (Vietinghoff-Riesch 1960; Bieber & Ruf 2009b, 2012). This extent of the hibernation season is remarkable because dormice live in the temperate zone in Western Europe where the growing season of plants exceeds their active season by up to 2 months. It has been suggested that dormice employ extended hibernation in underground burrows to minimize the risk of predation above-ground (Bieber & Ruf 2009b). Supporting this hypothesis, survival rates during winter were found to be extremely high in five dormouse populations across Europe (>98% monthly local survival probability) and significantly lower (80–94%) during the active season when dormice live nocturnal and arboreal in deciduous forests (Lebl *et al.* 2011a). Hence, hibernation is associated with decreased mortality in dormice. Consequently, prolonging phases of inactivity (i.e. hibernation) might have other positive effects, which previously were only rarely considered in the context of hibernation performance.

Because of their extended use of torpor, dormice provide an ideal model to investigate possible effects of energy reserves (i.e. body fat stores) on hibernation patterns. According to the hypothesis that hibernators should minimize torpor expression (Humphries, Thomas & Kramer 2003b), high body mass (as a proxy for body fat reserves, Schaefer, Piquard & Haberey 1976) should lead to a decreased use of torpor. If so, this could be achieved in two ways: Dormice with large fat reserves could either reduce the duration of the hibernation season in general, especially since the environmental conditions appear to allow emergence from hibernation much earlier than observed on average. This strategy may be beneficial for obtaining high-quality territories containing old productive beech trees, which are crucial for reproductive success (Lebl *et al.* 2011b). A drawback of this option could be increased activity and hence predation risk (Bieber & Ruf

2009b, 2012). Alternatively, dormice may maintain a long hibernation season but use less or less-pronounced torpor by (i) reducing the duration of torpor bouts, (ii) increasing the duration of interbout euthermia (IBE) and/or (iii) by maintaining a higher T_b during torpor. If dormice opted for this alternative, it would indicate that surplus fat reserves are not merely used to minimize the time spent torpid, but also to minimize the time spent above-ground, with its associated risks.

We analysed 42 complete T_b data sets from entire hibernation seasons to examine whether and how dormice individually adjust torpor expression in relation to body fat reserves. To strengthen analytical power, we experimentally increased the variation in prehibernation body mass. As other variables also might influence torpor use, such as reproduction prior to hibernation (e.g. Milesi *et al.* 1999), age (e.g. Michener 1978; French 1990; Bieber & Ruf 2012) and white adipose tissue (WAT) composition (e.g. Geiser & Kenagy 1987), these factors were also considered in our analysis.

Materials and methods

ANIMALS AND CLIMATE

We analysed two data sets generated from implanted temperature data loggers: (i) 11 female dormice kept permanently (mixed sex and age groups) in outdoor enclosures (data recorded 2005–2007; four animals were implanted twice, in two consecutive years) and (ii) 27 females captured in late summer in the field (study site Vienna Woods, Austria, about 40 km from the enclosures, see below) and kept only during the winter season in our enclosures (data recorded winter 2008/2009 and 2009/2010). Taken together, we obtained 42 data sets for complete hibernation seasons: 6 in 2005/2006, 9 in 2006/2007, 18 in 2008/2009, 9 in 2009/2010. After hibernation and logger removal, the females from the Vienna Woods were released at the site of capture. All dormice were marked individually (PIT tags, 13.8 × 2.1 mm; Virbac, Back-HomeBioTec, Bad Oldesloe, Germany).

The enclosures were located 364 m a.s.l. in Vienna, Austria (48°13' N; 16°16' E). Enclosure-housed dormice were provided with rodent chow *ad libitum* (Altromin 1314, FORTI, Altromin, Lage, Germany). Field-captured females also received a small amount of sunflower seeds prior to hibernation (~10 g) to facilitate the acclimatization to captivity. Enclosures contained nest boxes for shelter that were used during the active season. All dormice dug underground burrows in which to hibernate. Nest boxes were checked weekly during the active season, and body mass of captured animals was recorded to the nearest 1 g. In dormice, as in other hibernators, variation in body mass is highly correlated with variation in WAT depots ($r = 0.84$, $n = 27$, Schaefer, Piquard & Haberey 1976). Notably, the slope of this relation was close to 1 (0.98) indicating that variation in body mass directly reflects total body fat content. Therefore, although body mass is influenced by differences in structural size (Fietz & Weis-Dootz 2012) or the size of other tissues (Bieber *et al.* 2011), it provides an excellent proxy of energy reserves in this species. For a subset of analyses that involved body mass loss (autumn/spring mass) during the hibernation season, we included data only for individuals whose mass was measured within 1 week of onset and termination of hibernation ($n = 29$).

For field-captured animals, we could not determine their exact year of birth. However, since age is an important variable known

to influence patterns of hibernation (Bieber & Ruf 2012), we distinguished between two age classes: yearlings (after first hibernation) and adult animals (beyond second hibernation, for details see Bieber 1998). Because of the unknown date of birth in field-captured animals, we were not able to differentiate in more detail. However, since we considered only yearlings at the end of their second active season (>14 months), we assume that most structural body growth was complete at the beginning of our experiment.

Mean ambient temperature (T_a) was recorded at the weather station 'Hohe Warte', Vienna, Austria (48°15'N and 16°22'E, 203 m a.s.l., <http://www.zamg.ac.at>, 2 km from our site). The mean monthly T_a during the core hibernation period (October–April) was used as an indication of the severity of winter. Temperature was highest in 2006/2007 (8.4 ± 1.4 °C), all other winter seasons were colder T_a [2005/2006: 4.2 ± 2.1 °C, 2008/2009: 5.7 ± 2.1 °C (beech masting year), 2009/2010: 4.8 ± 1.8 °C].

Soil temperature (T_s) was recorded with an iButton (15 cm below ground) in one enclosure.

IMPLANTATION OF TEMPERATURE LOGGERS

Wax-coated iButtons (DS1922L, Dallas/Maxim, Maxim Integrated, San Jose, CA, US; resolution 0.5 °C) were calibrated in a water bath and implanted for the measurements of T_b in dormice. In 2005 and 2006, iButtons were implanted subcutaneously in the lateral area of the thorax, caudal to the scapula ($n = 15$, for further details see Bieber & Ruf 2009a), in 2008 and 2009, iButtons were implanted intraperitoneally ($n = 27$; this change was due to a change in animal ethics guidelines). Surgical anaesthesia was induced by subcutaneous injection of 50 mg kg⁻¹ ketamine (Ketamidol® 10%; Richter Pharma, Wels, Austria) and 8 mg/kg xylazine (Rompun® 2%; Bayer, Leverkusen, Germany) and maintained by 1.5% isoflurane in an oxygen stream via a face-mask. The animals were placed in dorsal recumbency, the operation field was prepared according to standard surgical procedures and covered by sterile surgical drapes. The abdominal cavity was opened through a ~1 cm incision in the *linea alba*. Postimplantation, peritoneum, abdominal muscles were sutured using synthetic absorbable surgical suture material USP 3/0 (Surgicryl PGA; SMI AG, Hünningen, Belgium) using the single-button suture technique. The skin was sutured separately using synthetic absorbable surgical suture material USP 4/0 (Surgicryl PGA; SMI AG) with intracutaneous suture technique. During the entire procedure, vital parameters [respiration rate, peripheral haemoglobin oxygen saturation as measured by pulse oximetry (SpO₂), heart rate] were monitored. Postsurgical analgesia (5 mg kg⁻¹ Ketoprofen, subcutaneously) was provided. One week after implantation, dormice were released from cages (individual postoperative care) into the outdoor enclosures. T_b was recorded at approximately hourly intervals (3850 s) to allow for 1 year of data recording. Implantation was carried out between June and September and replacements/logger removals between May and August.

REPRODUCTION

Dormice use nest boxes in the active season to rest during the daytime and as sites to rear their young. To assess the possible impact of reproduction on hibernation the following winter, we recorded the absence or presence of juveniles (reproductive output prior to implantation in our experimental females) during weekly nest-box controls in our enclosure-housed population and in biweekly nest-box controls ($n = 184$, height 2–3 m, irregular distribution) at our field study site in the Vienna Woods (48°05' N, 15°54' E; elevation 500–850 m, from 2006 to 2010, for details see e.g. Lebl *et al.* 2011b). Only females captured at least twice during the reproduc-

tion period (August/September) without litters or visible nipples were counted as nonreproductive (in our sample $n = 25$, 60 %). We collected females from the field study site with different reproductive output (range 1–9 weaned juveniles/litter) for our hibernation experiment. We recorded a total of 17 females with litters (mean litter size: 5.35 ± 0.47).

FATTY ACIDS

During logger implantations, we collected small amounts of subcutaneous or omental WAT to measure fatty acid (FA) composition. FA composition was determined using FA methyl ester (Garces & Mancha 1993); separation, identification and quantification, was based on integration of peak areas obtained by gas chromatography (for further methodological details see Valencak *et al.* 2003; Popescu *et al.* 2011). We only used the percentage of linoleic acid (most abundant omega-6 fatty acid) for further analyses, since this FA has been shown to be crucial for torpor patterns (e.g. Geiser & Kenagy 1987; Geiser 1991; Frank & Storey 1995). Because of the negligible amounts (median 0.3%) of alpha linolenic acid (omega-3 fatty acid) in our field samples, we did not analyse this essential FA, or the 'linoleic acid/alpha linolenic acid' ratio.

STATISTICS

We analysed T_b data using the statistical package R (Version 2.13.1, R Development Core Team 2011). We used a T_b of 25 °C as a conservative threshold for entering or leaving the state of torpor/euthermia. Onset of the hibernation season was defined by $T_b < 25$ °C for more than 24 h. The hibernation season was considered to be terminated when an animal remained at $T_b > 25$ °C for more than 72 h. We computed the duration of the hibernation season, torpor bout duration, number of arousals (i.e. periods of rewarming followed by several hours of IBE), as well as IBE duration for each recorded hibernation season.

To test simple hypotheses, we used ANOVA tables of linear regression models and Pearson's product-moment correlations (for normally distributed residuals).

We used lme models (linear mixed effect models, R-package lme4, Bates, Maechler & Bolker 2011) to analyse the effects of age-class (yearling vs. adult), reproduction (number of juveniles weaned prior to hibernation) and body mass prior to hibernation on duration of hibernation season, onset and end of hibernation season, mean and maximum torpor bout duration, mean and sum of IBE duration, number of arousals, body mass after hibernation and mean T_b minimum. Beside the fixed effects (age, reproduction and body mass), we also used the factors site (enclosure raised females vs. females captured in the field), and year (2005, 2006, 2008, 2009) as random effects in all modelling procedures. Thus, we were able to adjust for site-dependent variation (e.g. differences in implantation technique) and for variation between the years (e.g. climatic variation). Further, we adjusted for the mean minimum soil temperature (T_s , set as a random factor) except for the response variables onset of hibernation, end of hibernation, mean minimum T_b , and maximum torpor bout duration, because these single event variables could not conceivably be affected by long-term soil temperatures. Since mean minimum T_s and T_b are known to be closely correlated (e.g. Bieber & Ruf 2009b), we chose the latter because of more precise measurements (only one iButton was recording T_s at 15 cm depth), to correct for the influence of the surrounding temperature. The response variable mean minimum T_b , however, was adjusted for T_s . All models were assessed visually (histograms and quantile/quantile plots) for normal distribution of residuals. As this was the case for all response variables (even rates, such as number of arousals per hibernation season), all lme models were computed using the Gaussian family.

Initially, we tested for interactions between the variables in our models. However, since none of these interactions were statistically significant, we did not consider interactions in our further analyses. Also, since we did not observe a significant effect of linoleic acid proportions on hibernation patterns (e.g. mean torpor bout duration), we removed this variable from further modelling.

We used the multimodel inference approach (R-package MuMIn, Barton 2012) to determine the relative importance of predictor variables. We started with a global set of linear models including all additive effects of the above-mentioned variables. We then created a table ranked by minimizing the value of Akaike's Information Criterion (AICc, Akaike 1973), corrected for small sample size. We also calculated Akaike weights, which represent the relative likelihood of each model given the data and the entire set of models (Burnham and Anderson 2002). To identify influential variables, we made robust inferences based on a set of supported models ($\Delta\text{AICc} < 10$). We could then estimate the relative explanatory strength of each variable while simultaneously accounting for uncertainty in model selection. We calculated model-averaged coefficients for all variables by averaging the estimates, weighted by multiplication with that model's Akaike weight, over the set of supported models ($\Delta\text{AICc} < 10$) including each variable. We also derived the *P*-value associated with each coefficient (i.e. not dependent on a single model). The relative importance of all variables was calculated by summing the Akaike weights of each model containing that variable. The relative importance of a predictor variable reached a maximum value of 1, when it was included in all supported models (with $\Delta\text{AICc} < 10$).

If not stated otherwise, all mean values were given \pm standard error of the mean (SEM).

Results

BODY MASS, SITE, AGE-CLASS, WAT

Animals captured at our field study site had a significantly lower mean body mass (105.1 ± 2 g, range: 78–129 g)

than females kept year-round in enclosures (192.5 ± 11.6 g, range: 100–238 g; $F_{1,39} = 85.40$, $P < 0.0001$). However, since we did not observe significant interactions between body mass and site for any of our different response variables, we can rule out that only site differences in body mass were responsible for the effects of body mass on hibernation patterns. We did not observe an effect of age-class (yearling vs. adult) on body mass prior to hibernation ($F_{1,39} = 0.22$, $P = 0.64$).

Mean concentration of WAT linoleic acid differed significantly between the years. Its concentration was highest in 2008 ($39.6\% \pm 1.7$) and significantly lower in the other years (2005: $15.9\% \pm 0.6$, 2006: $22.3\% \pm 0.8$, 2009: $14.3\% \pm 0.3$; $F_{3,27} = 25.2$, $P < 0.0001$).

DURATION OF HIBERNATION SEASON

Animals hibernated on average for 5664.1 ± 89.1 h (equivalent to 236 days or 7.7 months, range 4293.5–6575 h).

None of the predictors (body mass prior to hibernation, age-class and reproduction) contributed substantially to explaining the variation in duration of the hibernation season (Table 1). Age-class explained the most, however, considering all models with a $\Delta\text{AICc} < 10$, its relative variable importance was only 0.44 and the model-averaged coefficient was not significant. Body mass prior to hibernation showed the lowest relative variable importance (0.20, Table 1) and did not affect the hibernation duration significantly (Fig. 1). The best model included none of the given predictors (best model weight: 0.34).

Table 1. Relative variable importance and corresponding *P*-values for the model-averaged coefficient of the predictor variables: body mass prior to hibernation, age-class (yearling vs. adult), and reproduction (number of weaned offspring) prior to hibernation, for the different response variables

Response variable	Predictor variables					
	Body mass		Age-class		Reproduction	
	Relative variable importance	<i>P</i>	Relative variable importance	<i>P</i>	Relative variable importance	<i>P</i>
Hibernation duration	0.20	n.s.	0.44	n.s.	0.25	n.s.
Onset of hibernation	0.95	0.0004***	0.35	n.s.	0.26	n.s.
End of hibernation	0.30	0.025**	0.67	0.037*	0.41	n.s.
Number of arousals	1	< 0.0001***	0.32	n.s.	0.40	0.047*
Mean IBE duration	0.22	n.s.	0.20	n.s.	0.26	n.s.
Sum IBE duration	0.96	0.001**	0.22	n.s.	0.36	0.088†
Maximum torpor bout duration	0.99	< 0.0001***	0.33	n.s.	0.20	n.s.
Mean torpor bout duration	0.97	< 0.0001***	0.64	0.035*	0.35	n.s.
Mean minimum T_b	0.62	0.022*	0.28	n.s.	0.36	n.s.
Body mass after hibernation	1	< 0.0001***	0.15	n.s.	0.15	n.s.

IBE, interbout euthermia; T_b , body temperature.

The highest relative variable importance with significant model-averaged coefficients is printed in bold.

Significance codes: 0> *** < 0.001 > ** < 0.01 > * < 0.05 > † < 0.1.

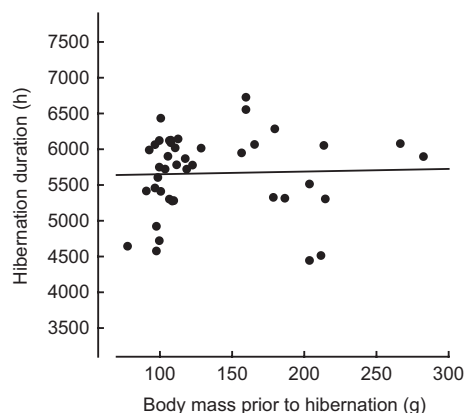


Fig. 1. Influence of body mass on hibernation duration in dormice. Shown are partial residual plots from the best linear mixed effects model, dots represent individuals.

ONSET OF HIBERNATION

Mean onset of hibernation was on 1 October (day 273.4 ± 2.2 d, range 21 August to 21 October).

Among the given predictors, only body mass prior to hibernation had a high relative variable importance (0.95) and a highly significant model-averaged coefficient (Table 1). The heavier a female was, the earlier she entered hibernation (Fig. 2a). Variation in the onset of hibernation was best explained by body mass prior to hibernation alone (best model weight 0.46). For each additional 10 g of body mass prior to hibernation, females entered hibernation 1.8 d earlier.

END OF HIBERNATION

The mean end of hibernation was on 25 May (day 147.2 ± 4 d, range 25 April–8 July).

The relative variable importance for age-class was high (0.67), and the model-averaged coefficient was significant (Table 1). Yearling females terminated hibernation significantly later than adult females (on average by 19.2 d, Fig. 2b). Age-class alone explained the observed variation in termination of hibernation best (best model weight 0.26). The model-averaged coefficient for body mass prior to hibernation, however, was also significant. Females with a higher body mass prior to hibernation terminated the hibernation season earlier than lighter ones (for an additional 10-g body mass gained at the onset of hibernation females terminated hibernation 1.7 days earlier). However, the relative variable importance for this predictor was low (0.30, Table 1). Thus, body mass prior to hibernation did not contribute much to the observed variation in termination of hibernation in general.

NUMBER OF AROUSALS, MEAN IBE DURATION, SUM OF IBE DURATIONS

Dormice aroused 23.7 ± 1 times per hibernation season (range: 12–43 arousals per animal). All models with a

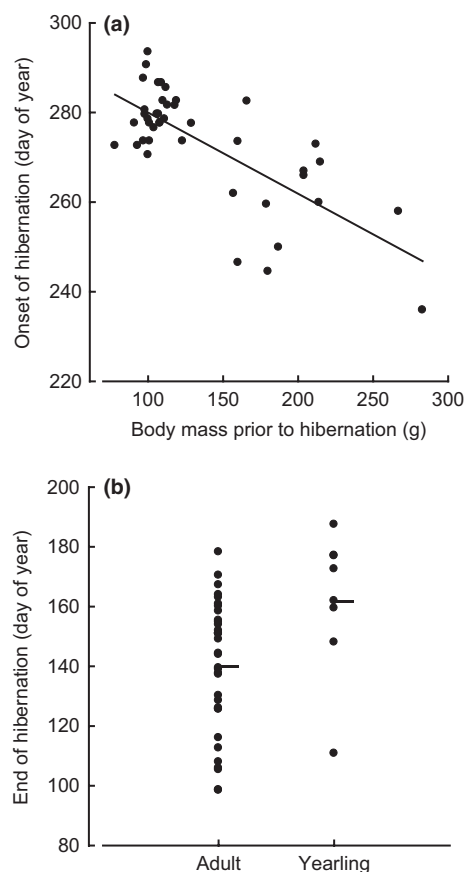


Fig. 2. Factors affecting the timing of the hibernation season in dormice; (a) influence of body mass prior to hibernation on onset of hibernation, (b) influence of age on termination of hibernation. Note that for yearlings, their second hibernation season was analyzed, for adults, their third or later seasons. Shown are partial residual plots from the best linear mixed effects model. Dots represent individuals, horizontal lines means.

$\Delta AICc < 10$ included the predictor body mass prior to hibernation (relative variable importance = 1). The heavier a female was at the beginning of hibernation the more often it aroused (Fig. 3a). The model-averaged coefficient was highly significant (Table 1). Variation in the number of arousals was best explained by body mass prior to hibernation alone (best model weight 0.39). Number of arousals increased on average by 1.1 for a 10-g body mass increment prior to hibernation. Although the relative variable importance of reproduction was moderate (0.40), we observed a significant model-averaged coefficient ($P = 0.047$, Table 1). Thus, the influence of reproduction on number of arousals had the same trend in all models including this predictor ($\Delta AICc < 10$). For each additional juvenile weaned, the females showed an increase in 0.5 arousals per hibernation season.

Mean IBE duration was 6.7 ± 0.3 h (range: 4.4–12 h per animal). The best model included none of the given predictors (model weight: 0.46; Table 1).

During the entire hibernation season, the animals were euthermic for on average 161.6 ± 10.2 h, or 2.8% of the

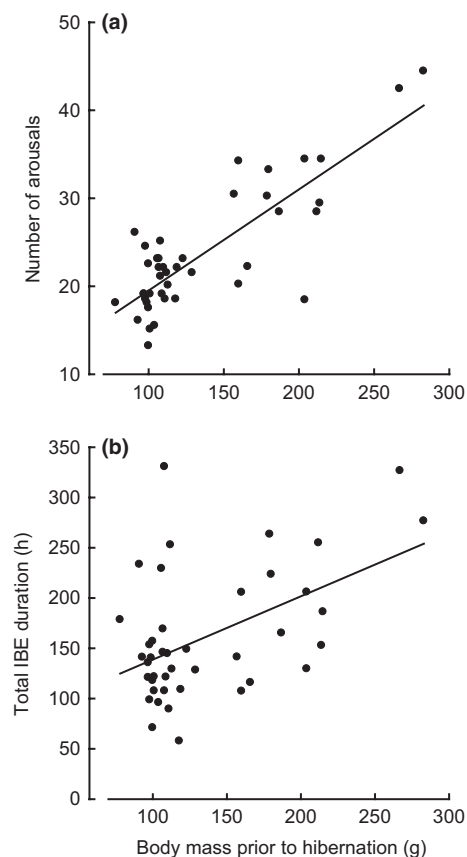


Fig. 3. Influence of body mass prior to hibernation on (a) number of arousals and (b) total duration of interbout euthermia [total IBE duration (h)] during hibernation in dormice. Shown are partial residual plots from the best linear mixed effects model, dots represent individuals.

time. Relative variable importance of body mass prior to hibernation on the sum of IBE durations was very high (0.98) and the model-averaged coefficient highly significant (Table 1). Animals increased the time spent euthermic during the hibernation season by 7 h for a 10-g body mass increment prior to hibernation (Fig. 3b). Among our predictors, only body mass prior to hibernation influenced the sum of IBE durations significantly (best model weight 0.36).

MEAN AND MAXIMUM TORPOR BOUT DURATION

Mean torpor bout duration was 237.7 ± 10 h (range: 124.5–392.5 h per animal, equivalent to 5.2–16.4 d per animal). The mean maximum torpor bout duration was 604.7 ± 23.7 h (range: 276.3–972.1 h per animal, equivalent to 11.5–40.5 d per animal). As expected, both mean and maximum torpor bout duration were explained by the same variables, with shorter torpor bouts occurring in heavier females (e.g. Fig. 4a). Body mass prior to hibernation, in both modelling procedures, had a high relative variable importance (0.97 and 0.99, respectively) in combination with highly significant model-averaged coefficients

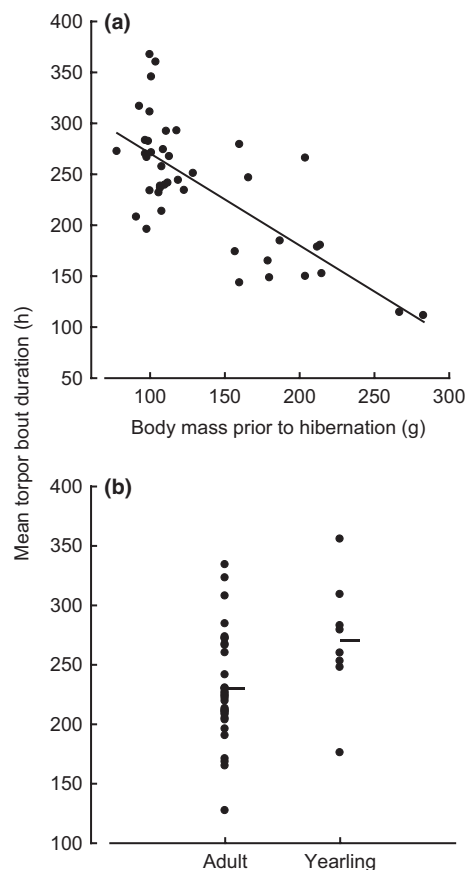


Fig. 4. Factors affecting mean torpor bout duration; (a) influence of body mass prior to hibernation and (b) influence of age-class. Shown are partial residual plots from the best linear mixed effects model. Dots represent individuals, horizontal lines means.

Table 1). Mean torpor bout duration was shortened by 7.6 h for each 10-g body mass increment and maximum torpor bout duration by 17.4 h for each 10-g body mass increment. However, only for mean torpor bout duration, we observed a medium-ranked relative variable importance of age-class with a significant model-averaged coefficient (Table 1). On average, a torpor bout was 39.8 h longer in yearling than in adult females (Fig. 4b). The best model for mean torpor bout duration included body mass and age-class (weight: 0.43) for maximum torpor bout duration only body mass (weight: 0.52).

MEAN MINIMUM T_b

The mean minimum T_b during hibernation increased with increasing pre-hibernation body mass (Fig. 5). The relative variable importance was 0.62 (Table 1). The best model included only body mass prior to hibernation (model weight: 0.30).

BODY MASS AFTER HIBERNATION

On average, the animals lost 37.1 ± 4.7 g during a hibernation season [range: 10–117 g (inset graph Fig. 6); on

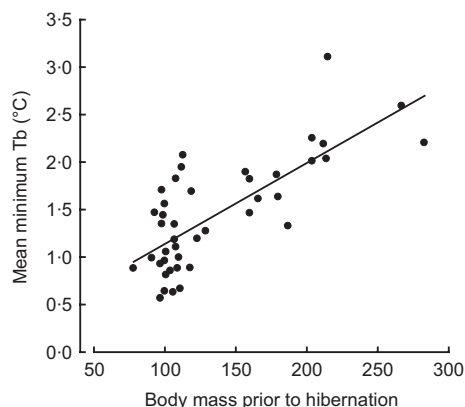


Fig. 5. Influence of body mass prior to hibernation on mean minimum T_b (°C). Shown are partial residual plots from the best linear mixed effects model, dots represent individuals.

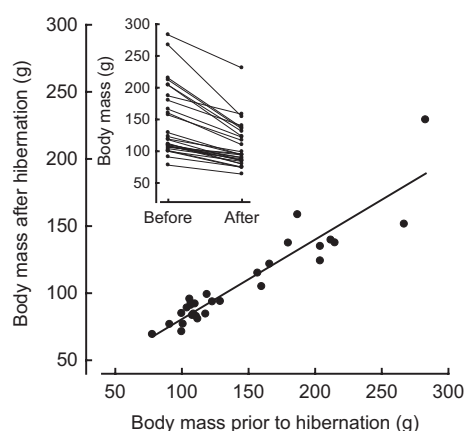


Fig. 6. Influence of body mass prior to hibernation on body mass after hibernation. Shown are partial residual plots from the best linear mixed effects model. The inset graph shows the individual body mass loss during hibernation. Dots represent individuals.

average $0.2 \pm 0.02 \text{ g day}^{-1}$). Body mass prior to hibernation and body mass loss during hibernation were strongly correlated ($r = 0.83$, $t = 7.86$, d.f. = 27, $P < 0.0001$) showing that body mass loss during hibernation was greater in heavy females (compare inset graph Fig. 6). Body mass loss during hibernation was positively affected by the number of arousals during hibernation [adjusted for hibernation duration (covariate), $F_{2,26} = 6.54$, $P = 0.003$].

Our analysis revealed a strong impact of body mass prior to hibernation on the body mass after hibernation. All models with an AIC < 10 included the predictor body mass prior to hibernation (relative variable importance = 1, Table 1). In general, females that were heavier prior to hibernation were also heavier after emergence (Fig. 6). A 10-g additional body mass prior to hibernation caused a 6 g higher body mass after hibernation. The best model included only the predictor body mass prior to hibernation (model weight: 0.54).

Discussion

Our study shows that in female dormice, prehibernation body mass, and thus fat mass (Schaefer, Piquard & Haberey 1976), affects most of the torpor variables during the hibernation season, but not the duration of the hibernation season per se. Heavier individuals aroused more frequently, had longer IBEs, a higher mean minimum T_b , and lost more body mass than lean individuals but still were heavier at the end of the hibernation season.

BODY MASS AND TORPOR

Different physiological pathways may explain the decrease in torpor expression associated with an increased body mass in fall observed here. Firstly, it is possible that body mass directly affected metabolic rate. One of the oldest hypotheses concerning periodic arousals proposed that they may be caused by some chemical imbalance resulting from the animal's metabolism that eventually triggers re-warming and correction of the imbalance during euthermic intervals (Fisher 1964). This hypothesis could indeed explain why heavier animals, with lower mass-specific euthermic MR at low T_a require longer IBEs. Increased arousals at higher body masses are also known from interspecific comparisons of hibernators (French 1982, 1985). This 'metabolic theory' of arousals would, however, also predict that the rate of accumulation of a chemical imbalance is proportional to MR during torpor. Hence, smaller animals with somewhat higher mass-specific torpor metabolic rates (Geiser 2004) should have shorter torpor bouts. Our data suggest the opposite (Fig. 4a) and comprehensive comparative analyses have shown that torpor bout duration is not related to body mass (e.g. Geiser & Ruf 1995; Malan 2010). Therefore, the hypothesis that our observations are simply effects of body mass on metabolism does not seem to be supported.

Secondly, animals with high-energy reserves may be able to minimize adverse effects of torpor, such as the possibility of increased exposure to reactive oxygen species (ROS, Buzadzić *et al.* 1990) which may lead to lipid peroxidation (Carey, Frank & Seifert 2000; Harlow & Frank 2001). However, the question of negative effects of torpor on ROS production and damage (e.g. telomere length) is still not fully resolved (i.e. positive effects of torpor, e.g. Brown *et al.* 2012; Turbill *et al.* 2012, 2013). Less controversial are the negative effects of torpor on immunocompetence. Since periodic arousals activate a dormant immune system, which can then combat pathogens (Prendergast *et al.* 2002; compare Canale & Henry 2011), it seems likely that an increased number of arousals may enhance immunocompetence during hibernation. Because body mass loss during hibernation was positively correlated with the number of arousals and a higher mean T_b during torpor, we conclude that animals with large fat depots can afford to minimize torpor use without jeopardizing their over-winter survival chances. This explanation is in line with the findings of

Humphries, Kramer & Thomas (2003a) that increased food stores (supplemental feeding) decreased the time chipmunks were torpid during the hibernation season. In our study, for every additional 10 g body mass gained prior to hibernation, the number of arousals increased by 1.1, total time spent euthermic increased by 7 h, and mean torpor bout duration decreased by 7.6 h. Since body mass prior to hibernation in the field can vary enormously among animals and years (adult animals 100–180 g, Lebl *et al.* 2010), the differences observed here are likely of biological relevance in terms of energy expenditure and minimizing the negative effects of torpor during hibernation.

BODY MASS, DURATION AND TIMING OF THE HIBERNATION SEASON

Interestingly, dormice did not use surplus body fat reserves to shorten the total duration of the hibernation season, in contrast to other species (e.g. Buck & Barnes 1999). Thus, even animals with higher energy reserves did not shorten the hibernation season, although environmental conditions almost certainly would have allowed this to happen (the latest emergence in the present study was 8 July). While our data show that dormice with higher body fat reserves arouse more frequently, the fact that high body fat reserves did not lead to a shorter hibernation season per se contradicts the hypothesis that hibernators should minimize the time spent torpid (Humphries, Kramer & Thomas 2003a). Apparently, factors other than energy saving and minimizing negative effects of torpor are involved in determining the duration of the hibernation season in dormice.

Arguably, the most probable explanation for the finding that even dormice with larger fat reserves do not shorten the hibernation duration is predator avoidance. We are aware that we cannot directly show the impact of predation on survival in this study, however, the support for this conclusion is manifold. For example, it could be shown that certain butterflies use estivation under otherwise benign environmental conditions to successfully evade 'predation' (i.e. infection by a parasitoid, Pörschmann & Spieth 2011). Moreover, in mammals, predation is known to be a major cause of mortality, especially in small mammals, and seems related to the amount of activity (e.g. Christe, Keller & Roulin 2006; Boon, Réale & Boutin 2008). In contrast, during hibernation, survival rates are extremely high (Schaub & Vaterlaus-Schlegel 2001; Bryant & Page 2005; Lebl *et al.* 2011a; Turbill, Bieber & Ruf 2011; Bieber *et al.* 2012), likely because of decreased exposure to predators (Lima 1998). At first glance, this may seem counter-intuitive, as torpid, sluggish animals should be particularly vulnerable to predation. Indeed, it has been shown that American badgers (*Taxidea taxus*), unlike European badgers, which feed on invertebrates and fruits, are very successful in digging up and depredating hibernating Richardson's ground squirrels (*Urocitellus richardsonii*, Michener 2004). However, a high risk of predation during hibernation seems to be the exception rather than the rule.

A recent comprehensive study on survival rates and longevity in hibernators (Turbill, Bieber & Ruf 2011) found that (i) most mammalian hibernators (93% of the populations investigated) survive the winter season significantly better than the active season, (ii) hibernators have an about 15% higher annual survival probability compared with similar sized nonhibernators, and (iii) small hibernating mammals have longer maximum life spans (50% greater for a 50 g species). Additionally, animals seem to benefit from the torpid state, in terms of predator avoidance, since they are motionless and emit minimal noise and body odour (Brown 1970).

In the case of the edible dormouse, the impact of hibernation on survival is particularly strong: Long-term mark-recapture studies found very high-winter survival rates (monthly survival >98%), determined in five free-ranging dormouse populations in Europe (Lebl *et al.* 2011a), indicating clearly that the impact of predation is negligible during the hibernation season. Additionally, in dormice high survival probabilities correlate with low recapture probabilities (Ruf *et al.* 2006). Thus, animals alive, but not recaptured (probably due to inactivity) survive significantly better than active individuals with high recapture rates.

Arguably, increased survival rates, as in dormice, have important consequences for life-history traits: Small hibernators have, on average, long maximum life spans and slower life histories (i.e. generation times), which are normally characteristic only for much larger nonhibernators (Turbill, Bieber & Ruf 2011). In fact, low extrinsic mortality (as caused by predation) is a major prerequisite for the evolution of mechanisms that might extend life in organisms (Kirkwood 2002; Ricklefs 2010). In other words, life-history theory predicts that animals with a high risk of predation should not invest into cellular repair mechanisms that delay senescence but instead invest into reproduction. Lower risk of mortality might therefore be interpreted as the key function for hibernators to evolve physiological adjustments that increase somatic maintenance and slow the processes of ageing during daily torpor and hibernation, as shown for Djungarian Hamsters (*Phodopus sungorus*, Turbill *et al.* 2012) and dormice (Turbill *et al.* 2013). Taken together, these facts underline that hibernation cannot be fully understood without considering its impact on survival probability beyond its role as energy saving mechanism.

We observed that females with higher body mass entered hibernation significantly earlier than leaner ones. Reaching sufficient body fat reserves likely facilitates the entry into hibernation. However, given the huge variation in body mass prior to hibernation in adult animals, we did not observe a 'body fat set point' (i.e. precisely regulated body mass levels prior to hibernation), as described for juvenile Belding's ground squirrels (Nunes, Muecke & Holekamp 2002). It seems that additional factors, such as food availability, climate, costs of foraging and decreased mobility (i.e. risk of predation), are likely to contribute to this decision in dormice.

BODY MASS AT EMERGENCE

Animals with high fat reserves prior to hibernation were also heavier in spring. Thus, dormice do not use all surplus fat reserves to minimize negative effects of torpor, but also save fat reserves for the upcoming active season. Also, free-ranging dormice showed a significantly higher body mass after emergence from hibernation following a mast year compared to emergence after a nonmast year (Fietz *et al.* 2005). In hibernators, these fat reserves are important for survival and reproduction during spring (e.g. Hackländer & Arnold 1999; Millesi *et al.* 1999; Karels *et al.* 2000). However, in dormice, the advantage of high fat stores in early summer appears to have two functions. Firstly, high-energy reserves allow earlier reproduction and thus optimal growth of the juveniles (Pilastro, Gomiero & Marin 1994). Secondly, in a year with mast failure of beech and/or oak (*Quercus* sp.) dormice do not reproduce (Bieber 1998; Schlund, Scharfe & Ganzhorn 2002; Fietz *et al.* 2005; Ruf *et al.* 2006; Bieber & Ruf 2009a). This skipping of reproduction does not depend on body mass or condition in spring (Bieber 1998; Pilastro, Tavecchia & Marin 2003), but fat stores may help to compensate for low food availability in years without mast. Thus, accumulated fat reserves from the previous autumn might facilitate summer dormancy (Bieber & Ruf 2009b) or an early entry into the next hibernation season.

LINOLEIC ACID AND HIBERNATION

Patterns of hibernation are not only affected by the quantity but also the quality of food. High values of linoleic acid in the WAT lowers minimum T_b , MR, and decreases the frequency of arousals in hibernators (e.g. Geiser & Kenagy 1987; Florant *et al.* 1993; Florant 1998). In 2008, we observed an extremely high content of linoleic acid in WAT (39.58%), during a beech mast year. Since beech seeds eaten during the prehibernation fattening period have a high content of linoleic acid (Fietz *et al.* 2005), the beech mast was likely responsible. However, the variation of linoleic acid content of WAT among years did not affect hibernation patterns significantly. Perhaps the amount of linoleic acid available for dormice was sufficient in all study years (lowest value 14.3%) and therefore did not affect torpor patterns unlike it does in herbivorous hibernators with limited access to linoleic acid (Geiser & Kenagy 1987; Ruf & Arnold 2008; Arnold *et al.* 2011).

AGE-CLASS AND HIBERNATION

Age-class contributed most to explaining the variation in termination of hibernation. Younger animals terminated hibernation significantly later than older animals, which is similar to other hibernators (e.g. Geiser & Kenagy 1987; Buck & Barnes 1999). Our data support earlier observations that age after the major growth period (after the second hibernation season) significantly influences duration and termination of

hibernation in dormice (Bieber & Ruf 2012). An age-dependent change in the trade-off between investment into current reproduction and future reproduction seems responsible for a shorter duration and earlier termination of hibernation in older animals (see also Bieber & Ruf 2012). Especially, in long-living species (up to 10 years in free-ranging dormice, J. Fietz, pers. comm.), younger adults (i.e. yearlings) should minimize the risk of predation and therefore increase survival probability by prolonging the hibernation season. Older adults, in contrast, should favour investment into reproduction (earlier termination of hibernation), since the opportunity for further reproduction is decreasing.

REPRODUCTION AND HIBERNATION

Reproduction was not important for explaining variation in any torpor variables (Table 1). We therefore rule out that the females investigated here suffered due to high reproductive output, independent from body mass. In contrast, we observed a weak positive effect of reproduction on the number of arousals. Yet, our sample might have been biased towards 'high quality' females, as we implanted only healthy females in a good body condition. In the field, however, we encountered females with low body mass and obviously depleted fat reserves after reproduction. Pathological examinations of dead females ($n = 5$) revealed a complete lack of WAT prior to hibernation. It seems therefore that some females invested all energy reserves into a last bout of reproduction and then died before hibernation.

Conclusions

In accordance with our hypothesis, our data show that dormice individually balance costs and benefits of torpor by partitioning their accumulated fat reserves into different pathways: (i) into maintaining a long-lasting hibernation season likely to minimize the risk of predation, (ii) into shallower and shorter torpor bouts and longer euthermic phases to avoid negative effects of torpor, and (iii) into larger fat stores at the beginning of the next active season probably to increase reproductive success or to facilitate summer dormancy. Although fat individuals showed an increase in euthermic phases during hibernation, they did not entirely avoid or shorten the hibernation season, even though the accumulated fat reserves would have allowed them to do so. Thus, our data suggest that hibernation should be seen as a flexible tool within life-history strategies and may not be fully understood as a response to energetic necessities due to harsh environmental conditions alone. Instead, it needs to be considered in context with other factors like predator avoidance as an important influence on patterns of hibernation and torpor in mammals. With regard to global climate change, our data indicate that climatic conditions alone may not be a good predictor for changes in hibernation patterns or survival in hibernating species.

Acknowledgements

We thank P. Steiger, K. Außerlechner, C. Skerget and K. Kürbisch, for their help with data collection and W. Zenker and F. Balfanz for implanting iButtons subcutaneously. This project was supported by the province of lower Austria, the city of Vienna, and the Austrian Science Fund (FWF, Projects 20534 and 25023). We declare that all experiments in this study comply with the current laws of Austria in which the study was performed (GZ 68.205/167-BrGT/2004, GZ 68.205/198-BrGT/2004, GZ 68.205/0041/II/10b/2008). We thank Mark Brigham and two anonymous reviewers for their useful comments.

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Received 25 February 2013; accepted 6 August 2013

Handling Editor: Craig Franklin