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SHORT COMMUNICATION

Summer dormancy in edible dormice (*Glis glis*) without energetic constraints

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Abstract Average longevity in free-living edible dormice (*Glis glis*) can reach 9 years, which is extremely high for a small rodent. This remarkable life span has been related to a peculiar life history strategy and the rarity of reproductive bouts in these seed eaters. Most females (96%) reproduce only once or twice in their lifetime, predominantly during years of mast seeding of, e.g., beech, but entire populations can skip reproduction in years of low seed availability. Surprisingly, in non-reproductive years, large fractions of populations apparently vanished and were never captured above ground. Therefore, we determined the duration of above-ground activity, and body temperature profiles in a subset of animals, of dormice under semi-natural conditions in outdoor enclosures. We found that non-reproductive dormice returned to dormancy in underground burrows throughout summer after active seasons as short as <2 weeks. Thus, animals spent up to >10 months per year in dormancy. This exceeds dormancy duration of any other mammal under natural conditions. Summer dormancy was not caused by energy constraints, as it occurred in animals in good condition, fed ad libitum and without climatic stress. We suggest that almost year-round torpor has evolved as a strategy to escape birds of prey, the major predators of this arboreal mammal. This unique predator-avoidance strategy clearly helps in explaining the unusually high longevity of dormice.

Keywords Aestivation · Hibernation · Torpor · Predation · Pulsed resources

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Introduction

Dormancy occurs in more than half of the mammalian orders in species that range from arctic ground squirrels to tropical primates (Geiser and Ruf 1995; Dausmann et al. 2004). However, mammals are generally thought to restrict torpid hypometabolic states such as hibernation [i.e., prolonged (>24 h) torpor in winter], aestivation or summer dormancy (prolonged torpor in summer) and daily torpor (<24 h) to times when environmental conditions are unfavourable for proficient foraging (e.g., Geiser and Ruf 1995; Webb and Skinner 1996). Typically, states of dormancy are restricted to cold or dry seasons and last, even in extremely harsh climates such as the Arctic, not more than approximately 8 months (Buck and Barnes 1999). Most previous reports on mammalian summer dormancy indicate that torpor occurred in response to adverse environmental conditions during periods of drought (Bartholomew and Hudson 1961; Kenagy and Bartholomew 1985; Dausmann et al. 2004) or, sporadically, in animals that fail to reproduce due to a poor body condition (Nicol and Andersen 2002; Nicol et al. 2004). Indeed, mammals are thought to minimise the duration of hypometabolic states whenever possible because it may be associated with costs such as reduced immunocompetence (Prendergast et al. 2002; Luis and Hudson 2006), neuronal damage (Arendt et al. 2003), cardiac dysfunction (Ruf and Arnold 2008), or impairment of memory (Millesi et al. 2001).

Edible (or fat) dormice (*Glis glis*) are hibernators closely adapted to the temporally limited availability of beechnut and acorn, their major food source in autumn in central and northern Europe (Bieber 1998; Schlund et al. 2002; Pilastro et al. 2003; Fietz et al. 2005; Ruf et al. 2006). In this distribution range, females give birth to a single litter per year only late in the summer season (July/August) and nurse young in early autumn when these energy-rich seeds are available (Bieber 1998; Schlund et al. 2002; Pilastro et al. 2003). However, whilst beech and oak can swamp seed eaters with overabundant food in mast seeding years, beechnuts and acorn can be rare or completely absent in years of seeding failure (Silvertown 1980; Ostfeld and Keesing 2000). Dormice have responded to this pulsed resource fluctuation by evolving a 'sit-and-wait' strategy of reproduction (Pilastro et al. 2003; Ruf et al. 2006). In years with low seed availability, large fractions or even entire populations of dormice can skip reproduction. In those years, dormice consume leaves, flowers and fruits (Fietz et al. 2005), which allow them to gain weight during summer but are insufficient to cover the additional costs of reproduction (Bieber 1998). In addition, in the absence of high-caloric seeds, the rapid fattening of juveniles within a small time window in fall, and hence their survival over the first hibernation season, seems impossible (Bieber and Ruf 2004).

Data from a long-term field study have demonstrated a strong trade-off between reproduction and future survival in dormice (Ruf et al. 2006). This at least partly explains why frequent reproduction skipping can lead to a mean longevity of up to 9 years in certain dormouse populations, which is extremely high for a ~150-g rodent (Pilastro et al. 2003). However, up to now, it remains unclear how dormice increase survival probability in years with lower food availability. Does the lack of investment in reproduction, and hence decreased metabolic stress, sufficiently explain for this phenomenon? Capture–recapture field studies revealed that dormice in mast failure years were captured over a shortened active season (Bieber 1998). Additionally, the probability to capture individuals at least once during the summer season in the field was significantly reduced (by ~45%) in years of low mast seeding and low reproduction (Ruf et al. 2006). Hence, parts of the population seemed to vanish during years of reproduction skipping, but were recaptured later in reproductive years. Further, in free-living male dormice, the occurrence of daily torpor (bouts <24 h) was found to significantly increase in years with reproduction skipping (Fietz et al. 2004). The aim of our study was to investigate whether reproduction skipping affects the use and extension of hibernation or other dormant states in dormice.

Materials and methods

All dormice (n=44, colony established in 1996) were held in mixed groups (age and sex) year-round in three outdoor enclosures (6×4×3.5 m each). The enclosures were located at 370 m a.s.l. in Vienna, Austria (48°10′ N, 16°20′ E). Mean air temperature at the enclosures during the study period (2005–2007) was 11.1°C (range, −7.4 to 31.2°C). The coldest month in our study site was January (mean maximum, 2.9°C; mean minimum, −2.0°C), the warmest July (mean maximum, 25.6°C; mean minimum, 15.4°C). iButtons (DS1922L, Maxim/Dallas) were used to record burrow temperature (15 cm below ground) and air temperature (shaded, 2 m above ground).

The outdoor enclosures were shaded and provided with branches. One nest box was available for each individual (positioned at heights of 1.2–2 m). However, we frequently observed two to six individuals sharing a single nest box. Food (rodent chow, Altromin 1314 FORTI), vitamins and water were available ad libitum. At the constantly good food supply, we observed in both years females which skipped reproduction whilst the others raised their litters successfully.

Animals were captured in their nest boxes once a week during their active season, and enclosures were searched carefully to assure that all dormice were captured. However, we cannot completely rule out that some dormice occasionally escaped our control. During weekly checks, body mass was recorded to the nearest 1.0 g. Whilst the animals occupied the offered nest boxes during the active season, all dormice exclusively used underground burrows dug by the animals for hibernation and summer dormancy. Comparisons between records of subcutaneous body temperatures and the nest box presence indicated that the median time interval between termination of hibernation and occurrence in the nest boxes above ground was 6 days (range, 0–28 days; interquartile range, 4–11 days). Thus, active animals were detected rapidly above ground.

Wax-coated iButtons (DS1922L, Maxim/Dallas) were implanted for measurements of subcutaneous temperature in the lateral area of the thorax, caudal of the scapula in 23 dormice (18 males, 15 females). Anesthesia for implantation was introduced with 4 mg ketamine + 0.8 mg xylazine and maintained with inhalation anesthesia (isoflurane in oxygen). At the date of implantation, animals weighed on average 153±30 g. Implanted dormice were released 1 week after implantation to their groups in the outdoor enclosures. Subcutaneous temperature was recorded at approximately hourly (3,650 s) intervals to cover 1 year. Implantation (and start of iButtons) was carried out between June and August 2005, explantation and new implantation/replacement of loggers between May and August 2006. Ten out of 23 dormice were implanted in the two subsequent years (resulting in 33 datasets). Since our study was planned to be terminated after hibernation 2006/2007, we explanted most iButtons immediately after emergence from hibernation in May–June 2007. However, three dormice of our colony unexpectedly retreated again into their underground burrows before we were able to retrieve the iButtons. In these three dormice, we explanted the iButtons later, in August 2007.

Arousal and torpor duration were determined from the times spent above and below a subcutaneous temperature of 25°C, respectively. We calculated body mass loss during dormancy only for animals that were weighed within 6 days after termination of hibernation.

Statistical analyses, i.e., linear models with subsequent ANOVA, linear mixed models with a random factor "animal" for repeated measurements, and generalised linear models (GLM), were carried out in R (R Development Core Team 2007) partly using the package "nlme" (Pinheiro et al. 2007). The tests used are specified in the text. Means are given ±SEM.

Results

In fall of both years, all implanted animals (n=23) retreated to their burrows and entered hibernation for approximately 8 months (mean duration, 234.41±4.58 days, n=33) from September/October to May/June. Whilst we found no evidence for summer dormancy in 2006 (Fig. 1a), T_b profiles of those three animals (two females, one male) recorded until August 2007 revealed that 2–4 weeks after hibernation, they reentered dormancy during summer for up to 4 months (Fig. 1b). Another eight non-implanted individuals of our colony showed long phases of absence from above ground (i.e., from nest boxes or elsewhere in the enclosures) in summer 2007 (for periods of 49 to 157 days between early April and late August; Fig. 2). These animals lost body mass at rates (0.69±0.12 g day^{-1}) similar to those of the three animals in which summer dormancy was directly recorded in the same year (0.83± 0.24 g day^{-1}; ANOVA, $F_{1,9}$=0.305, P=0.594). In contrast, active (not summer-dormant) dormice were captured regularly (every 7–21 days) and showed a mean increase in body mass of 0.87±0.11 g day^{-1} during the active season. Together, these data suggest that 11 animals (five females, six males, 25% of the colony) used prolonged dormancy during summer 2007, and, as during hibernation in this species (von Vietinghoff-Riesch 1960), solely relied on body fat reserves to fuel energy demands during these periods. This conclusion was further supported by the fact that we never found any food or food remnants in the hibernacula. Following phases of summer dormancy, eight out of the 11 dormice (three animals were dug up from their burrows) emerged again in autumn. All animals dug up from their burrows, including one non-implanted individual, felt cold to the touch and were clearly torpid. Subsequently, some showed a brief period of pre-hibernation fattening (Fig. 2) before they entered hibernation in September/ October 2008.

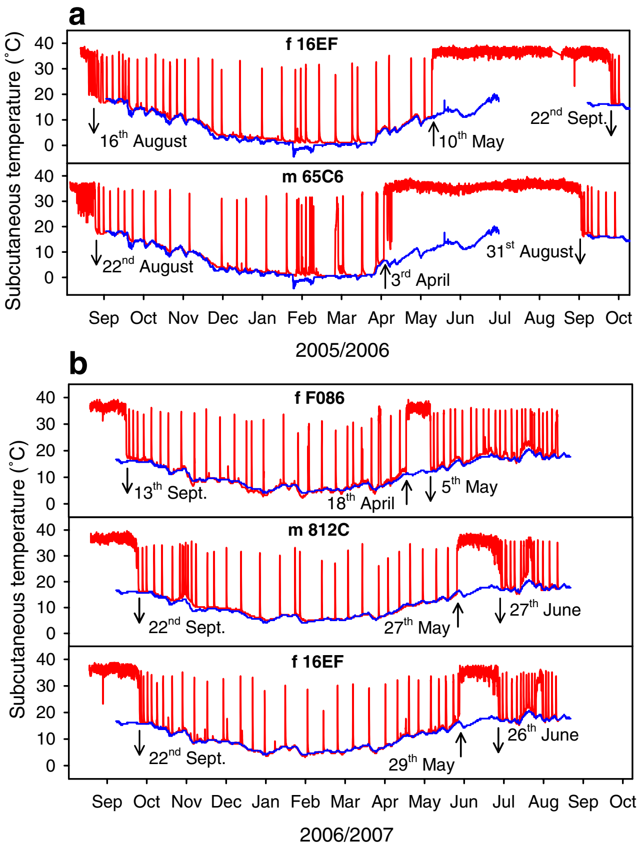

Fig. 1 Year-round records of subcutaneous body temperature in **a** 2005/2006 for two dormice with normal temperature pattern during active season (animals were sexually active) and **b** 2006/2007 for three individuals with an extremely shortened active season after hibernation (animals were sexually inactive). All three animals entered a state of dormancy long before the expected onset of hibernation under natural climatic conditions with food provided ad libitum. *Arrows* indicate the date of emergence and immergence into natural hibernacula, dug by the animals. *f* female, *m* male. *Red* (*grey*) *line* = body temperature, *blue (black) line* = ambient temperature recorded in an artificial burrow. Please note that all three animals were recaptured alive after the hibernation season in 2007/2008. Thus, they spent approximately 19 out of the last 21 months in dormancy below ground

All of the five females among the 11 summer-dormant animals did not reproduce in 2007. However, reproductive activity was certainly not the only decisive factor for summer dormancy, since 54% of those females that were regularly encountered in nest boxes during summer 2007 also failed to reproduce. Further, in the previous year (2006), only two out of 16 adult females had young, but activity and T_b records gave no evidence for summer dormancy in either females or males.

Importantly, all animals that entered summer dormancy did so in good body condition and in the presence of energy-rich food. In spring of 2007, the mean body weight of dormice after emergence was even significantly higher than in the previous year (2005/2006, 131±6 g; 2006/2007, 159±8 g, ANOVA, $F_{1,23}$=6.83, P=0.015). Also, body mass

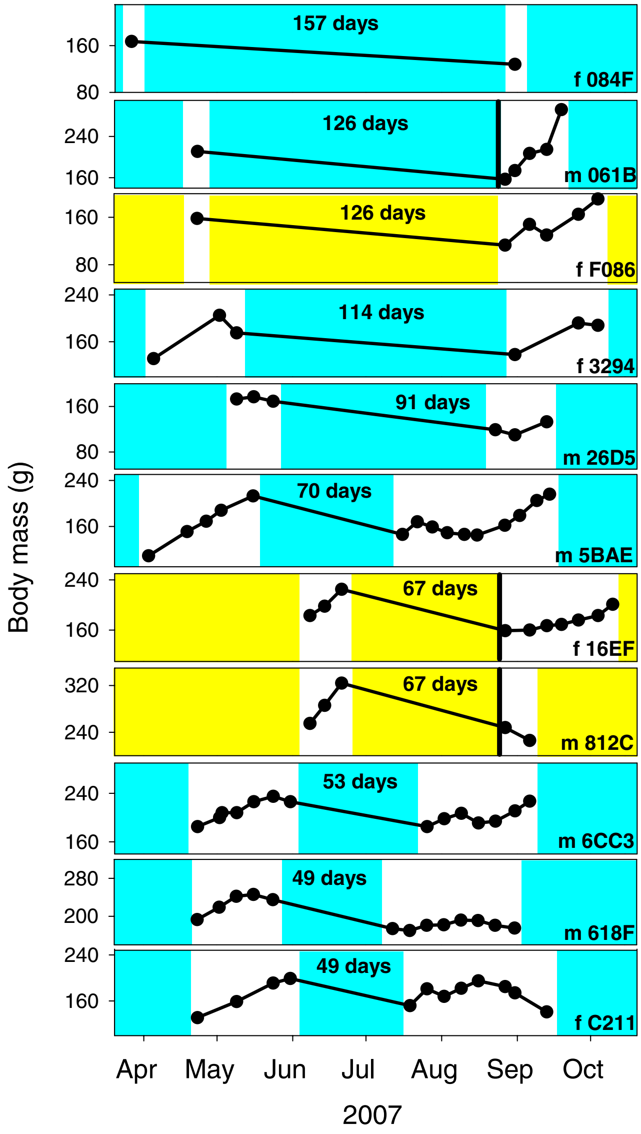

Fig. 2 Body mass change in edible dormice showing summer dormancy in 2007. Prolonged periods of summer dormancy (i.e., absence from above ground for at least 7 weeks accompanied by body mass loss) were observed in 11 animals. Whilst the animals occupied offered nest boxes during the active season, all dormice used exclusively earth holes dug by the animals for hibernation and summer dormancy. *Coloured* (*grey*) *areas* show periods of presumed dormancy; animals with T_b records available (Fig. 1) are shown in *yellow* (*light grey*). *White areas* indicate periods of activity above ground. *Vertical black lines* indicate cases in which we dug up torpid animals from their burrows

after emergence was not a significant predictor of whether or not an individual would enter summer dormancy (GLM, family 'binomial', P=0.198) or of the total duration of the time spent dormant (range, 49–157 days, GLM on log-transformed data, family 'Poisson', P=0.671).

As during hibernation, T_b alternated during summer dormancy between bouts of torpor lasting several hours to 6.8 days and intermittent brief periods of arousal to normothermia (Fig. 3). Dormice displayed torpor at burrow temperatures ranging between –4.6°C in winter and 20.2°C in summer and with minimum T_bs varying between 0.6°C and 21.2°C (arousal temperatures not considered). Pooling torpor bouts from summer dormancy and hibernation, we found that arousal duration increased and torpor bout duration decreased as burrow temperature increased (Fig. 3). However, adding a factor "season" to a repeated measurements regression (linear mixed effects) did not improve the model, but caused slight increases in AICs in both cases (from 577.9 to 579.6 for arousal duration and from 1634.7 to 1635.9 for torpor bout duration). Body mass loss during summer dormancy was significantly higher (0.73 ± 0.10 g day^{-1}, n=11) than during the two preceding hibernation seasons (0.29 ± 0.03 g day^{-1}, n=14; ANOVA, $F_{1,23}$=20.07, P<0.001).

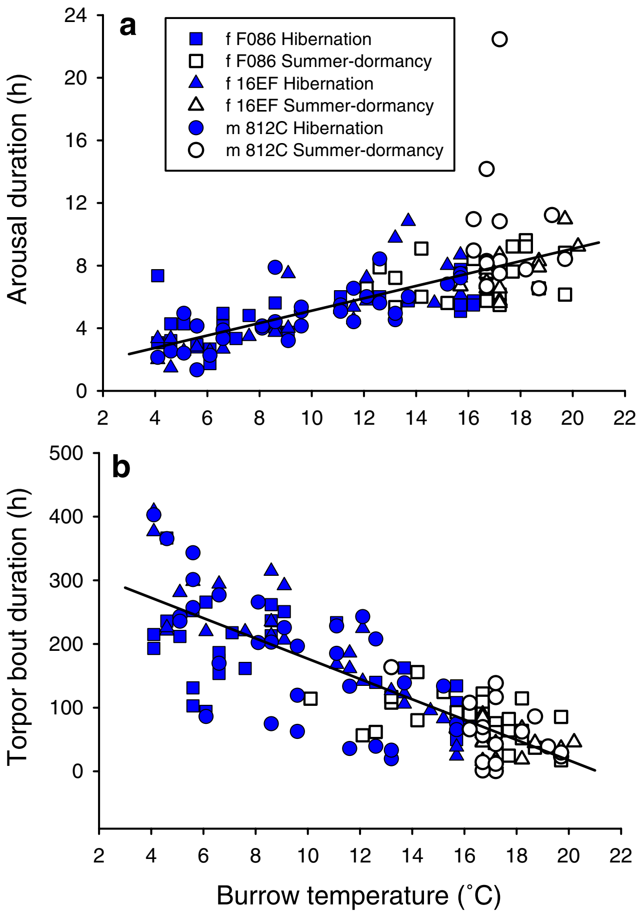

Fig. 3 Relation between dormancy pattern and burrow temperatures. **a** Relation between arousal duration and burrow temperature (duration= $1.32+0.374\times T_a$, R^2=0.60). **b** Relation between torpor bout duration and burrow temperature (duration=$336.20-15.94\times T_a$, R^2=0.66). Arousal and torpor duration were determined from the times spent above and below a subcutaneous temperature of 25°C, respectively. There was no evidence for a difference in these relations between hibernation (*closed symbols*) and summer dormancy (*open symbols*)

Discussion

There are two characteristics of our observations that differ from previous reports on summer dormancy in other mammals: First, dormice entered summer dormancy in good body condition and in the presence of abundant food with an energy content that would have allowed them to rapidly gain weight. Second, summer dormancy in dormice showed a temporal pattern that differs from typical summer dormancy, i.e., aestivation. In desert rodents, aestivation appears to actually represent an early onset of hibernation after much longer periods of activity (Kenagy and Bartholomew 1985) than in the summer-dormant animals observed here. In contrast, dormice showing summer dormancy emerged again in autumn, and most of them showed a brief period of pre-hibernation fattening. Also, periods of continuous summer dormancy in dormice were much longer (up to 4–5 months, Figs. 1 and 2) and more regular than occasional episodes of prolonged torpor during summer in echidnas (a few days, Nicol et al. 2004) or of brief bouts of torpor in other mammals, e.g., bats (4–5 h, Turbill et al. 2003).

However, whilst the pattern and characteristics of summer dormancy in dormice seems highly unusual, our data support the view that hypometabolic states during summer and winter dormancy are regulated by the same physiological mechanisms (i.e., cooling rates and rates of metabolic depression during entrance into the torpid state are identical, Wilz and Heldmaier 2000; see also Bartholomew and Hudson 1961). As in other hibernators (French 1982, 1985), arousal duration increased and torpor bout duration decreased as burrow temperatures increased. Importantly, there was no indication for different slopes or elevations of the relation between torpor and arousal duration to ambient temperature between summer and winter. The relation between burrow temperature and frequency of arousals, the most energy-consuming processes during hibernation, explains why dormice lost body mass at significantly higher rates during summer dormancy than during hibernation. Also, summer dormancy was performed at a level of body temperatures which incurs higher energetic costs (e.g., Wilz and Heldmaier 2000).

Our current data give reason to suggest that previous observations of the disappearance of free-living non-reproductive dormice during summer (Ruf et al. 2006) may indicate their return to dormancy in underground burrows. Summer dormancy in dormice is clearly linked to their adaptation to strongly pulsed resources with the associated skipping of reproduction in years with low tree seeding (Ruf et al. 2006). Apparently, dormice employ a unique ‘sit-and-wait’ tactic with long phases of dormancy below ground, which may have evolved as a strategy to maximise survival. However, our observation of a number of reproductively quiescent animals that did not use summer dormancy but remained active above ground in both study years indicates that reproduction skipping alone, whilst it may be a prerequisite, does not directly trigger summer dormancy. Therefore, it remains to be clarified which other factors elicit this strategy in certain years and individuals.

We suggest that the main function of summer dormancy in dormice is predator avoidance. Retreating to underground burrows entirely protects arboreal and nocturnal dormice from their main predators, i.e., nocturnal birds of prey such as owls (von Vietinghoff-Riesch 1960), which should significantly contribute to the extremely high longevity of free-living dormice (Ruf et al. 2006). We can only speculate that dormice may asses the density of predators, e.g., by perceiving an increased number of owl calls (possibly leading to increased stress levels), which could act as a proximate factor causing dormice to retreat and employ summer dormancy. Extrinsic mortality (e.g., predation) is thought to be one of the main factors influencing the evolution of senescence and longevity (Williams 1957; Kirkwood 2002; Wilkinson and South 2002; Williams et al. 2006). The extremely high longevity in many bats, for example, has been related to two factors that lower the risk of predation: (1) the ability to fly and (2) hibernation (e.g., Brunet-Rossini and Austad 2004). In years of reproduction skipping, which typically follow years of full mast seeding (Ruf et al. 2006), predation pressure is particularly high in dormice. This is because the density of predators (e.g., birds of prey) increases following the resource pulse of increased prey abundance such as seed-eating mice (Schmidt and Ostfeld 2008). In dormice, this pattern of pulsed resource cascades should further enhance the benefits of predator avoidance by remaining below ground in years of low food abundance, which typically follow a full masting event. Decreased predation risk was also thought to explain previous findings of a higher survival probability over the hibernation season than over the active season in the closely related garden dormouse (Schaub and Vaterlaus-Schlegel 2001). Future studies focusing on the influence of predator density on the performance of summer dormancy and hibernation duration are needed to clarify this hypothesis. However, survival may be additionally enhanced by prolonged hypometabolism as such, as there is evidence for an association between the use of hibernation and increased longevity (e.g., Lyman et al. 1981; Wilkinson and South 2002).

At least in some individuals, the combination of hibernation and summer dormancy in dormice can sum up to a total time of hypometabolism of >10 months per year (see Fig. 1 animal f F086) during which no food is consumed. Similar (or even slightly longer) yearly times spent in prolonged torpor have been observed only in hibernators placed in cold rooms (Mrosovsky 1977) in the laboratory and/or following the complete removal of food (French 1985; Geiser 2007). Irrespective of whether or not summer dormancy in dormice indeed primarily serves to avoid predators, in our experiments, it was clearly not caused by poor body condition or climatic stress. Thus, its adaptive value seems unrelated to energetic constraints. Therefore, our findings question the common view of torpor as a 'last resort' strategy that should be employed only under conditions of negative energy balance (Humphries et al. 2003).

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