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Seasonal differences in the feeding ecology and behavior of male edible dormice (*Glis glis*)

Michaela M. Sailer, Joanna Fietz*

Institute of Experimental Ecology, University of Ulm, Germany

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Abstract

Mammalian hibernators undergo dramatic seasonal changes of food intake and the use of their gastrointestinal tract. During several months of hibernation fat-storing hibernators do not use their intestinal tract for nutritional intake. However, during the rest of the year they have to increase their energy intake in order to compensate high reproductive investment and store sufficient body fat to survive the following hibernation period. Edible dormice (*Glis glis*) are obligate fat-storing hibernators which hibernate in Germany from September until June. Males incur high energetic costs during mating and as soon as reproduction is terminated they have to accumulate high quantities of fat to survive hibernation. In order to understand how fat-storing hibernators like edible dormice cope with these energetically demanding situations, we measured body mass changes of captured male edible dormice in the field and studied their feeding ecology. Furthermore, we measured seasonal changes in food ingestion and assimilation rates by feeding experiments carried out in captivity.

Results of this study revealed that during the mating season males significantly lowered their body mass, while food ingestion and assimilation rates remained constant. The body mass reduction showed that they used their body fat reserves to pay at least part of the energetic costs of reproduction. During the pre-hibernation fattening period males increased their body mass but held their assimilation rates on a constant level. Nevertheless, they increased the amount of ingested food and subsequently the amount of energy intake. Furthermore, they changed their dietary spectrum in the field by turning to lipid-rich seeds. These behavioral adaptations enable them to restore their energy losses during reproduction and to accumulate sufficient body fat to survive hibernation.

Keywords: *Glis glis*; Assimilation efficiency; Body mass; Feeding ecology; Hibernation

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Introduction

During the European winter ambient temperature is low and food availability for herbivores is reduced. In order to cope with or evade energetically unfavorable environmental conditions animals show a variety of different physiological and behavioral adaptations such as diet switching, migration, fasting tolerance, as well as entering hibernation (Lyman et al. 1982; Vogt and Lynch 1982; Totzke et al. 2000; Ganzhorn et al. 2003; Heldmaier and Neuweiler 2004). During hibernation body temperature and metabolic rate are reduced to a fraction of the normothermic values (Lyman et al. 1982; Heldmaier and Ruf 1992). While food-storing hibernators such as chipmunks (*Tamias* sp.) and the European hamster (*Cricetus cricetus*) rely mainly on cached food

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*Corresponding author. Tel.: +49 731 5022668; fax: +49 731 5022683.
E-mail address: Joanna.Fietz@uni-ulm.de (J. Fietz).

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during winter, fat-storing hibernators stop feeding during hibernation season and rely entirely on the products of lipid hydrolysis obtained from the white adipose tissue as an energy source (Lyman et al. 1982; Carey 2005). Members of the latter group, which includes rodents like ground squirrels (*Spermophilus* sp.), marmots (*Marmota* sp.) and edible dormice (*Glis glis*), are therefore much longer in a fasted state than any non-hibernating mammal species (Carey 2005). In most mammalian species, intestine is energetically very costly and assumed to be responsible for 25% of whole body oxygen consumption (Cant et al. 1996). Due to these high energetic costs the intestine should be reduced if not used in order to conserve energy (Piersma and Lindström 1997; Hume et al. 2002). And indeed, hibernation was shown to have profound effects on the structure of the gastrointestinal tract (Carey 1992; Hume et al. 2002). Alpine marmots (*Marmota marmota*) as well as 13-lined ground squirrels (*Spermophilus tridecemlineatus*) reduce their intestine in size and activity during hibernation. This size reduction comprise about 50–75% of peak values in midsummer (Carey 1990; Carey 1992; Stevens and Hume 1995; Hume et al. 2002). After hibernation is terminated the gastrointestinal tract enlarges again (Carey 1992) and in marmots (*M. marmota*) it was shown, that this enlargement is a response to food intake at the beginning of the activity period in spring (Hume et al. 2002). This reduction of the intestinal tract prior to hibernation can be assumed to profoundly affect the digestive functioning directly after emergence from hibernation in spring.

With the exception of bats, hibernators mate and reproduce at the beginning of their activity period in spring, when food is still limited (Lyman et al. 1982; Millesi et al. 2000). In mammals, reproduction is energetically extremely costly especially for females due to gestation and lactation (Clutton-Brock and Harvey 1978; Clutton-Brock et al. 1989). But as well mammalian males may incur high costs during their reproductive period (Clutton-Brock et al. 1979; Jönsson et al. 1998; Wolff 1998; McElligot et al. 2003; Fietz et al. 2004). After this energetically expensive period of reproduction fat-storing hibernators have to deposit enormous quantities of body fat to survive the following hibernation period. This pre-hibernation fattening period is usually restricted to a tight timeframe directly before the onset of hibernation. Thus, mammalian hibernators undergo dramatic seasonal changes of energy demands, food intake and use of the gastrointestinal tract (Carey 2005). Fat-storing hibernators are therefore excellent examples for mammals that shift between the use and disuse of the intestine (Carey 2005) and the ecological implications of these seasonal variations.

In order to ensure sufficient energy and nutrition intake during energy demanding periods, hibernators as well as non-hibernating species can simply increase their food consumption (Millar 1979; Petter-Rousseaux and Hladik 1980; Bairlein 1985; Bairlein 1987; Pereira 1993; Pereira et al. 1999; Speakman et al. 2001) or switch their diet (Simons and Bairlein 1990; Ganzhorn et al. 2003). Nevertheless, some species were shown to change the morphology and physiology of their gastrointestinal tract maximizing their assimilation efficiency, which is partially determined by intestinal surface (Gross et al. 1985; Weiner 1987; Starck 2005). This enables them to compensate for elevated energetic costs, while the food intake may stay constant. In some species like in Djungarian hamsters (*Phodopus sungorus*), it was demonstrated that food assimilation rates are maximized by acclimation to low ambient temperatures (Weiner 1987; Starck 2005).

Edible dormice are nocturnal rodents with an arboreal life style occurring in deciduous forests in middle and southern Europe. They belong to the group of obligate fat-storing hibernators (Vietinghoff-Riesch 1960) and in Germany they hibernate from September until June in burrows 50–100 cm underground (Morris and Hoodless 1992). During their active period, they use tree holes and nest boxes for sleeping and raising their offspring. As typical in solitary hibernation species, females emerge from hibernation 2–3 weeks after their males. They mate during July and after approximately 30 days 5–7 (up to 11) juveniles are born (Vietinghoff-Riesch 1960; Schlund 2005). In Germany females give birth to only one litter each year, which is weaned after 30 days (Vietinghoff-Riesch 1960; Schlund 2005). At the beginning of their active period, they feed fleshy fruits, leaves and sprouts but also eat small amounts of arthropods (Gigirey and Rey 1999; Fietz et al. 2005), while their diet consists mainly of fatty fruits and seeds like beechnuts and acorns before re-entering hibernation (Gigirey and Rey 1999; Fietz et al. 2005). Shortly before the onset of hibernation in September, they increase their body mass by 80–100% to 180–200 g (Fietz et al. 2005). Edible dormice show unusual strong fluctuations of reproductive output between years, which are synchronized with the masting pattern of beech/oaks trees (*Fagus sylvatica*/*Quercus* sp. L.; Pilastro et al. 2003; Ruf et al. 2006) and feed mainly on beech and oak seeds during reproduction and pre-hibernation fattening (Bieber and Ruf 2004; Fietz et al. 2005). During the reproductive period male as well as female dormice have high energetic costs. While females invest energy primarily in gestation and lactation (Kager 2004; Zoufal 2005), Jallageas and Assenmacher (1983) showed that high testosterone values of the blood plasma in males inhibit the occurrence of daily torpor, which enables them to potentially conserve as much as 20–80% of their energetic requirements (Wilz and Heldmaier 2000). Even though the effect of hormones on torpor ability in females has not yet been studied in detail, field data