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ORIGINAL PAPER

Behavioural and physiological consequences of male reproductive trade-offs in edible dormice (*Glis glis*)

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Abstract Testosterone mediates male reproductive trade-offs in vertebrates including mammals. In male edible dormice (*Glis glis*), reproductivity linked to high levels of testosterone reduces their ability to express torpor, which may be expected to dramatically increase thermoregulatory costs. Aims of this study were therefore to analyse behavioural and physiological consequences of reproductive activity in male edible dormice under ecologically and evolutionary relevant conditions in the field. As we frequently encountered sleeping groups in the field, we hypothesized that social thermoregulation should be an important measure to reduce energy expenditure especially in sexually active male edible dormice. Our results revealed that the occurrence of sleeping groups was negatively influenced by male body mass but not by reproductive status or ambient temperature. In reproductive as in non-reproductive males, the number of individuals huddling together was negatively influenced by their body mass. Thus in general males with a high body mass were sitting in smaller groups than males with a low body mass. However, in reproductive males group size was further negatively affected by ambient temperature and positively by testes size. Thus breeders formed larger sleeping groups at lower ambient temperatures and males with larger testes were found in larger groups than males with smaller testes. Measurements of oxygen consumption demonstrated that grouping behaviour represents an efficient strategy to reduce energy expenditure in edible dormice as it reduced energy requirements by almost 40%. In summary, results of this field study showcase how sexually active male edible dormice may, through behavioural adjustment, counterbalance high thermoregulatory costs associated with reproductive activity.

Keywords Oxygen consumption · Social thermoregulation · Reproduction small mammal

Introduction

Testosterone mediates male reproductive trade-offs in mammals and other vertebrates (Galeotti et al. 1997; Garamszegi et al. 2005; Hau 2007; Fusani 2008). While testosterone may increase male reproductive success by promoting courtship, aggression, sexual behaviour, and sperm production, it has also disadvantageous affects by suppressing immunocompetence and paternal care, and by increasing metabolic rate and body mass loss (Feuerbacher and Prinzinger 1981; Wingfield et al. 1990; Zielinski and Vandenbergh 1993; Buchanan et al. 2001; Place 2000; Hume and Wynne-Edwards 2005; Soma 2006; Hau 2007; Peters 2007).

Interestingly, several studies in small mammals have demonstrated that testosterone also influences their ability to enter torpor or hibernation (*Cricetus cricetus*: Darrow et al. 1988; *Spermophilus lateralis*: Lee et al. 1990; *Phodopus sungorus*: Ouarour et al. 1991; *Spermophilus parryii*:

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Hochstetler and Barnes 1993; *Saccostomus campestris*: Mzilikazi and Lovegrove 2002; *Glis glis*: Jallageas and Assenmacher 1983, 1984). Torpor represents the most efficient physiological adaptation of small mammals and birds to facultatively reduce energy expenditure during environmentally unfavourable conditions (Geiser and Ruf 1995; Heldmaier and Neuweiler 2004; Namekata and Geiser 2009). It is characterized by a substantial drop of metabolic rate and body temperature, by which energy requirements may be reduced by more than 95% of normothermic values (Heldmaier and Ruf 1992; Geiser and Ruf 1995; Heldmaier and Elvert 2004; Namekata and Geiser 2009). However, in males of some species the incidence of torpor decreases with increasing levels of testosterone. Thus, high levels of testosterone are linked to a reduced ability to express torpor with the consequence that reproductively active males may therefore have to maintain high and energetically costly levels of body temperature (T_b; Jallageas and Assenmacher 1983; 1984; Darrow et al. 1988; Lee et al. 1990; Ouarour et al. 1991; Mzilikazi and Lovegrove 2002). Hence, the effect of testosterone on the ability to use torpor can therefore have tremendous fitness-relevant consequences for the energy budget of an organism, especially since normothermic thermoregulation is one of the most costly physiological processes (Schmidt-Nielsen 1983; Heldmaier and Neuweiler 2004).

A limited range of options is available to animals to reduce thermoregulatory costs other than through entering torpor. Behavioural adaptations such as nest building and social thermoregulation (Vogt and Lynch 1982; Hayes et al. 1992; Boix-Hinzen and Lovegrove 1998; Perret 1998; Willis and Brigham 2007) are seen as key components for thermoregulation in small endotherms, where huddling individuals reduce their thermoregulatory costs due to a reduction of the collective surface exposed to the environment and by local heating (Hayes et al. 1992).

The edible dormouse (*G. glis*) is an obligate hibernator that also enters torpor during environmentally unfavourable conditions in spring and summer. Like in some other small mammals, this capacity is reduced in sexually active males with high circulating blood plasma levels of testosterone (Jallageas and Assenmacher 1983, 1984). Accordingly, breeders were shown to maintain T_b above 30°C, while non-breeders in the field had significantly lower T_b and entered torpor more frequently (Fietz et al. 2004). In breeders, T_b fluctuated diurnally between 37° and 30° which suggests that they may try to lower their T_b as much as possible to reduce thermoregulatory demands while maintaining a low normothermic T_b (Fietz et al. 2004). Furthermore, in comparison to non-breeders, reproducing edible dormouse males showed a severe decrease in body mass during mating season which can be attributed to higher thermoregulatory costs, energy consuming mating activities connected with less time spent foraging, and had a lower chance of survival in the following winter (Fietz et al. 2004; Ruf et al. 2006; Fietz et al. 2009). Thus reproducing edible dormice are in a negative energy balance which seems to decrease their chance to survive. As we frequently encountered in our field studies nest boxes with males sleeping in groups containing up to 13 individuals and these males were to more than 99% euthermic (two out of 277 groups; Fietz unpubl. data), we hypothesized that social thermoregulation might represent an efficient strategy to reduce energy expenditure for breeding males which may be unable to enter torpor.

Aims of this study were therefore to analyse behavioural and physiological consequences of reproductive activity in male edible dormice under ecologically and evolutionarily relevant conditions in the field. As testes are regarded as the major sources of androgens (Denk and Kempenaers 2006; Hau 2007), and Jallageas and Assenmacher (1983) showed a clear annual cycle of plasma testosterone levels in edible dormice which coincide with their annual testes development (Fietz et al. 2004), we assumed testes sizes to be positively linked to levels of testosterone in the blood plasma.

Based on previous observations in the field, we hypothesized that especially sexually active male edible dormice should use social thermoregulation to counteract high thermoregulatory costs, caused by their reduced ability to enter torpor. We therefore expected reproductive males to form sleeping groups depending on their energy reserves (body mass), reproductivity (testes size) and ambient temperature (T_a). To further evaluate the efficiency of social thermoregulation we measured oxygen consumption of euthermic individual males in the field sitting alone and in groups and compared their energy expenditure.

Materials and methods

Species

The edible dormouse (*G. glis*) is an obligate hibernator and occurs preferentially in deciduous mixed forests dominated by European beech (*Fagus sylvatica*; Schlund et al. 1997; Schlund 2005). They feed predominantly on beech nuts during offspring raising and pre-hibernation fattening but also consume leaves, buds, and fruits (Storch 1978; Fietz et al. 2005). In Germany, adult edible dormice hibernate for 7–8 months from September/October until May/June and have only one litter per year. Mating takes place at the end of June and in July. The proportion of reproductively active males depends on food availability of a certain year. In years with intermediate food availability, breeders as well as non-breeders occur during the same time, whereas in years with low food availability all males might remain sexually quiescent and completely skip reproduction (Bieber 1998; Schlund et al. 2002; Ruf et al. 2006; Fietz et al. 2009). Similar to most other hibernators (e.g., Christian et al. 1972; Darrow et al. 1988; Lee et al. 1990; Place and Kenagy 2000) males regress their testes before the onset of hibernation and retreat them into their abdomen (Jallageas and Assenmacher 1983; Fietz et al. 2004). Consequently, male edible dormice emerge from hibernation with regressed gonads. In reproductive years testes descend and increase in size after emergence from hibernation, reaching their maximal volume during the mating season in July (Fietz et al. 2004).

Study sites

This study was conducted at two sites located in Southwestern Germany. The study area "Hohenentringen"comprises a mixed deciduous forest of 12 ha with 128 nest boxes (for details see Schlund et al. 1997), situated on the southern rim of the "Schönbuch" Nature Reserve (48°33′N, 8°59′E). The second study site is within the Botanical Garden of the University of Ulm (48°25′N, 9°57′E). It is about 6 ha in size, contains 70 nest boxes and is covered by mixed deciduous forest. A grid system with 30×30 m squares was established at both study areas and nest boxes were installed at the intersections of the grid lines. Each nest box was mounted to a tree at a height of approximately 3 m aboveground. Nest boxes are used frequently by dormice and provide easy access to the animals for research. Minimal and maximal ambient temperature (T_{amin} and T_{amax}) were automatically recorded with dataloggers (DS 1921L, resolution: 0.5°C; Thermochron iButtons, Dallas semiconductor, Dallas, USA) on a daily basis at both study sites.

Individual marking and morphological measurements

We performed weekly checks of nest boxes from June to October during daytime in both study areas (Hohenentringen 2003–2007, Botanical Garden in Ulm 2007). Upon first capture, we marked individuals by subdermal injection of transponders (Trovan, EURO I.D. Usling, Weilerswist, Germany) that carried unique identification numbers. We recorded sex and assessed body mass for each capture to the nearest gram using a 300 g spring balance (Pesola, Baar, Switzerland; division: 2 g, accuracy: 99.7%). In males, testes lengths of the right testis were measured to the nearest mm using callipers. Males with palpable testes at the time of capture were categorized as sexually active or breeders, those without as sexually quiescent or non-breeders. At the end of the procedure, animals were returned to their nest boxes. By definition, individuals that had overwintered at least 2 years were classified as adults and as yearlings if they had overwintered only once. Adults and subadults were discriminated by their body size and the colour of their fur (Schlund 1997).

Oxygen consumption

Oxygen consumption was measured in 2004 and 2006 in Hohenentringen and in 2007 in the Botanical Garden of Ulm University. Measurements of oxygen consumption were always carried out between June and July during the daytime for at least 6 h. Metabolic rate was measured as rate of oxygen consumption (VO2) per individual or group (between two and seven individuals) and was recorded continuously using a portable 2 channel gas analyser (oxbox; designed and constructed by Thomas Ruf, Research Institute of Wildlife Ecology, Vienna; for further information see Schmid et al. 2000) with chemo-electric sensors (Bieler and Lang, Achern, Germany; accuracy <0.02 vol.%). Oxygen sensors were calibrated directly before the field measurements in the laboratory using a calibration gas (Linde Gas GmbH). The VO2 of individuals and groups was measured by using their nest box (3SV; Schwegler; Schorndorf; vol. 1.5 l) as a metabolic chamber. The entrance of the nest box (diameter 34 mm) served as air inlet. Small crevices between the lid of the nest box and the nest box itself were sealed beforehand with plasticine to avoid gas diffusion during measurements of oxygen consumption. Gas was sampled from the side opposite to the entrance by inserting a gastight tube (diameter: 20 mm) between the lid and the nest box.

This gastight tube was connected to the analyser system, which was powered by a car battery (12 V). During the experiments air flow through the chamber was controlled at about 100 l/h. Air was filtered and dried with silica gel (volume: 500 ml) prior to analysis. Flow rate of dry air was measured by a thermal mass flow meter based on the heat transfer property of air, through measuring the temperature difference before and after passing a heated tube. Oxygen consumption was calculated as described previously (Heldmaier and Ruf 1992). In addition, T_{a} was measured to the nearest 0.1°C by a copper-constantan thermocouple located near the animals' sleeping corner at middle height in the nest box. T_{a} in the chamber, the output of the flow meter, the oxygen sensor cell, and voltages of the power supply were stored on a datalogger (Hobo) at 1-min intervals and transferred to a laptop each day. To control for any drift of the oxygen sensor, reference air from the outside was analysed for 5 min each hour to obtain a zero reading of O_2 in reference air at hourly intervals. The entire set-up except the car batteries was housed in a weather proof aluminium box (Zarges, 60×40×24 cm). The box was thermally insulated from the inside to improve temperature stability and was opened only to retrieve the data.

We defined the lowest measured 10 min moving averages as resting metabolic rates (RMR). Subsequently, RMR was divided it by the total body mass (in grams) from all individuals (between two and seven) located within the respective nest box to achieve mass-specific RMR. Dormice in our study were removed from the nest box, weighed with spring balance and returned into the nest box immediately (5–10 min) before the measurement started. After measurements were finished, we checked whether the same individuals were still within the nest boxes to exclude that dormice had entered or exited.

In this study oxygen consumption was measured only of euthermic individuals, because we wanted to investigate the effect of huddling on energy consumption and not that of torpor. Individuals were regarded as euthermic, if they did not feel cold to the touch and showed normal locomotor activity and behaviour, when taken out of the nest box. As edible dormice are nocturnal they enter daily torpor during the early morning hours. Thus it is extremely unlikely that if we encountered an individual euthermic during the day, they would enter torpor afterwards. We are aware of the fact, that the mass-specific metabolic rate is a theoretical value with limited ecological significance. However, in this paper we used mass-specific metabolic rates to evaluate reductions of energy expenditure achieved by social thermoregulation because we could not separately measure oxygen consumption of huddling individuals.

Statistics

Generalized linear mixed models were used to investigate whether reproductive status, body mass and T_{amin} influence grouping behaviour and to analyse the influence of body mass, T_{amin} and testes size on the number of individuals found within a nest box in reproductive males. Furthermore, we calculated a generalized linear mixed model to assess the influence of body mass and T_{amin} on group size in non-reproductive males. We used T_{amin} as an indicator for the climatic condition of any given day, as in a nocturnal rodent like the edible dormouse, the decision to spend the day either in a group or alone will be made late at night or early in the morning, that is, close to T_{amin}. For the analysis of the influence of testes size on grouping behaviour, only captures of adult males with palpable testes were considered. While, for investigation of the influence of the factor reproductive status on grouping behaviour all males with known reproductive status (palpable testes: yes or no) were considered and classified accordingly. As several individuals were included more than once into the analyses, we further included „individual“ as a random factor into the different models (R Developement Core Team 2007; Package: lme4).

For mass-specific RMR measurements below the lower threshold of the thermal neutral zone (TNZ), we analysed the influence of the factors grouping (yes or no), and T_a as a covariable on mass-specific RMR with a linear model. However, as the effect of T_a was not significant ($p=0.7$) we excluded it from the final model. For measurements carried out within the TNZ, we compared mass-specific RMR between groups and single individuals with the student's *t* test.

Statistical analyses were generally performed using SPSS 13.0. Generalized linear mixed model procedures were carried out with the statistical package R version 2.9. (R Developement Core Team 2007). Significance levels were two-tailed. A probability of less than 0.05 was considered significant, while a probability less than 0.1 was treated as a tendency. Data are presented as mean±SD.

Results

Grouping behaviour

During 2007, 67 individual adult males were captured and recaptured 141 times within the Botanical Garden of the University of Ulm. Forty-three of these adult males were captured 82 times in 32 groups of two up to eight individuals. In 75% ($n=24$) of all cases at least two adult males were found together within one group, while in 25% of all cases only one adult male was present within one group. The proportion of captures in groups was highest during the mating season in July (Fig. 1), while adult males were always captured alone in September.

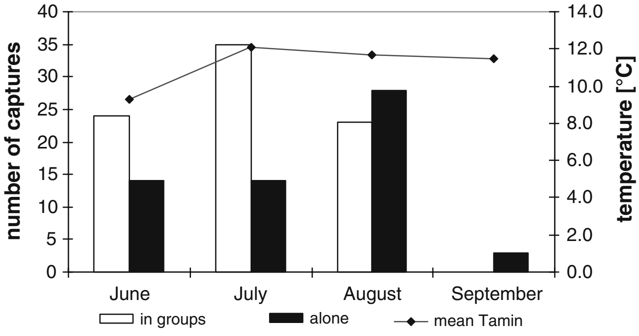

Fig. 1 Captures of adult males in the Botanical Garden of Ulm University in groups or alone during their activity period 2007 note that the figure presents dependent and independent data, as it shows 141 capture occasion of 63 males

Grouping behaviour and group size in dependence of body mass, T_{amin}, and reproductive status and testes size

We captured 67 individual adult males of known reproductive status 138 times.

The fact whether or not males were detected in groups or alone was significantly influenced by their body mass, while reproductive status and T_{amin} failed to show a significant effect. Thus males with a higher body mass were significantly more often captured alone than in groups irrespective of their reproductive status and T_{amin} (Table 1).

In order to analyse the effects of testes size body mass and T_{amin} on huddling behaviour in reproductive males, respectively, we eliminated males without palpable testes from the analysis. In reproductive males, huddling behaviour of adult males was significantly influenced by their body mass, testes size and T_{amin} (Table 2). As body mass negatively influenced group size, males with a lower body mass were more likely to huddle with conspecifics than males with a higher body mass. Testes size was significantly linked to huddling behaviour. Males with larger testes were huddling in larger groups than males with smaller testes. Finally, group size was negatively correlated with T_{amin}. Thus, after cold nights reproductive males dormice were more likely to be found with conspecifics than after warm nights. T_{amin} and T_{amax} were significantly correlated (Pearson's correlation: $r=0.6$; $n=110$; $p<0.001$), thus cold nights were followed by cold days.

Like in reproductive males, group size was negatively influenced by body mass in non-reproductive males. However, here T_{amin} failed to show a significant effect on group size (Table 3).

Comparison of the mass-specific RMR rate between single individuals and groups

In this study, oxygen consumption of altogether 49 individuals was measured with 42 of these individuals measured only once. Below the lower threshold of the TNZ mass-specific RMR was significantly higher in individuals sitting alone than of those sitting in groups (Fig. 2; general linear model: grouping: $F_{1.11}=19.14$; $R^2=63.5$; $p=0.001$).

Table 1 Summary of the generalized linear mixed model fit by the Laplace approximation

	Estimate	Standard error	*z* value	*P*
Intercept	6.1	1.53	3.98	<0.001***
Body mass	−0.049	0.013	−3.8	<0.001***

Formula: group~body mass+(1 Individual), family=binomial; number of obs: 133, groups: individual, 65

Table 2 Summary of the generalized linear mixed model fit by the Laplace approximation for reproductive males

	Estimate	Standard error	*z* value	*P*
Intercept	2.53	0.53	4.73	<0.001***
Body mass	−0.01	0.005	−2.56	0.01 *
Testes length	0.05	0.018	2.82	0.005**
T_{amin}	−0.08	0.02	−3.35	<0.001 ***

Formula: groupsize~body mass+testes size+T_{amin}+(1 Individual), family=Poisson; number of obs: 66, groups: individual, 40

Mass-specific RMR measured within the TNZ did not differ significantly between groups and single individuals, but showed a tendency towards lower values in individuals sitting in groups (Student's *t* test: $t=2.04$; $p=0.055$; $df=19$). The comparison of mass-specific metabolic rates at corresponding T_a below thermoneutrality revealed reductions of energy expenditure of about 38.8% (pairs: $n=6$ measured at the same T_a) of individuals sitting in groups (paired samples Test: $t=3.76$; $p=0.013$; $df=5$; Table 4) compared with individuals sleeping alone.

Discussion

Our results revealed that reproductive as well as non-reproductive males are encountered in sleeping groups and that the reduction of energy expenditure by social thermoregulation can be regarded as one of the main driving factors to form sleeping groups in male edible dormice.

In contrast to reproductive males non-reproductive males are able to enter torpor which represents physiologically the more efficient way to reduce energy expenditure in comparison to social thermoregulation (Heldmaier and Elvert 2004; Namekata and Geiser 2009). It could therefore be expected that non-breeders should prefer to sleep alone because the reduction of energetic expenditure by torpor can assumed to be maximized by sitting alone to avoid passive warming and disturbance by normothermic conspecifics. However, non-breeders have both options to reduce their thermoregulatory costs they can form sleeping groups or enter torpor, depending on the availability of energy resource like food

Table 3 Summary of the generalized linear mixed model fit by the Laplace approximation for non-reproductive males

	Estimate	Standard error	*z* value	*P*
Intercept	2.41	0.34	7.1	<0.001***
Body mass	−0.01	0.003	−4.37	<0.001***

Formula: groupsize~body mass+(1 Individual), family=Poisson; number of obs: 138, groups: individual, 67

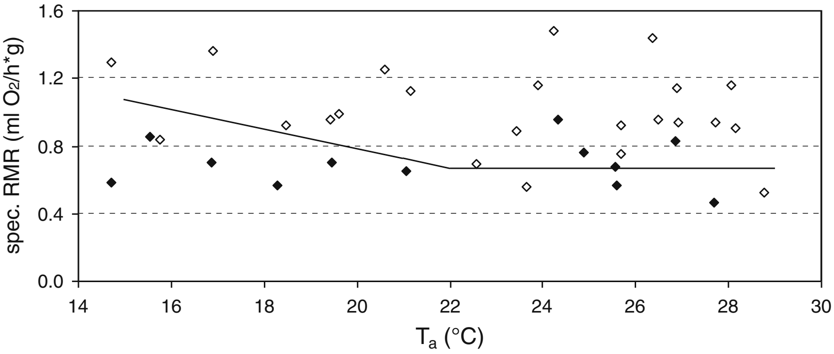

Fig. 2 Mass-specific RMR measured in single (*open symbols*) and groups (*closed symbols*) of edible dormice in the field and nest box temperature. The *line* gives the expected values of mass-specific RMR for edible dormice measured by Heldmaier and Elvert (2004) in captivity

availability or internal fat stores. Accordingly, our results revealed that the decision to form a sleeping group was not influenced by reproductive status or ambient temperature but by body mass. Thus males with sufficient internal energy stores preferred to sleep alone, while light males were associating in groups, irrespective of their reproductive status. Even though torpor represents the more efficient measure to reduce energy expenditure, the disadvantage of torpor is that torpid individuals are much more vulnerable to predators entering sleeping holes than normothermic individuals sleeping in groups. Thus predation pressure might be another factor influencing the cost benefit ratio between entering torpor and forming a sleeping group.

In breeders which do not have the ability to enter torpor and depend mainly on social thermoregulation to reduce their energy expenditure, group size was positively affected by decreasing T_a and body mass, while testes size had a positive impact on the number of individuals sleeping together.

The fact that the number of individuals huddling together was increasing with decreasing T_{amin} can be explained by the fact that energy budgets of animals are strongly affected by the surrounding T_a and metabolic rates of birds and mammals that regulate T_b on euthermic levels increase with decreasing T_a below their TNZ. Previous studies that have investigated the effect of group size on oxygen consumption in small mammals and birds in the lab point towards a reduction of energy consumption with the increase in numbers of individuals huddling together (Canals et al. 1989; Hayes et al. 1992; Perret 1998, McKechnie and Lovegrove 2001). However, there seems to be a critical number of grouped individuals beyond which the reduction of energetic requirement does not change significantly (Canals et al. 1989). Moreover, the addition of other individuals may even increase energetic demands (Perret 1998) because of an increase in social stress occurring in larger groups. Although we did not investigate energetic benefits of different group sizes, measurements of oxygen consumption revealed that grouping fully compensates temperature effects on mass-specific RMR below the lower limit of the TNZ (Fig. 2). Thus the flexibility of this behavioural adaptation allows edible dormice to respond quickly to daily climatic changes by adjusting their group size.

Table 4 Mass-specific RMR of individuals sitting in groups or alone at comparable T_a

	Mean spec. RMR (ml O2/g*h)	SD
Group (*n*=6)	0.68	0.10
Alone (*n*=6)	1.10	0.22

Results of our study further confirm the negative effect of body size, corrected for T_a and reproductive status, on grouping behaviour. Small individuals have generally a lower surface area to volume ratio and thus a higher proportional heat loss across their body surface than larger individuals (Heldmaier and Neuweiler 2004). This makes thermoregulation comparatively more expensive for smaller individuals than for larger ones. To compensate small dormice form groups to reduce thermoregulatory costs.

We observed that males with larger testes and thus presumably higher levels of testosterone were more often captured in larger groups than males with smaller testes. The ability to enter torpor is reduced with increasing levels of testosterone (Mzilikazi and Lovegrove 2002); accordingly, males with larger testes can be assumed to have higher thermoregulatory costs than males with smaller testes. Thus, as observed for differing T_a, male edible dormice seem to be able to compensate the effects of varying testosterone levels on their thermoregulatory capacity by adjusting the size of their sleeping groups. The finding that group size was shown to be negatively correlated with energy expenditure in small endotherms (Canals et al. 1989; Hayes et al. 1992; Perret 1998, McKechnie and Lovegrove 2001) supports this assumption.

These findings imply that dormice indeed use social thermoregulation as a strategy to cope with high thermoregulatory demands. This assumption was further supported by our finding that below the lower threshold of the TNZ euthermic individuals sleeping in groups consumed 40% less energy than euthermic individuals sleeping alone. As predicted, social thermoregulation represents an efficient way for small mammals like edible dormice to reduce energy expenditure (Hayes et al. 1992; Namekata and Geiser 2009), in particular for reproductively active edible dormice that have a reduced ability to enter torpor.

To characterize the impact of different testosterone concentrations on thermoregulatory costs and on social thermoregulation, plasma testosterone levels need to be experimentally modified, for instance by implanting testosterone filled capsules (Place 2000; Mzilikazi and Lovegrove 2002) and by simultaneously measuring testosterone levels, T_b, metabolic rate and in consequence the preferred sizes of formed sleeping groups.

Previous findings (Jallageas and Assenmacher 1983; Fietz et al. 2004) in combination with results of this study demonstrate that testis sizes and levels of testosterone in male edible dormice are highest during the mating season. During mating, testosterone increases male reproductive success by promoting aggressive behaviour and territorial defence, as shown in other bird and mammal species (Beletsky et al. 1989; Zielinski and Vandenbergh 1993; Romero et al. 1998; Hume and Wynne-Edwards 2005; Hau 2007). In accordance with this general link between testosterone and aggressive behaviour, old edible dormouse males are often covered with numerous scars that are mainly ascribed to intrasexual combats during the mating season (Ruf et al. 2006). It is therefore surprising, that the frequency of sleeping groups was highest during the mating season and in most cases observed, males were found to form sleeping groups with other adult males. Based on this finding, it can be assumed that males are under a strong selection pressure to reduce energy expenditure during this period, which further coincides with limited food availability (Bieber and Ruf 2004). This assumption is further supported be the finding that reproductively active males lose body mass during the mating season, while body mass of sexually quiescent males remain stable (Fietz et al. 2009). This energetic pressure seems to subsequently translate into the survival rate of male edible dormice in the field, as their survival rates after high reproductive years were much lower than after low reproductive years (Ruf et al. 2006). One has to bear in mind that males experienced body mass loss and lower survival rates, although they used social thermoregulation to compensate part of energetic costs. Without this behavioural adaptation, fitness consequences would be probably even more severe. However, it cannot be excluded that other factors like a suppressed immune system or intrasexual combats and reduced time spend foraging also influence body mass development and chances for survival in reproductive male edible dormice.

In addition to the energetic benefit of forming sleeping groups at low T_a our results revealed, that even within the TNZ energy consumption of huddling individuals tended to be lower than that of single individuals. This finding is somewhat unexpected, because temperature effects should have no influence on oxygen consumption at thermoneutrality. However, it is possible, that individuals sitting alone consume more energy, because they have to be more vigilant against potential predators, than individuals huddling in groups. RMRs of single individuals measured within the TNZ of this field study were generally above values measured in captivity at corresponding T_a (Heldmaier and Elvert 2004). This discrepancy could possibly be explainded by the heat increment of feeding, as wild individuals were in contrast to captive individuals not fasted and therefore not in a post-absorptive state (Heldmaier and Neuweiler 2004).

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