

RESEARCH ARTICLE

The insensitive dormouse: reproduction skipping is not caused by chronic stress in *Glis glis*

Jessica S. Cornils^{1,*}, Franz Hoelzl¹, Nikolaus Huber¹, Richard Zink¹, Hanno Gerritsmann¹, Claudia Bieber¹, Franz Schwarzenberger² and Thomas Ruf¹

ABSTRACT

Entire populations of edible dormice (*Glis glis*) can skip reproduction in years without mast seeding of deciduous trees (particularly beech or oak seed), because juveniles require high-calorie seeds for growth and fattening prior to hibernation. We hypothesized that, in mast failure years, female dormice may be forced to spend larger amounts of time foraging for low-quality food, which would increase their exposure to predators, mainly owls. This may lead to chronic stress, i.e. long-term increased secretion of glucocorticoids (GC), which can have inhibitory effects on reproductive function in both female and male mammals. We monitored reproduction in free-living female dormice over 3 years with varying levels of food availability, and performed a supplemental feeding experiment. To measure stress hormone levels, we determined fecal GC metabolite (GCM) concentrations collected during the day, which reflect hormone secretion rates in the previous nocturnal activity phase. We found that year-to-year differences in beech mast significantly affected fecal GCM levels and reproduction. However, contrary to our hypothesis, GCM levels were lowest in a non-mast year without reproduction, and significantly elevated in full-mast and intermediate years, as well as under supplemental feeding. Variation in owl density in our study area had no influence on GCM levels. Consequently, we conclude that down-regulation of gonads and reproduction skipping in mast failure years in this species is not caused by chronic stress. Thus, in edible dormice, delayed reproduction apparently is profitable in response to the absence of energy-rich food in non-mast years, but not in response to chronic stress.

KEY WORDS: Fluctuating environment, Mast, Predation, Owl, Fecal glucocorticoids, Pulsed resources

INTRODUCTION

Fluctuating resource pulses are common in many ecosystems, including deciduous forests (e.g. Crone and Rapp, 2014; Curran and Leighton, 2000; Letnic et al., 2005; Yang et al., 2010). One example of a highly fluctuating food source are mast seeding events in trees, such as oak and beech (Hilton and Packham, 2003; Norton and Kelly, 1988; Övergaard et al., 2007). Large mammals like wild boar, deer or bears are highly mobile and can select areas with mast seeding (Bogdziewicz et al., 2016). Small rodents, in contrast, are inescapably exposed to resource pulses. This can impair reproductive success in mast failure years (Bieber, 1998; Pilastro

et al., 2003) but favors reproductive effort in full-mast years (Bergeron et al., 2011; Boutin et al., 2006; Lobo and Millar, 2013; McShea, 2000; Ostfeld et al., 1996; Ostfeld and Keesing, 2000). Full-mast years are normally followed by non-mast years, because oak or beech trees typically cannot produce massive amounts of seeds in two consecutive years (Hilton and Packham, 2003; Övergaard et al., 2007; Pearse et al., 2014; Ruf et al., 2006). However, there are intermediate years in which only a few trees produce seeds (e.g. Ruf et al., 2006; Lebl et al., 2011a).

One of the small rodent pulsed-resource consumers is the edible dormouse (*Glis glis*), a hibernator which produces a single litter per year. Adult dormice can live and even gain fat for hibernation on low-calorie food, such as fruits and leaves (Fietz et al., 2005; Schlund et al., 2002). Juveniles, however, require energy-rich beechnuts, acorns or similar seeds for rapid growth and pre-hibernation fattening in autumn (Pilastro et al., 2003; Ruf et al., 2006). Consequently, edible dormice have evolved the ability to anticipate food quality in the upcoming autumn, probably from the presence or absence of seed-buds in spring, and entire populations may forego reproduction in years without seed production in beech or oak (Fietz et al., 2009; Lebl et al., 2010, 2011a,b; Ruf et al., 2006). In years of seeding failure, the animals may remain in a state of gonadal regression, in which they enter hibernation (Bieber, 1998; Hoelzl et al., 2015; Schlund et al., 2002).

Currently, it is unclear which physiological pathway is responsible for this downregulation of the gonadal axis. Supplemental feeding with high-calorie seeds in an intermediate mast year caused significant increases in the proportion of reproducing females and reproductively active males (Lebl et al., 2010). Interestingly, however, the decision to reproduce was not the result of increased body energy reserves due to the consumption of surplus food, as body weight did not differ significantly between dormice receiving supplementary food and controls. These findings confirmed previous observational studies showing that differences in body mass (and highly correlated body energy reserves) are not related to reproductive decisions in dormice (Bieber, 1998; Schlund et al., 2002).

If energy intake facilitates reproduction, but is not the primary regulator of reproductive investment in dormice, which other physiological pathway is altered in response to large fluctuations in food resources? We hypothesized that the strong year-to-year variation in food quality could lead to chronic stress; that is, a long-term increase in the activity of the hypothalamic-pituitary–adrenal axis (HPA). Arguably, a scarcity of high-quality food may lead to potentially stressful changes in foraging behavior of dormice. In particular, in intermediate years, seeding beech or acorn trees may provide rare resources that may be defended, leading to increased intraspecific competition and aggression and therefore stress.

Scattered high-quality food patches may also lead to foraging over larger distances and exposure to predators. It is known that dormice clearly prefer forest patches which impede exposure to owls, their

¹Research Institute of Wildlife Ecology, Department of Integrative Biology and Evolution, University of Veterinary Medicine, Vienna, Savoyenstrasse 1, 1160 Vienna, Austria. ²Institute for Medical Biochemistry, Department for Biomedical Sciences, University of Veterinary Medicine, Vienna, Veterinärplatz 1, 1210 Vienna, Austria.

*Author for correspondence (jessica.cornils@vetmeduni.ac.at)

 J.S.C., 0000-0001-9930-6226; H.G., 0000-0002-9093-8611

main predators, such as areas with closed canopies (Cornils et al., 2017). In years with high local variation of food quality, dormice may be tempted to increasingly forage in more open forest in which owls are able to maneuver more easily and have higher hunting success (Glutz von Blotzheim, 2001; Hunter et al., 1995). This need for increased or altered foraging activity may have been reduced by supplemental feeding of seeds, which was associated with increased reproduction in females (Lebl et al., 2010).

Both intraspecific aggression and exposure to predators can act as major stressors (e.g. Baird et al., 2014; Boonstra, 2013; Clinchy et al., 2004; Koolhaas et al., 2011; Sands and Creel, 2004; Sheriff et al., 2009). Also, it is well known that stress in mammals can have a negative effect on reproduction, in both males and females. For instance, elevated glucocorticoid (GC) concentrations, induced by stress, were shown to decrease reproductive output in the 'sensitive' snowshoe hare (Sheriff et al., 2009). Stress has inhibitory effects on the release of gonadotropin-releasing hormone (GnRH) and greatly reduces the amount of luteinizing hormone (LH). Further, GCs act at the level of the gonads to decrease responsiveness to LH (Oakley et al., 2009; Sheriff et al., 2009; Wingfield and Sapolsky, 2003). GC can also indirectly impair reproduction through effects on the immune and digestive systems (Munck et al., 1984; Romero, 2004; Romero and Wikelski, 2001; Sapolsky, 2005). Experimental studies have demonstrated that exposure to predators or their odors can cause immediate increases in the circulating GC levels of prey and significantly impair reproductive success (e.g. Canoine et al., 2002; Cockrem and Silverin, 2002; Eilam et al., 1999; Hubbs et al., 2000; Monclús et al., 2005; Sheriff et al., 2009; Thaker et al., 2009).

Given these links between stress and reproduction, we hypothesized (i) that reproduction skipping in dormice may be caused by chronic stress (e.g. Boonstra et al., 1998; Oakley et al., 2009), triggered by the alternation between high and low tree seeding. This implies (ii) that year-to-year differences in mast seeding are associated with different levels of GC secretion. We further hypothesized (iii) that levels of GC may be affected by year-to-year differences in predation pressure, rather than by variation in food resources. To test these hypotheses, we assessed reproduction in dormice inhabiting nest boxes at a field site in the Vienna woods in a year without tree seeding, an intermediate (low-mast) year and a full-mast year. In the intermediate year, we additionally supplemented food in approximately half of the animals, to see whether surplus food affects stress hormones. We focused on females, because this allowed monitoring of actual reproduction, whereas in males only reproductive capability (e.g. testes size) could be measured. To measure GC levels, we used assays determining fecal GC metabolite (GCM) concentrations, as this method is minimally invasive and feces collected during the day reflect GC levels during foraging in the previous night in nocturnal dormice. To assess predation pressure, we estimated the density of owls in an area including our field site.

In brief, our results show that, as hypothesized, yearly differences in mast seeding were associated with significantly different levels of GCMs, which were particularly elevated in the intermediate seeding year. However, GCM levels were unaffected by predator density and – contrary to our hypotheses – reproductive decisions of females were not associated with fluctuations of GCM levels.

MATERIALS AND METHODS

Ethics permission

This study was approved by the institutional ethics and animal welfare committee and the national authority according to §§ 26ff.

of the Animal Experiments Act, Tierversuchsgesetz 2012-TVVG2012 (GZ 68.205/0092-WF/V/3b/2015).

Validation experiment

At the beginning of July 2015, we captured seven free-living adult female edible dormice, *Glis glis* (Linnaeus 1766), at our field site in the Vienna Woods (Lower Austria, Austria, 48°05'N, 15°54'E; 400–600 m asl; for details, see 'Study site and feeding experiment' below). Only newly captured individuals that have never been used for previous experiments were equipped with a PIT tag for individual recognition and their body mass was measured at the field site (for capture protocol, see Lebl et al., 2010). Edible dormice were transported by car to the Research Institute of Wildlife Ecology in Vienna in individual Makrolon cages (Type II, 26.5×20.5×14.5 cm) in a cotton bag. The minimum transport time from the field site to the institute was 2 h, with an additional maximum of 2 h in the cotton bag (including handling time and sampling) until they were placed under final housing conditions, which is sufficient to trigger an acute (short-term) stress response (Canoine et al., 2002; McLaren et al., 2003). Fecal samples for comparison between field and housing conditions were taken on average at 10:30 h at the field site and before transfer into the experimental cages at around 14:45 h (Figs 1 and 2). After capture, fecal samples were collected at 4 h intervals from 20:00 h to 08:00 h with a pooled period over the day from 08:00 h to 16:00 h, resulting in five sampling events within 24 h. The time associated with each fecal sample corresponded to the end of the interval during which they were shed (e.g. feces collected at 20:00 h were excreted between 16:00 h and 20:00 h). The experiment started at 16:00 h on 2 July 2015 and ended at 16:00 h on 6 July 2015. To cover the peak of the stress-induced GCM response and the subsequent decline of GCM levels, we chose a 4 day sampling interval. We injected the animals with adrenocorticotropin (ACTH, 100 µg kg⁻¹; Synacthen[®], Novartis) subsequent to the biological validation on

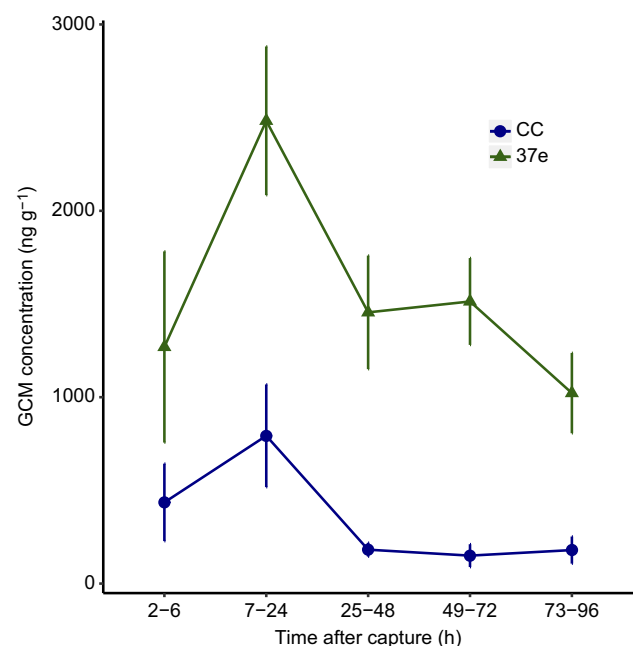


Fig. 1. Glucocorticoid metabolite (GCM) assay comparison. GCM levels during the validation experiment (2–6 July 2015). Data are means±s.e.m. for the corticosterone assay (CC) and corticosterone metabolite 37e assay (37e) ($n=7$).

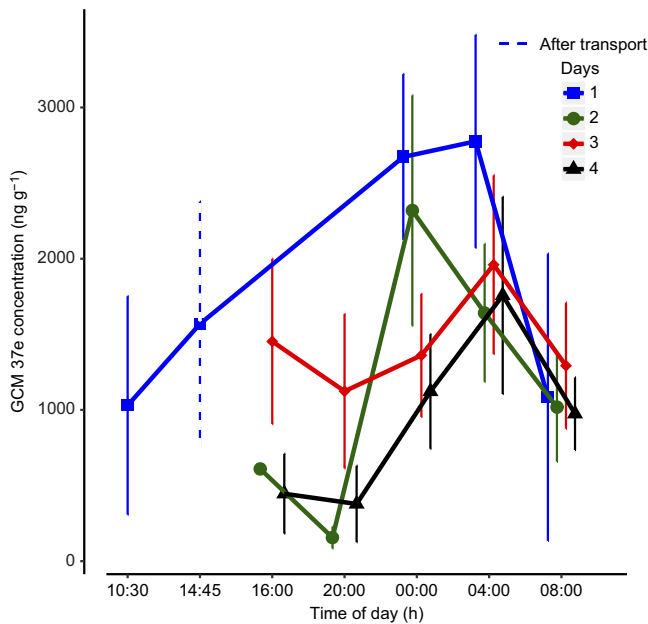


Fig. 2. Daily comparison of GCM values during the validation experiment. GCM 37e concentration (means \pm s.e.m.) during the validation experiment, compared between the sampling days ($n=7$) in a 72 h period. The first two sample times (10:30 h and 14:45 h) are pre- and post-transport; remaining samples were taken within a 24 h period on each day, as indicated.

day 6 at around 17:00 h. However, the response triggered via the ACTH challenge was significantly diminished compared with capture-, handling- and transport-induced GCM peak levels and was therefore not included in the current study (mean peak GCM 37e concentration after ACTH injection: 1449.9 ± 490.7 ng g $^{-1}$). At the end of the experiments, all animals were released back into their nest boxes in the field. Individual body mass was assessed only prior to and after the experiment, to ensure minimal disturbance. Prior to their release, all animals were examined by a veterinarian and classified as healthy.

During the experiment, the animals were housed in individual, commercially purchased and slightly modified cages (155 \times 66 \times 66 cm; Happypet[®]) under natural light and temperature conditions (indoors, with ventilation and windows). The cages contained screen floors and removable drop pans that allowed for non-disruptive collection of fecal samples. Non-transparent plastic foil between the individual cages prevented direct visual contact between the animals. Each of the cages was equipped with a nest box with hay bedding as well as branches, to provide some structure. Water and food (rodent chow, ssniff[®] V164x, ssniff Spezialdiäten GmbH, Soest, Germany) were provided *ad libitum* and were replenished once a day (16:00 h). Additionally, animals were fed with a piece of apple every day. After fecal sampling, all removable drop pans were cleaned and equipped with new paper towels to avoid urine contamination of fecal samples.

Study site and feeding experiment

The field study was conducted in the Vienna Woods next to St Corona am Schöpfl in Lower Austria, Austria (see above). The site is composed of mixed forest dominated mainly by beech (*Fagus sylvatica*, 60%), but conifers are also common (e.g. *Picea abies*, 15%). Randomly positioned nest boxes ($n=124$) were checked every second week over a period of 3 years during the active season (April–October). The fortnightly interval should be sufficient to rule out handling effects on stress hormone levels during the

subsequent capture (Hämäläinen et al., 2014; Koolhaas et al., 2011). Encountered animals were PIT tagged (BackHome BioTec[®], Virbac Limited, Bury St Edmunds, UK; Tierchip Dasmann[®], Greven, Germany), weighed to the nearest gram using a 300 g spring balance (Pesola[®], Baar, Switzerland) and aged (juveniles: before first hibernation; yearling: after first hibernation; adult: after second hibernation; von Vietinghoff-Riesch, 1960; Schlund et al., 1997). We focused on female edible dormice in this study and defined animals as reproductively inactive if we captured them at least twice without young and/or visible mammae during the time of young rearing (week 31–39 of the year; Lebl et al., 2010) or once during peak reproduction in mid-August. This caused a considerable reduction of the overall sample size, but minimized possible errors due to misclassification (Table 1). Generally, dormice are relatively philopatric (Cornils et al., 2017; Ruf et al., 2006). If they change site between seasons, females appear to pick nesting sites early after emergence and typically stay in the same nest box over the active season. Fecal samples were taken for later analysis.

During the field work from 2012 to 2014, there was a non-mast year (2012, no seeds) followed by a full-mast year (2013) where most of the beech trees developed seeds (Table 1). To mimic a mast situation, during the intermediate (low-mast) year 2014, we divided the study site into a control area (48 nest boxes; 18 females) and a supplemental feeding area (76 nest boxes; 20 females). The three categories of non-mast, low mast (intermediate year) and full mast were defined by the amount of pollen in the air close to the study site (Maria Brunn, Lower Austria, Austrian Research Centre for Forests; gravitation traps; Litschauer, 2000) and collected beech seeds (Table 1). Collection of seeds was conducted in the study area from August until the end of October using 4 \times 4 m nets, which were emptied out every second week. We confirmed these findings with visual inspection of the trees at the field site. Weather conditions at the study site (Lascar Electronics EL[®]-USB-2 temperature and humidity loggers) were similar over the course of the 3 years, with an average annual temperature difference of $\leq 0.94^{\circ}\text{C}$. The average annual relative humidity varied between 85% and 92%. Precipitation close to the study site (Klausen-Leopoldsdorf, Lower Austria, Austria) had yearly sums between 762 and 993 mm.

Table 1. Environmental variables, occupied tawny owl nest boxes and percentage of sexually active dormouse males and reproductive dormouse females from 2012 to 2014

Variable	2012	2013	2014	
			Control	Supp.
Pollen density (pollen cm $^{-2}$)	10	1630	30	
<i>Fagus sylvatica</i> seeds per 10 m 2	0	670.1	20.9	
% Occupied owl nest boxes in the area*	69%	19%	63%	
% Occupied owl nest boxes at the study site ‡	100%	0%	100%	
% Dormouse males with tangible testis (n)	7% (106)	68% (149)	22% (93)	70% (86)
% Reproducing dormouse females (n)	0% (56)	85% (107)	0% (69)	14% (88)

*Tawny owl nest boxes in Vienna Woods Biosphere Reserve, $n=140$ –183 per year.

‡ Tawny owl nest boxes at the study site, $n=6$ –7 per year.

2012 corresponds to a non-mast year and 2013 to a full-mast year. In 2014, an intermediate (low-mast) year, the study site was separated into a control and a supplemental feeding area. Data on testes sizes and reproduction were collected over the entire active season, which includes periods prior to and after actual reproduction.

During the supplemental feeding experiment, the two areas were separated by a road and did not differ in habitat characteristics or in demographic population structure (none of our marked animals was encountered in the other part of the forest; Hoelzl et al., 2016). Reproduction took place in the full-mast year and to a very limited extent also at the supplemental feeding site in 2014 (Table 1). In the supplemental feeding area, we supplied the animals with 200 g unhulled sunflower seeds every second week in the nest box prior to reproduction (first feeding: 21 May 2014, last feeding: 23 July 2014, 6 times in total). We provided the sunflower seeds directly in the nest box to ensure that only dormice had access to the food. Birds (in this area, mostly great tits) breed and therefore use the nest boxes mainly in April to May (i.e. mainly before dormice emerge), and avoid nest boxes occupied by dormice, as dormice occasionally feed on eggs and nestlings (Adamík and Král, 2008). Red squirrels are too large and do not fit through the entrance of the nest box. Thus, we assumed that dormice readily consumed the provided seeds. We chose sunflower seeds because, similar to beech seeds, they are rich in fat and energy content (24.1 kJ g⁻¹ for beech seeds and 24.5 kJ g⁻¹ for sunflower seeds; USDA Food Composition database). During supplemental feeding, nest boxes were shared by, on average, 1.8 females. Among supplementary fed females there was no significant difference in the number of nest mates that did (1.5 females per nest) or did not reproduce (2.3). Thus, given a gross energy intake of non-reproducing females of ~100 kJ day⁻¹ (Zoufal, 2005), the energy content of the sunflower seeds provided (~350 kJ day⁻¹) was sufficient to entirely cover energy demands.

In a parallel study on owls, tawny owl density in the Vienna Woods Biosphere Reserve (10,000 km²) was estimated by determining nest box occupancy. The number of nest boxes occupied by owls per year over the whole area was included in our models, because it reflects breeding activity of tawny owls and hence predator pressure on edible dormice (Table 1). Six to seven nest boxes were also distributed inside the study site and followed the pattern of the total area (Table 1).

Enzyme immunoassay analysis

Fecal samples collected in the field as well as under laboratory conditions were immediately frozen on dry ice before storage at -80°C. Prior to extraction, samples were mixed carefully and subsequently dried in a drying kiln at 60°C overnight; 0.05 g of every sample was extracted using 1 ml of methanol (80%) and placed in a thermoshaker for 15 min at 22°C, 550 rpm. If there were only low amounts of feces available, we adjusted the methanol quantity accordingly. Subsequently, every sample was centrifuged for 5 min on 1550 g and the supernatant (800 µl 0.05 g⁻¹ sample) was transferred into a new Eppendorf tube (1.5 ml) and frozen at -20°C until further analysis.

The extracted samples were analyzed via enzyme immunoassay analysis (EIA). We used a pregnanediol and a total estrogen assay (5β-pregnane-3α, 20α-diol 3HS:BSA; estradiol-17β-OH 17-HS:BSA; see Flacke et al., 2017; only for the field samples) to control for the influence of pregnancy and the sexual hormone metabolites.

For fecal corticosterone metabolites (GCM), we compared two different assays within our validation experiment: 5α-pregnane-3β,11β,21-triol-20-one (lab code 37e; Touma et al., 2003) and corticosterone (4-pregnene-11β,21-diol-3,20-dione; Palme and Möstl, 1997) and we used the better performing 37e assay (Fig. 1) for our field experiment. The GCM 37e assay has a less than 1% cross-reactivity with gonadal steroids (Touma et al., 2003). The samples were diluted 1:10 and then diluted further if the overall

concentration was too high for EIA analysis. Intra- and inter-assay coefficient of variation was <10% and <15%, respectively. Hormone concentrations are given as ng g⁻¹ dry mass.

Statistical analysis

For the field study, we calculated linear mixed effects models (package nlme: <https://cran.r-project.org/package=nlme>; <https://www.r-project.org/>) with GCM level as the response variable including animal ID as a random factor, because of repeated measurements for some of the individuals. To achieve normality of the residuals, the response variable was log transformed, with subsequent visual confirmation of normality by a quantile–quantile plot (<https://www.r-project.org/>). We included all potentially relevant variables, i.e. hour and season (spring/summer/autumn) of sampling, age and body mass of the animals, owl density, reproduction during the season (yes/no) and the mast situation (including supplemental feeding) as fixed factors. In addition, we included progesterone and estrogen metabolite levels as covariates, to correct for the potential bias of sexual hormones in the samples. We calculated a type 2 ANOVA and a *post hoc* Tukey-like all-pairwise comparison for the variable mast using function glht (package car: Fox and Weisberg, 2011; package multcomp: Hothorn et al., 2008, respectively).

We calculated two separate models to compare field samples with samples after exposure to capture and transport and to show that the treatment significantly affected GCM 37e levels. A linear mixed-effects model (package lme4: Bates et al., 2015) was calculated with GCM level as the response variable and animal ID as a random factor. The days of sampling (day 1–4) and the treatment (three levels: field, after capture and cage) were used as fixed factors.

For comparison between experimental days, we used GCM levels again as a response variable and included only samples from caged animals. Sampling day (day 1–4) and time of sampling were used as fixed factors, and animal ID was used as a random factor in this linear mixed-effects model.

RESULTS

Validation experiment

We confirmed the sensitivity of our hormone assay by performing a biological validation experiment using capture, handling and transport as a standardized stressor.

GCM levels of edible dormice follow a strong daily rhythm (Fig. 2). During the night, GCM levels were 3–6 times higher than during the day. The comparison between days showed that exposure to our standardized stressor, i.e. capture and transport, significantly affected HPA axis activity and consequently fecal GCM levels ($\chi^2=14.6$, $P=0.003$).

Post hoc comparisons showed that GCM 37e levels were significantly higher on day 1 than on day 2 ($z=-2.66$, $P=0.039$), day 3 ($z=-2.89$, $P=0.02$) and day 4 ($z=-3.74$, $P<0.001$; Fig. 2). There was no notable body mass loss or gain during the experiment.

Field population

We analyzed $n=104$ samples from 38 females over 3 years (2012–2014). Mast level was the only variable that had a significant influence on GCM 37e levels (Table 2). Females had significantly lower GCM levels in the non-mast than in the full-mast year (Fig. 3; $z=-3.847$, $P<0.001$) or the intermediate (low-mast) year (Fig. 3; $z=-11.096$, $P<0.001$). In the supplemental feeding condition, GCM levels were significantly higher compared with those in the full-mast year (Fig. 3; $z=3.093$, $P=0.01$) and the non-mast year (Fig. 3; $z=8.223$, $P<0.001$), but there was no significant difference between

Table 2. ANOVA table of effects on concentrations of fecal GCM 37e

Fixed effects	χ^2	d.f.	P-value
Reproduction during the season (yes/no)	1.450	1	0.23
Food availability	150.330	3	<0.001
Season (spring/summer/autumn)	2.420	2	0.29
Owl density (% of used nest boxes)	1.860	1	0.17
Hour of sampling	0.610	1	0.44
Body mass	0.050	1	0.82
Age class (yearling, adult)	0.063	1	0.8
Progesterone	5.940	1	<0.02
Estrogen	4.820	1	<0.03

Note that the factor food availability had the levels non-mast, low mast (intermediate year), full mast and supplemental feeding. For reproduction, yes indicates the female had a litter, no indicates the female was not captured lactating or with juveniles between weeks 31 and 39.

levels in the low-mast (intermediate) condition and the supplement feeding condition in the same year (Fig. 3; $z=-2.37$, $P=0.078$).

GC levels of reproducing and non-reproducing females were not significantly different (Table 2, Fig. 4). We corrected for estrogen (Table 2) and progesterone levels (Table 2), to adjust for the potential bias of sexual hormones on fecal GCM levels.

Season, body mass, time of fecal sampling, age and tawny owl density had no significant influence on GCM levels (Table 2).

DISCUSSION

Validation, sampling regime and the effect of sexual hormones

Our validation experiment showed that fecal GCM levels can be used as a measure of HPA axis activity and thus as a proxy for stress in edible dormice, and that this method is applicable under field conditions. The highest GC peak at 04:00 h on the first night indicates an approximate delay of around 14–18 h from occurrence

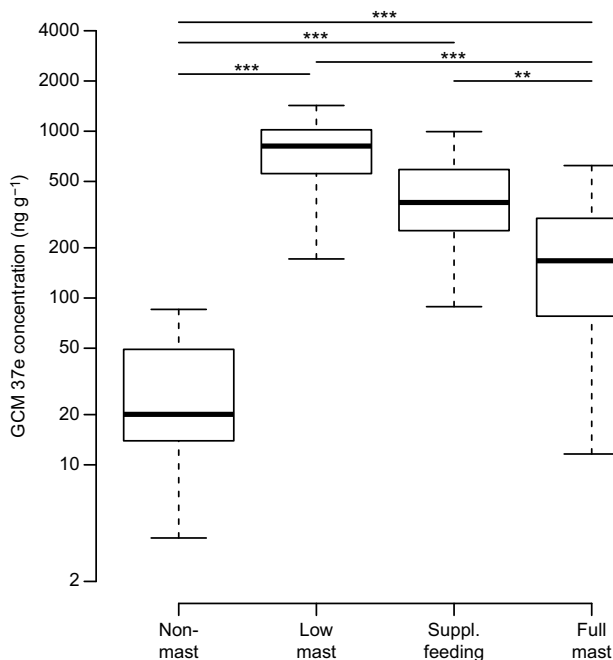


Fig. 3. Influence of mast level on GCM concentration in the field. Partial regression plot of the effect of different mast levels (non-mast, low mast, supplementary feeding and full mast) on GCM 37e concentration at the field site. Asterisks indicate significant differences (*** $P<0.0001$ and ** $P<0.001$; $n=38$; linear mixed-effects model, *post hoc* Tukey-like all-pairwise comparison).

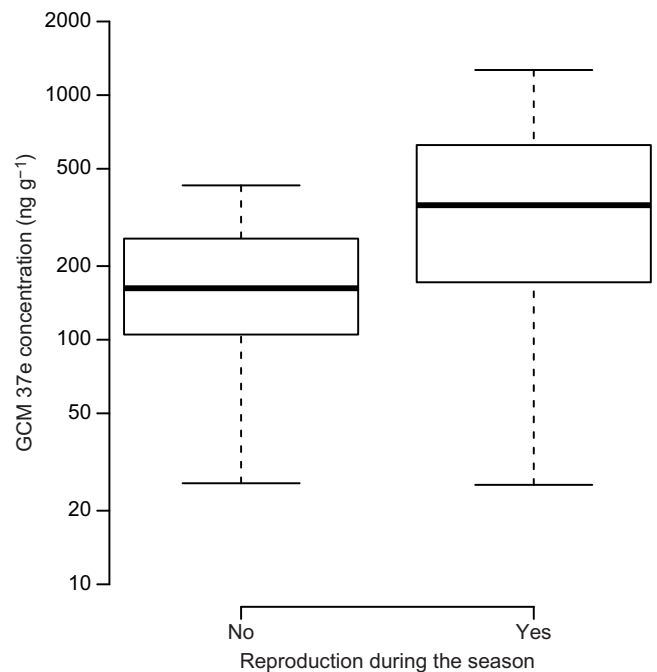


Fig. 4. Influence of reproduction on GCM concentrations in the field.

Partial regression plot of the effect of female reproductive status (yes: reproduced in that season, no: did not reproduce in that season) on GCM 37e concentration ($n=38$; $P=0.23$, $z=1.2$; linear mixed-effects model, *post hoc* Tukey-like all-pairwise comparison).

of the stressor to the peak of GCs in the feces. Thus, our field samples reflect the situation of the previous night. Similar to data from other rodents (e.g. Bosson et al., 2009), we found a large daily variation of GCM with the highest peak at around 00:00 h–04:00 h, corresponding to the nocturnal activity phase of the animals (Rodolfi, 1994). Nonetheless, we found a steady and significant rise of GCM after confinement and transport of the animals to the laboratory (Figs 1 and 2). GCM assays, and the metabolite 37e assay in particular, have already been successfully used in other small rodent studies (e.g. Bosson et al., 2009; Lepschy et al., 2007), and we used only females before the main reproductive season to ensure an adequate validation of the assays (Touma and Palme, 2005). The significant effects of estrogen and progesterone metabolites on GCM concentrations warrant further investigation and additional experiments, which, however, were beyond the scope of this study.

Food availability and the influence of predation

GCM levels were significantly affected by tree masting, with the lowest levels detected in the non-mast year (Fig. 3). One could have expected the opposite, i.e. high levels of stress hormone due to higher exposure to stressors in non-mast years, assuming that dormice have to increase foraging activity when only low-calorie food is available. However, as we subsequently determined in independent studies on the same population, this is not the case. In non-mast years, dormice do not spend more time foraging but compensate for the lack of high-calorie food by frequently using short bouts of torpor during their daily resting phase (Bieber et al., 2017; Hoelzl et al., 2015). In fact, in non-mast years, animals with large body fat reserves may even give up foraging entirely, retreat to underground burrows after only 2–3 weeks of activity and hibernate for more than 11 months into the next year (Hoelzl et al., 2015).

In contrast, locomotor activity is extremely high in reproducing and lactating animals in full-mast years, which can lead to elevations

of body temperature to $>40^{\circ}\text{C}$ for several hours during nocturnal foraging (Bieber et al., 2017). Importantly, this evidence for high activity in masting years and low activity in mast failure years was collected at the same site and in the same years as the current study. For intermediate years, we have no direct estimate of foraging activity. A recent environmental niche factor analysis has revealed that, interestingly, dormice do not prefer territories with a maximum density of beech trees (and energy-rich food in mast years), but preferentially inhabit areas that also provide alternative food sources (cherries, elder berries, conifer needles, conifer cones, etc.) in years without full mast (Cornils et al., 2017). Conceivably then, intermediate mast years may well be accompanied by increased foraging to exploit these less energy-rich foods, or find interspersed masting trees. Competition for food on rare seeding beeches or for alternative food sources, which would increase the likelihood of antagonistic intraspecific encounters, may also explain why GCM levels were highest in the intermediate year. An alternative explanation for this finding would be based on the fact that part of the population vanishes below ground and estivates in non-mast and intermediate years (Hoelzl et al., 2015; Lebl et al., 2011b). This will increase the effective predator/prey ratio and may lead to increased predation pressure on those dormice remaining above ground in summer. However, as we found no general association between predator density and GCM levels (see below), we attribute elevated stress hormones in years of low, locally concentrated food abundance to competition and intraspecific aggression.

Consequently, all our results are consistent with the hypothesis that differences in average GC levels are caused by changes in foraging behavior, which lead to increased predator exposure and possibly territorial conflicts in beech seeding years, especially in intermediate years (Fig. 3). This explanation also fits our observation of GCM levels in food-supplemented dormice, which were lower than those in control animals, but higher than those in full-mast years. This suggests that the availability of sunflower seeds in their nest boxes led the animals to somewhat reduce, but not to abandon, foraging and risk exposure.

Increased GCM levels may be caused by encounters with, or perception of the presence of, predators. We know that predation pressure plays a role in the habitat selection and distribution of edible dormice. In particular, owls, the main predators of edible dormice, prefer to hunt in relatively open stands and, consequently, dormice prefer dense canopy cover (Cornils et al., 2017). However, we could not connect the overall owl density in the three study years to mean GCM levels. In fact, GCM levels were high (in the full-mast year) when owl density was lowest. Partly, this lack of association could be due to the availability of alternative prey species (e.g. voles, woodmice, yellow-necked mice), which also varies heavily between years (Clotfelter et al., 2007; Ostfeld and Keesing, 2000; Wolff, 1996). Alternatively, edible dormice may be adapted to the permanent presence of predators, which could be predictable and may fail to cause 'allostatic overload' (Landys et al., 2006; Sterling and Eyer, 1988; Wingfield, 2005) and detectable stress responses. In that case, elevated GCM concentrations would be caused only by competition for food resources and repeated aggressive interactions with conspecifics, which can increase HPA axis activity (Kitaysky et al., 2007; Koolhaas et al., 2011; Landys et al., 2006).

The fact that GCMs were lowest in the non-reproductive year and elevated in the full-mast, reproductive year corresponds to the observation that males and females (even with fully developed gonads) may share nest boxes, probably to benefit from social huddling at cold ambient temperatures, but pregnant and lactating females typically fiercely defend nest boxes (Hönel, 1991; Fietz

et al., 2010; J.S.C., F.H. and C.B., unpublished observations). As tree holes and nest boxes probably represent a limited resource in working forests (Juškaitis and Šiožinyte, 2008), such as our study site, their defense may have contributed to stress responses in the reproducing females.

Irrespective of the causes of elevated GCM levels in certain years, our results do not support the hypothesis that chronic stress is the mechanism which governs – or even affects – reproduction skipping in edible dormice. While our fecal measurements do not allow us to discriminate between baseline and maximum GCM levels, one would have expected elevations in both measures during non-mast years according to the chronic stress hypothesis (Clinchy et al., 2004). However, GCM levels were lowest when no female reproduced in the non-mast year, and were almost 10 times higher when the vast majority of females had offspring, in the full-mast year (Fig. 3). Even within the same year, females that did reproduce under conditions of supplemental feeding had slightly higher median GCM levels (513 ng g^{-1}) than non-reproductive females under the same conditions (302 ng g^{-1}). Thus, there was no negative association between the decision to reproduce and the activation of the HPA axis in females. This finding is in accordance with the observation that chronic stress effects are present in some species but not others (reviewed in Boonstra, 2013). For instance, snowshoe hares seem highly sensitive towards chronic stress caused by predation, while these effects are not detectable in microtines (Boonstra, 2013). As emphasized by Boonstra (2013), it has been shown that delayed reproduction is only optimal when the number of future offspring produced by not breeding exceeds that of breeding immediately (Kokko and Ranta, 1996). In edible dormice, delayed reproduction apparently is profitable in response to the absence of energy-rich food in non-mast years, but not in response to chronic stress.

Thus, the question remains, if reproductive decisions in dormice are not governed by chronic stress, which signals and pathways are involved in reproduction skipping in this species? Arguably, energy intake is involved, but it is probably not the crucial signal. This is because supplemental feeding, as carried out previously (Lebl et al., 2010) and in the present study, increased reproduction probability only moderately, in the intermediate (low-mast) year from 0% to 14.3% (Table 1). This weak effect occurred despite the fact that the energy content of the food provided was sufficient to cover *ad libitum* intake of females prior to reproduction. Thus, it seems that the availability of high-calorie food alone is insufficient to trigger reproduction in the majority of females, as it occurs in full-mast years. We can only speculate that anticipatory investment in reproduction requires encountering high-calorie food during foraging (rather than during the daily resting phase), or may even be caused by a substance present in beechnuts or acorns but not in sunflower seeds.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.B., T.R.; Methodology: J.S.C., F.H., H.G., C.B., T.R.; Formal analysis: J.S.C., N.H., F.S., T.R.; Investigation: J.S.C., F.H., R.Z., H.G., F.S.; Writing -

original draft: J.S.C., N.H., T.R.; Writing - review & editing: J.S.C., F.H., N.H., R.Z., H.G., C.B., F.S., T.R.; Visualization: J.S.C.; Supervision: C.B., T.R.; Project administration: T.R.; Funding acquisition: T.R.

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Data availability

Data are available from the Dryad digital repository (Cornils et al., 2018): <https://doi.org/10.5061/dryad.s9m4qt0>

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