University of Natural Resources and Life Sciences, Vienna

Sharing is Caring?
Why Edible Dormice (*Glis glis*) Share Nest Boxes.

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Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

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Date   Signature

Figure 1: 13-year-old edible dormouse (*Glis glis*, Isabella Samweber 2018)

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Abbreviations

AIC	Akaike`s information criterion
all	total number of animals captured in the same week
ANOVA	Analysis of Variance
Apr	April
Aug	August
°C	degree Celsius (°C)
e.g.	exempli gratia
g	gram
glm	generalized linear model
glmer	generalized linear mixed-effects model
group	group formation (yes/no)
gsize	group size, total number of animals captured in the same nest box/day
ID	identity
Jul	July
Jun	June
m	meter
mage	average age of individuals per nest box/day in years
mast	mast year (yes/no)
mmass	average mass of animals per nest box/day in gram (g)
nb	nest box
numfam	number of familiar animals per nest box/day
Oct	October
propfam	proportion of familiar animals per nest box/day (propfam=numfam/gsize, 0-1)
propmales	proportion of males per nest box/day (0-1)
proptestes	proportion of males with palpable testes per nest box/day (0-1)
rainfall	precipitation in mm
Sep	September
T_a	ambient temperature in degree Celsius (°C)
znumfam	number of familiar animals by chance

Abstract

The definition of sociality in animals is still a controversial issue amongst ethologists. However, it is mostly agreed upon that sociality, in general, is reflected by cooperative group living. While some rodent species, like the naked mole-rat (*Heterocephalus glaber*), can easily be assigned to eusociality, group living and the social organization within these groups is less evident in other species, like edible dormice (*Glis glis*). Indeed, nocturnal dormice can frequently be encountered huddling in sleeping groups in nest boxes during the daytime and were therefore described as partly-social. However, up to now, very little is known about what factors are influencing group building and group size in dormice. Huddling, as the active and close aggregation of animals, has already been observed in a variety of species. So far, this behavior has mostly been linked to thermoregulatory reasons, yet in several species, a social component has proven to play a role as well. For this study, two years of continuous capture-recapture data based on nest box controls in the Vienna forest were evaluated. The data set included a mast year (2018) and a mast failure year (2017). Based on the continuous marking of the animals in this study area and the assignment of the pubs to their respective mothers, it was possible to determine their relatedness and familiarity. Firstly, it was tested whether the external variables ambient temperature, precipitation, total number of animals captured in the same week and mast affected the formation of groups in the nest boxes. Secondly, it was evaluated if the before mentioned external variables and internal variables, i.e., proportion of familiar animals, proportion of males, proportion of sexually active males, average mass, and average age of individuals, influenced the group size. The gained results revealed that the probability of group formation was consistently high in the mast failure year and negatively correlated with increasing temperatures in the mast year. The positive effect on group size, observed in males with tangible testes, only applied if the proportion of males within groups was small. Also, group sizes were on average larger in 2017, the mast failure year, and the proportion of familiar animals was positively correlated with group size in both active seasons. Although thermoregulation seems a driving force of group formation, animals were more likely to be found with a related conspecific, indicating an active decision process preferring a familiar individual as a groupmate in a nest box. Hence, the results of this study enable the discussion of the social classification of edible dormice and emphasize the importance of further investigations to unveil further social traits in this cryptic living species.

Keywords: *Glis glis* · sociality · huddling · group building · group size

Zusammenfassung

Der Begriff der Soziabilität ist nach wie vor ein umstrittenes Thema in der Wissenschaft. Heutzutage herrscht größtenteils jedoch Einigung darüber, dass Soziabilität durch kooperatives Leben in einer Gruppe definiert werden kann. Während manche Tierarten eindeutig als sozial klassifiziert werden können, sorgen Siebenschläfer (*Glis glis*) seit jeher für Diskussionen. Da Siebenschläfer in Nestboxen tagsüber häufig mit anderen Artgenossen zu finden sind, werden sie in aktuelleren Publikationen zumeist als teil-sozial beschrieben. Das sogenannte „Huddling", also die aktive und enge Aggregation von Tieren, wurde bereits bei mehreren Tierarten beschrieben. Bisher wurden diesem Verhalten vor allem thermoregulatorische Gründe zugesprochen, jedoch konnte in einigen Arten bewiesen werden, dass darüber hinaus auch soziale Komponenten eine Rolle spielen. Bis heute ist wenig über die Faktoren bekannt, die die Gruppenbildung und Gruppengröße bei Siebenschläfern beeinflussen. Auf Grund der kontinuierlichen Markierungen der Tiere im Untersuchungsgebiet und der Zuordnung des Nachwuchses zu ihren jeweiligen Müttern war es möglich Verwandtschafts- und Bekanntschaftsverhältnisse darzustellen. Für diese Studie wurden die Daten des Mastjahres 2018 und des Ausfalljahres 2017 gemeinsam mit „Mast" als Variable untersucht, um mögliche Unterschiede zwischen den Jahren aufzuzeigen. Zum einen wurde getestet ob die externen Variablen Umgebungstemperatur, Niederschlag, Gesamtanzahl der gefangenen Tiere in der jeweiligen Woche und Mast einen Effekt auf die Wahrscheinlichkeit zur Gruppenbildung hatten. Zum anderen wurde überprüft, ob die soeben genannten externen Variablen und internen Variablen (Anteil der sich bekannten Tiere, Anteil der Männchen, Anteil der Männchen mit Hoden, durchschnittliche Masse und durchschnittliches Alter der Individuen) einen Einfluss auf die Gruppengröße hatten. Die Ergebnisse dieser Studie zeigten, dass die Wahrscheinlichkeit einer Gruppenbildung in Ausfalljahren stets hoch war, während sie in Mastjahren negativ mit steigender Temperatur korrelierte. Der positive Effekt von Männchen mit Hoden auf die Gruppengröße galt lediglich für Gruppen mit einem kleinen Anteil an Männchen. Des Weiteren waren Gruppen im Jahr 2017 durchschnittlich größer. Der Anteil an sich bekannten Tieren korrelierte in beiden Jahren positiv mit der Gruppengröße. Diese Erkenntnisse legen nahe, dass Siebenschläfer vorwiegend aus Gründen der Thermoregulation Gruppen bildeten, die Wahrscheinlichkeit mit einem verwandten Tier in einem Nistkasten zu liegen jedoch höher war. Dies setzt einen aktiven Entscheidungsprozess voraus, welcher die Gesellschaft eines bekannten Artgenossen, die eines Fremden vorzieht. Die gewonnenen Erkenntnisse können einen wichtigen Beitrag für die Diskussion der sozialen Klassifikation von Siebenschläfern liefern und unterstreichen die Bedeutung weiterer Forschungsarbeiten, um die Soziabilität dieser kryptisch lebenden Spezies zu entschlüsseln.

1 Introduction

To determine whether an animal is social, it is necessary to define the concept of sociality. Among ethologists, however, there are up to now various controversies regarding the terminology of sociality (Lee 1994; Wcislo and Danforth 1997; Costa and Fitzgerald 2005; Korb and Heinze 2008; Rubenstein and Abbot 2017). One reason for the unprecise and challenging definition of sociality is that "solitary" and "social" are not discrete alternatives, but, rather endpoints along a continuum of spatial and social interactions among conspecifics (Wolff and Sherman 2007). After all, nearly all animals are social at some point during their lives: individuals often exhibit affiliative or aggressive social interactions with members of their own species, and individuals in nearly all species must come together to mate (Rubenstein and Abbot 2017).

For the sake of simplicity, it is nowadays agreed upon that sociality, in general, reflects cooperative group living (Alexander 1974; Rubenstein and Abbot 2017). By necessity, that definition encompasses a range of forms of social organization (Rubenstein and Abbot 2017). Groups of different species vary dramatically in size, structure, and degree of cohesion (Wolff and Sherman 2007). Even within species, the tendency to form groups may differ between populations due to environmental conditions or population density, and individuals may shift between a solitary and social existence during their lifetime (Ebensperger 2001; Wolff and Sherman 2007; Lott 2018). Therefore, social and group behavior is a mix of environmental factors and genotypes based on evolutionary advantages and disadvantages, while influenced by natural selection (Lee 1994; Bolhuis and Giraldeau 2005; Campbell and Reece 2015).

The categorizations range from eusociality, the highest and most sophisticated form of sociality, to solitary individuals that spend the majority of their activity period without another adult conspecific (Korb and Heinze 2008; Kappeler 2019). Within the order of Rodentia, which also includes the family of Gliridae, all types of sociality are described. For example, typical characteristics for eusocial behavior, including overlapping generations, cooperative care of young, and reproductive division of labor, are found in the naked mole-rat (*Heterocephalus glaber*) but are generally missing in hamsters (*Cricetinae spp.*, Dieterlen 1959; Michener 1969; Wilson 1971; Jarvis et al. 1994; Crespi and Yanega 1995).

For most rodent species, however, a more extensive range of classification needs to be applied. Consequently, species exhibiting various combinations of permutations of only one or two of the traits of eusociality have been classified as solitary, subsocial, communal,

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quasi-, or semi-social, respectively and therefore as representing less socially complex or somehow less social (Michener 1969; Wilson 1971; Crespi and Yanega 1995; Costa and Fitzgerald 2005; Dew et al. 2016).

While some species, such as the previously mentioned hamster or naked mole-rat, can doubtlessly be assigned to their associated categorizations of sociality, dormice are still a subject of discussion (Čanády et al. 2016). While some researchers have described dormice as solitary or asocial (Brehm 1918; Schwagmeyer 1988), others have proven that the social life of this species is more complicated than formerly expected. The potential non-solitary habits were firstly in detail described by Vietinghoff-Riesch (1960), who characterized the edible dormouse as a sociable animal and König (1960), who described it as a partly-social animal which is compatible also outside of the mating season.

Based on the preceding definition of sociality, depending on group building (Alexander 1974), huddling could fall into a category within the social system (Dreiss et al. 2016). Huddling, as the active and close aggregation of animals (Gilbert et al. 2009), has already been observed in a variety of species. The behavior is performed throughout several classes of the fauna such as Insecta like honey bees (*Apis mellifera,* Southwick and Heldmaier 2006), Aves like barn owls (*Tyto alba,* Dreiss et al. 2016) and emperor penguins (*Aptenodytes forsteri,* Ancel et al. 2015), and Mammals like rats (*Rattus norwegicus,* Alberts 1978b, a; Bowen et al. 2013), alpine marmots (*Marmota marmota,* Arnold 1988), barbary macaques (*Macaca sylvanus,* Pastor-Nieto 2001), white-footed mice (*Peromyscus leucopus*, Vogt and Lynch 1982) and dormice (*Glis glis,* Vietinghoff-Riesch 1960; Koenig 1960). So far, huddling has mostly been linked to thermoregulatory reasons (Madison et al. 1984; Hayes 2000; Fietz et al. 2010), due to the improved surface to body volume ratio a group has compared to a single individual (e.g., Contreras 1984).

In several species, a social component has proven to play a role in huddling as well. Arnold (1988) described social thermoregulation during hibernation in alpine marmots (*Marmota marmota*), Takahashi (1997) showed huddling was performed most frequently among kin dyads in Japanese macaques (*Macaca fuscata*), Porter (1981) claimed preferential huddling with foster littermates in spiny mice (*Acomys cahirinus*) and Call (1996) observed direct disproportionate amounts of grooming, huddling, and agonistic support toward maternal kin in rhesus monkeys (*Makaka mulatta*). Striped mice (*Rhabdomys pumilio*) merely huddle with unrelated individuals when resources are limited, and no close kin are available (Schradin et al. 2006). Schradin (2006) therefore concluded that the instability of non-kin sleeping groups indicates the potential for the conflict being higher between non-kin than between kin,

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suggesting non-kin sleeping groups may represent a trade-off between thermoregulatory requirements and kin selection.

Dormice are described to huddle in groups in nest boxes that are used in lieu of naturally occurring tree holes (Koenig 1960). Nest boxes are used by these arboreal, nocturnal animals as a safe location to sleep during the day and to raise the offspring during the breeding time (Vietinghoff-Riesch 1960; Koenig 1960). It has been described that communally breeding female dormice are close kin (Pilastro 1994). Dormice are hibernators, and the occurrence of groups in nest boxes is strongly affected by the season (Vietinghoff-Riesch 1960; Koenig 1960). While the hibernation is spent below ground, group sizes in nest boxes during the active season vary from 1-17 animals, depending on the population density and climate of the area (Fietz et al. 2010; Weber et al. 2018). Males emerge prior to females from their hibernacula and thus, occur more frequent in nest boxes than females in spring (Bieber 1998; Bieber and Ruf 2009). During the entire active season, dormice can also be found in nest boxes without any conspecifics (Vietinghoff-Riesch 1960). Shortly after the beginning of the mating period by the end of June, females tend to fight off males and stay solitary in their nest boxes as a preparation to giving birth to their young (Vietinghoff-Riesch 1960). Males are not involved in the upbringing of the offspring; hence, they are mostly found by themselves or in small groups of the same gender (Koenig 1960). By the age of six weeks, juveniles leave their family group and join nest boxes with peers of the same age or adult dormice (Vietinghoff-Riesch 1960). Accumulations of dormice by the end of the active season in October are often dominated by adult females or juveniles that were born late in the active season and therefore have not gained sufficient weight yet (Bieber et al. 2018).

The occurrence or absence of mast-seeding events of large seed trees, like beech (*Fagus sylvatica)* or oak (*Quercus* spec.), have a large impact on the annual life cycle of dormice and thus on the presence in nest boxes (Vietinghoff-Riesch 1960; Krystufek 2010). Dormice reproduce only in so-called mast years and skip reproduction in mast failure years (Bieber 1998; Schlund et al. 2002; Ruf et al. 2006; Hoelzl et al. 2015). In consequence, the presence of age classes differs between years, since juveniles only occur in mast years, and yearlings are observed in high numbers in years following a mast year (Ruf et al. 2006; Weissensteiner 2012). Even though group preferences by male dormice have already been investigated (Fietz et al. 2010), the present study includes both genders for its evaluation to consider a possible influence of females. Dormouse males, however, seem to huddle especially in mast years, in a situation where they have competent testes and high levels of testosterone, which prevent the occurrence of torpor as an energy-saving strategy (Fietz et al. 2010). However, the influences of external and internal variables on group size, as well as on group

composition, such as the mass and age of individuals, the familiarity, the gender distribution or the sexual activity within groups, remain unclear when both genders are taken into account.

This study aims to investigate whether group building and group composition are solely caused by thermoregulation, or is affected by the familiarity of the individuals as well. While one aspect does not rule out the other (i.e. social thermoregulation between kin), it is expected that familiarity or relatedness in group composition plays a more important role in dormice than expected so far. I hypothesize that (i) external variables are influencing group building, (ii) external as well as internal variables are influencing group size, (iii) there is a higher probability of familiar or related animals sharing a nest box and (iiii) there is, therefore, a social component to their huddling behavior. The results of my study can contribute to classifying dormice more accurate within the social spectrum.

2 Material and Methods

2.1 Study Species

The natural habitat of the edible dormouse *(Glis glis)* in Central Europe is mainly extensive connected forests dominated by the European beech (*Fagus sylvatica*) and oaks (*Quercus spec.*, Vietinghoff-Riesch 1960; Krystufek 2010). The aforesaid trees produce a large amount of nutrient and energy-rich seeds, at irregular intervals ranging from two to six years, depending on factors such as the climate of the area (Hilton and Packham 2003; Övergaard et al. 2007; Vacchiano et al. 2017). Reproduction in dormice is strongly adapted to the occurrence of so-called mast years, in which a high proportion of trees produce synchronized seeds (Fietz et al. 2005; Hoelzl et al. 2015; Bogdziewicz et al. 2016; Cornils et al. 2017). Mast events guarantee dormice enough food during the mating period and the phase of lactation when they feed on seed buds. For pre-hibernation fattening, the developed seeds provide an energy-rich food resource for adults, as well as for juveniles (Schlund et al. 2002; Pilastro et al. 2003). Masts lead, therefore, to synchronous high reproduction rates within dormouse populations in which most females are found with offspring (Bieber 1998; Schlund et al. 2002; Pilastro et al. 2003; Bieber and Ruf 2004; Ruf et al. 2006). Nevertheless, diminishing survival probabilities for these years have been observed for both male and female adults as a result of the high energy costs invested in reproduction (Ruf et al. 2006). A sharp contrast to this can be observable in mast failure or intermediate years when the majority of a population skips reproduction. In correlation to other hibernating animals, males regress their testes and retreat them into their abdomen before the onset of hibernation (Jallageas and Assenmacher 1983; Lee et al. 1990; Place and Kenagy 2000; Fietz et al. 2004, 2010). Males emerge from hibernation with regressed gonads, and only a small proportion of them develop gonads in years of mast failure. As a consequence of the scarcity of resources, some individuals even hibernate for up to 11 months (average hibernation period is 9.4 months), resulting in an abridged active season (Bieber and Ruf 2004; Hoelzl et al. 2015).

Adult dormice have a body length of approximately 130-160 mm and a weight between 80-120 g during the active season, reaching up to 260 g before entering hibernation (Vietinghoff-Riesch 1960; Koenig 1960). With an average life expectancy of 3.4 years and maximum longevity of 14 years (Trout et al. 2015), most females (96%) reproduce only once or twice in their lifetime (Ruf et al. 2006). While most females solely reproduce in years of food superabundance, older individuals (> five years) also breed under the poorer environmental

conditions in intermediate years, due to their diminishing chances of future reproduction (Hoelzl et al. 2016; Bieber et al. 2018). In central Europe, females give birth to a single litter each year, with a litter size of *Glis glis* varying between 4.8 and 6.8 pups (Ruf et al. 2006; Krystufek 2010; Lebl et al. 2010). Offspring are born in between late July and August when high-caloric seeds reach their peak of abundance in the treetops (Ruf et al. 2006).

2.2 Study Site

The study site enclosed St. Corona am Schöpfl (Lower Austria, 48°07'N/15°92'E, 400-600 m asl.), a village situated southwest of Vienna in the *Wienerwald* Biosphere Reserve. The area is covered with deciduous forest, dominated by beech (*Fagus sylvatica*). Since 1984, wooden nest boxes were randomly installed on trees along forest roads at the height of 2-3 m. The distance between those boxes varied from approximately 2 m to more than 100 m (Lebl et al. 2011; Hoelzl et al. 2015; Cornils et al. 2017, Figure 2).
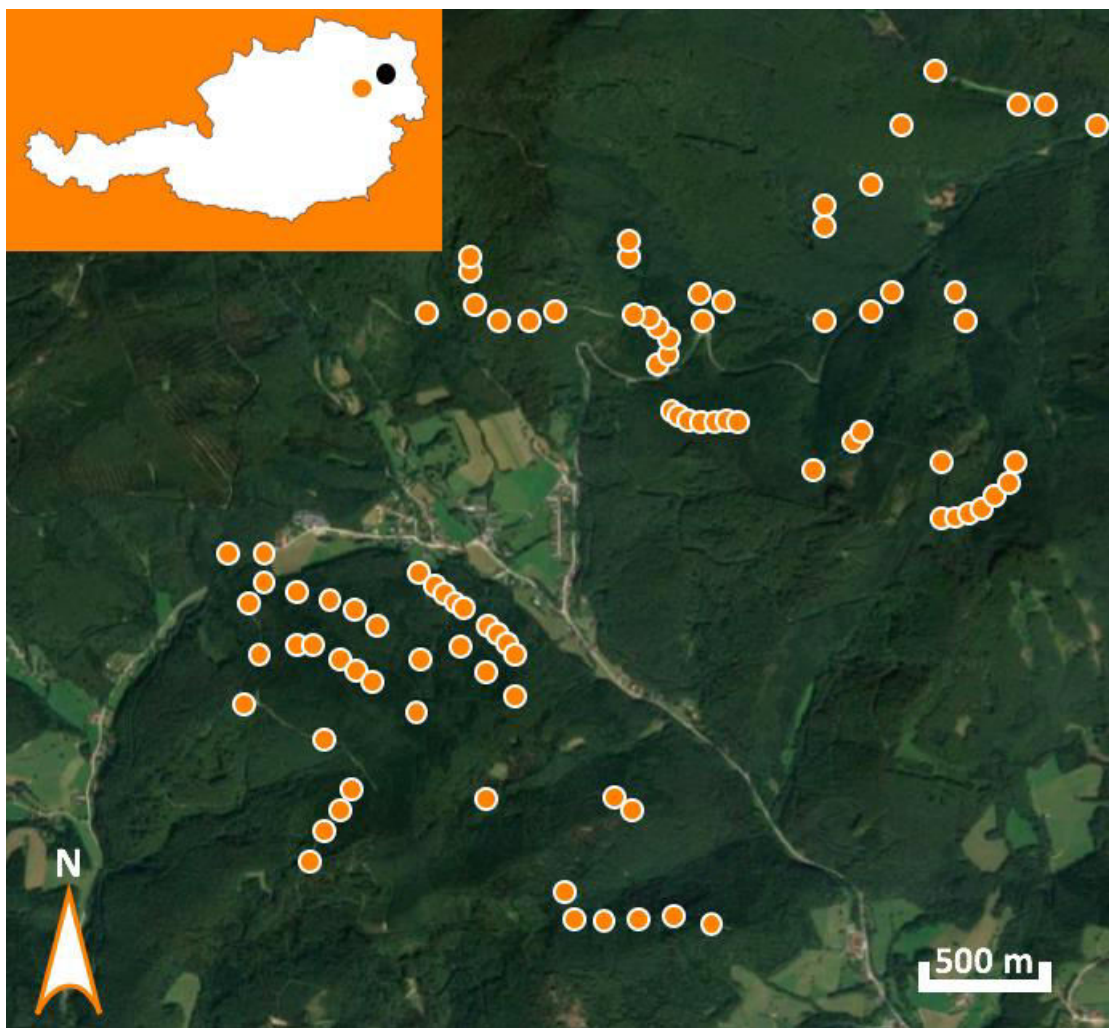

Figure 2: Location of study site within Austria in the top left corner (right spot/ black: Vienna, left spot/ orange: study site). Spots in satellite picture mark nest boxes within the study area, while some spots equal two nest boxes.

2.3 Data Collection and Nest Box Surveys

Within a long-term study, supervised by C. Bieber and T. Ruf (Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna), capture-mark-recapture data of dormice have been collected continuously between 2006 and 2018. I contributed to this long-term data set and participated alongside other scientists (see Acknowledgements) in the controls of a total of 124 nest boxes for the presence of edible dormice between April and October 2018. The nest box controls and the capturing of the animals were carried out every second week during daytime when boxes were used as sleeping sites. Once dormice were captured by hand with protective leather gloves, they were immediately transferred separately into opaque cotton bags. First, the sex of every individual was determined by the distance of the external sexual organ to the anus (Bright and Morris 1989). If palpable, measurements of scrotal testes were taken to conclude the sexual activity of males (Niessing 1956). Second, dormice were classified into three age categories based on body mass and fur characteristics. The categorization differentiated between juveniles (before the first hibernation period), yearlings (before the second hibernation period, sexually mature), and adults (after the second hibernation period). Date of birth in juveniles was based on fur growth, degree of the finger and toe separation and developmental stage of eyes and ears with an accuracy of ±1 day in the first week and ± 2 days in the second week of age, established by Koenig (Koenig 1960) and Vietinghoff-Riesch (1960).

Since 2006 dormice were individually marked with passive integrated transponder chips (Tierchip Dasmann[®], Tecklenburg, Germany). Animals captured for the first time were transferred into a handling cone and injected subcutaneously with a new chip on the dorsal side lateral to the spine (Koprowski 2002). After the second scanning process (Mini Max II, Backhome BioTec[®], Virbac[®], Carros, France; Tierchip Dasmann®, Tecklenburg, Germany) to assure (Brehm 1918; Schwagmeyer 1988) the successful implantation of the chip, all individuals were transferred separately into one-liter plastic bags to ascertain their body mass to the nearest 1 g with a spring balance (Pesola[®] Präzisionswaagen AG, Schindellegi, Switzerland). Juveniles up to the age of three weeks were not marked and only weighted collectively to obtain the litter weight. Females were described as mothers if they had visible, enlarged mammae and were found in a nest box with juveniles up to the age of 35 days. Within this timeframe, weaning takes place, and juveniles have not left the nest boxes yet indefinitely (Koenig 1960; Pilastro 1992). Ambient temperature (T_a) was recorded at hourly intervals at approximately 2 m height. The temperature loggers (iButtons, DS1922L, Maxim, San Jose, USA, accuracy: ±0.5 °C) were positioned at a tree in the center of the study site, in the shadow. Precipitation was not recorded at the study site. Data were used from the

weather station *Hohe Warte*, which is located 30 km east of the study area (https://rp5.ru/Wetterarchiv_in_Wien,_Hohe_Warte_(Wetterstation), 11.01.2019). Mean T_a and mean precipitation were calculated from an interval of 24 hours (first 12 hours of capture day and last 12 hours of the day before). This specific timeframe was chosen to cover the active phase of the nocturnal living dormouse. Subsequently to foraging during the night, individuals chose their sleeping sites (e.g., nest boxes) in the early morning hours.

2.4 Statistics

The data of this study, including the years of 2017 (mast failure year) and 2018 (mast year), were examined jointly with mast year (mast) as a variable to ascertain possible differences between these two active seasons. The effects of variables were evaluated on the one hand on the formation of groups and the other hand on the group size. Potentially relevant internal variables were the proportion of familiar animals per nest box/day (propfam), the average mass of individuals in gram per nest box/day (mmass), average age of individuals per nest box/day in years (mage), the proportion of males per nest box/day (propmales), the proportion of males with palpable testes per nest box/day (proptestes). Potential external variables were, i.e., the total number of animals captured in the same week (all), ambient temperature (T_a), mast year (mast), and precipitation (rainfall). Numerical variables with different units were scaled in order to be processed jointly. Propfam was created to bypass the logical positive correlation between the number of familiar animals per nest box/day (numfam) and group size (gsize, propfam=numfam/gsize).

A model-selection based on AIC was conducted for both, the formation of groups and group size. For the formation of groups a generalized linear mixed-effects model (glmer, family "binominal", R Core Team 2018, R-package: lme4, Bates et al. 2015) and for the group size, a generalized linear model (glm, family "poisson", R Core Team 2018) were chosen. Both models showed no sign of overdispersion. Subsequently, after the glm, a backward stepwise regression based on AIC was performed to determine the best model for group size. Afterwards, an ANOVA type III was calculated for both models.

To test whether the above mentioned external variables had an effect on the formation of groups (yes/no), a generalized linear mixed-effects model was calculated with group formation (group) as the response variable and nest box as a random factor, due to repeated measurements for some nest boxes. Rainfall was excluded from the further modelling procedure due to a significantly decreased AIC omitting this variable (Δ AIC 5.19, Akaike's information criterion, Akaike 1973).

To determine whether the above mentioned external and internal variables affected group size, a generalized linear model was calculated with group size (gsize) as the response variable. At first, the variable nest box was included in a generalized linear mixed-effects model (glmer) as a random factor, due to repeated measurements for some nest boxes. However, due to a lower AIC omitting the variable nest box (Δ AIC = 2.00), this variable (i.e., the random effect) was removed from the model for further evaluations. The variable average age of individuals per nest box/day (mage) was excluded due to a lack of data. Although the age-class was always recorded, the exact age in years could only be determined in animals which were marked as juveniles.

Based on the consequent marking of the animals, including young juveniles still together in the litter with their mother, the assignment of the pubs to their respective mothers and their siblings (i.e., relatedness) was possible. However, for this study, only related and, therefore, familiar animals from the same litter were included in calculations. Offspring from other breeding seasons sharing the same mother were excluded and not regarded as related. Accordingly, the variable propfam refers to related individuals originating from one litter, therefore, being familiar with each other.

A Monte-Carlo-Simulation was used to calculate the number of familiar animals by chance (znumfam). Subsequently, a Test of Equal or Given Proportions (R Core Team 2018) was implemented on the number of familiar animals per nest box/day (numfam) and znumfam to test whether the null hypothesis (familiarity of individuals within nest boxes is coincidental) can be rejected. Juveniles were excluded from the model and, therefore, the kinship analysis based on the individuals not being able to choose a nest box within the first few weeks.

To evaluate whether demographic parameters varied within and between the two study periods, Tests of Equal or Given Proportions were conducted for sex, age, and the number of captured animals. Significance levels were corrected for multiple comparisons using the method of False Discovery Rates (FDR) as recommended for investigations including testing with multiple loci (Benjamini and Yekutieli 2001). To display all effects and interactions visually, effect plots were created (R-package: effects, Fox and Weisberg 2019).

3 Results

3.1 Demographic Parameters

During the sampling period, a total of 1518 dormice were captured. A significant difference of captured animals was observed between the two study years with 1118 animals in the mast year 2018 and 400 animals in the mast failure year 2017 (χ^2 = 338.66, df = 1, p < 0.0001). This included a total of 329 yearlings and 71 adults in 2017, as well as 637 juveniles and 481 adults in 2018. Since no reproduction was observed in 2017, no yearlings were captured in 2018. In both years the number of captured non-adults was significantly higher than the number of adults (2017: χ^2 = 165.12, df = 1, p < 0.0001; 2018: χ^2 = 21.48, df = 1, p < 0.0001, Figure 3). While the abundance of yearlings in 2017 peaked in July (129 dormice), most juveniles were found in September 2018 (269 dormice).
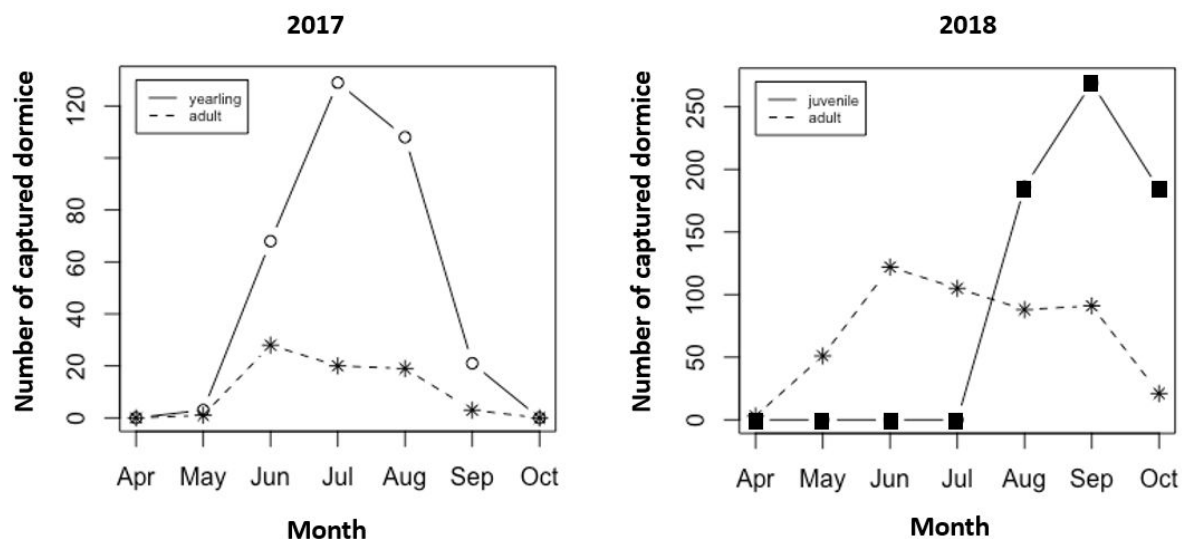

Figure 3: Number of captured dormice per month in 2017 (mast failure year, no reproduction) and 2018 (mast year with successful reproduction). Please note the different scaling of the y-axis.

Although significantly more adult males were captured in 2017 (46 males : 25 females; χ^2 = 5.63, df = 1, p = 0.0176), the gender ratio was significantly skewed toward adult females in 2018 (195 males : 286 females; χ^2 = 16.84, df = 1, p < 0.0001). In 2017 the first adult individual was found in a nest box in May, whereby sex ratio was significantly male-biased until June (χ^2 = 16.69, df = 1, p < 0.0001), changing to be more balanced throughout the rest of the active season (χ^2 = 0.02, df = 1, p = 0.8774). In 2018 the first adult animals occurred in nest boxes in April, whereby the sex ratio was male-biased for April and May (χ^2 = 20.16, df = 1, p < 0.0001) changing to be predominantly female based for the remaining investigated months (χ^2 = 36.01, df = 1, p < 0.0001). The highest number of adult animals were counted in June for 2017 (28 adults) and 2018 (122 adults), reflecting the maximum population densities of active animals for each year. The capture rate decreased in both years during the fall season, with an onset of hibernation for most animals in September in 2017 and October in 2018. In both study years, no significant gender ratio in adults was observable for the start of hibernation (Figure 4). On the contrary, juveniles showed a significantly delayed onset of hibernation in 2018 (χ^2 = 128.02, df = 1, p < 0.0001, Figure 3).
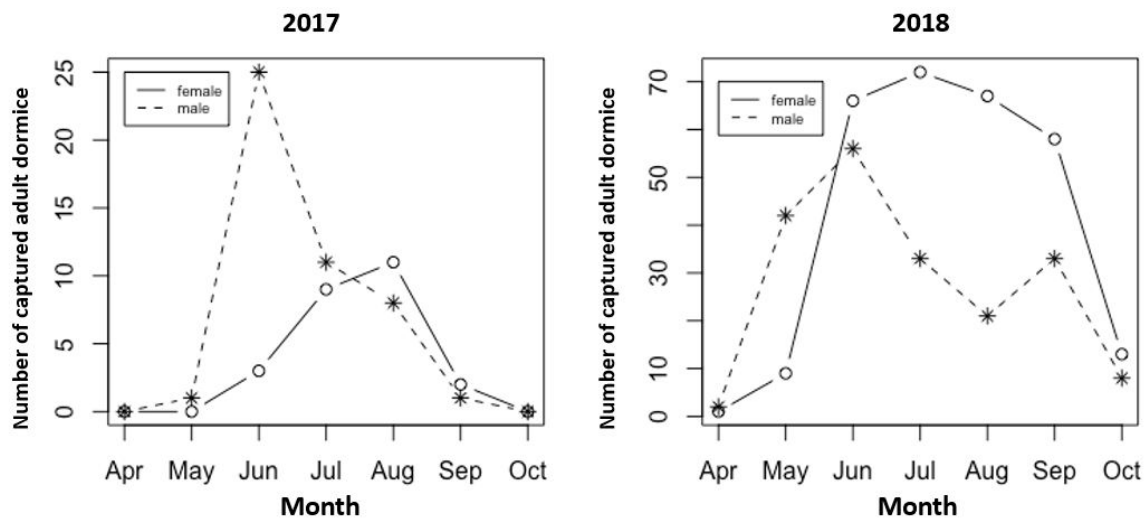

Figure 4: Number of captured adult dormice per month in 2017 (mast failure year, no reproduction) and 2018 (mast year with successful reproduction). Please note the different scaling of the y-axis.

3.2 Influence of External Variables on Group Building

Based on the combined data of 2017 and 2018, the effect of ambient temperature (T_a) and mast situation yielded a significant interaction on the probability of group building (p = 0.0017, Table 1, juveniles not considered). While the effect of increasing T_a on group building was slightly positive in the mast failure year (2017), there was a strong negative correlation between group building and T_a in the mast year (2018, Figure 5).
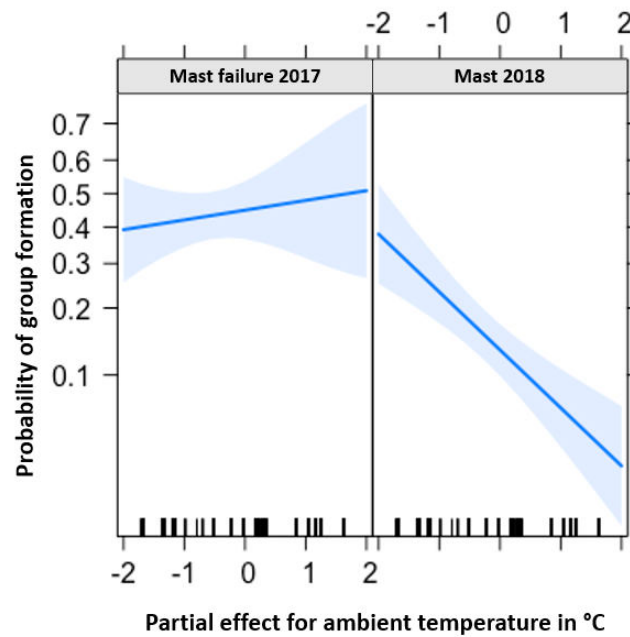
Figure 5: Effects plot of the probability of group formation depending on the partial effect ambient temperature (T_a) in °C and the mast situation (i.e., Interaction temp:mast,

Table 1: Anova table of the best model (glmer) with the variables affecting group building. Significant terms are printed in bold

	df	χ2	P
all	1	1.4293	0.232
temp	1	0.1797	0.672
mast	**1**	**44.667**	**<0.001**
all:temp	1	1.4048	0.236
all:mast	1	1.6407	0.200
temp:mast	**1**	**9.8768**	**0.002**

Results

3.3 Influence of External and Internal Variables on Group Size

The results from the generalized mixed model with group size as the response variable showed a significant effect of mast (p<0.0001, Figure 6a) and a significant effect of the proportion of familiar animals per nest box/day (p<0.0001, Figure 6b). The interaction between the proportion of males with palpable testes per nest box/day and the proportion of males per nest box/day was significant as well (p<0.0001, Figure 7 and Table 2). While the group sizes were significantly larger in the mast failure year (2017), the proportion of familiar animals was positively correlated with group size in both investigated active seasons (Figure 6).
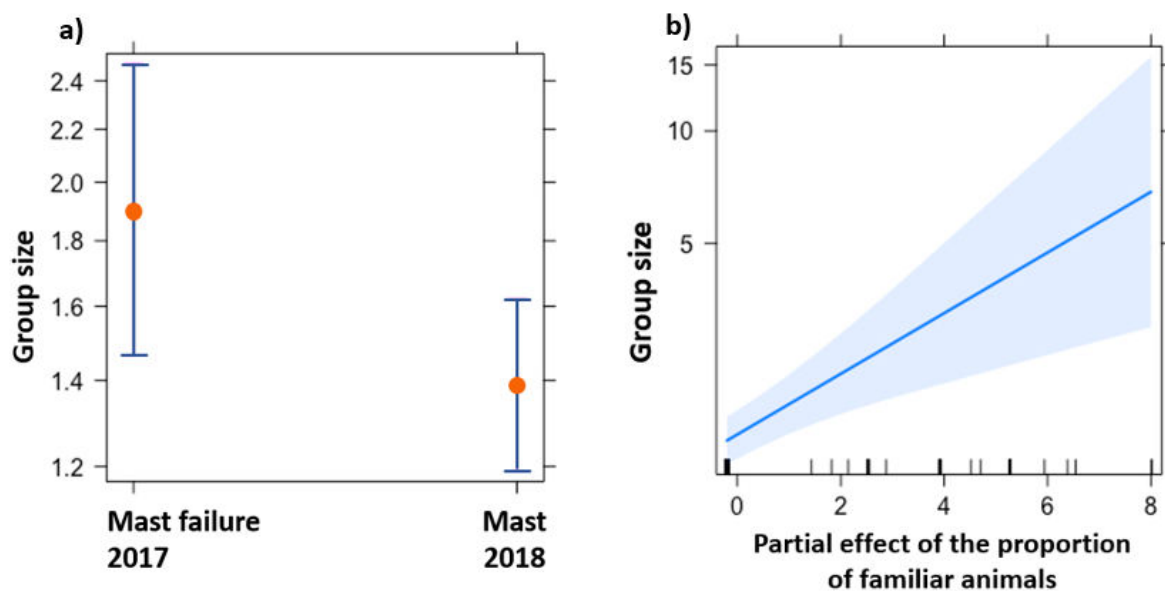
Figure 6: a) Influence of mast (left figure) and b) partial effect of proportion of familiar animals (right figure) on group size.

Furthermore, the results revealed that the positive effect of males with testes on group size only applies if the proportion of males within groups is small (Figure 7). Therefore, males with palpable testes were predominantly found in larger groups when only a few other males were present in those nest boxes. In general, it was found, the higher the proportion of males and the proportion of males with palpable testes in groups were, the smaller was the observed group size. The average mass of individuals in gram per nest box/day had no significant effect on the size of groups.

Results
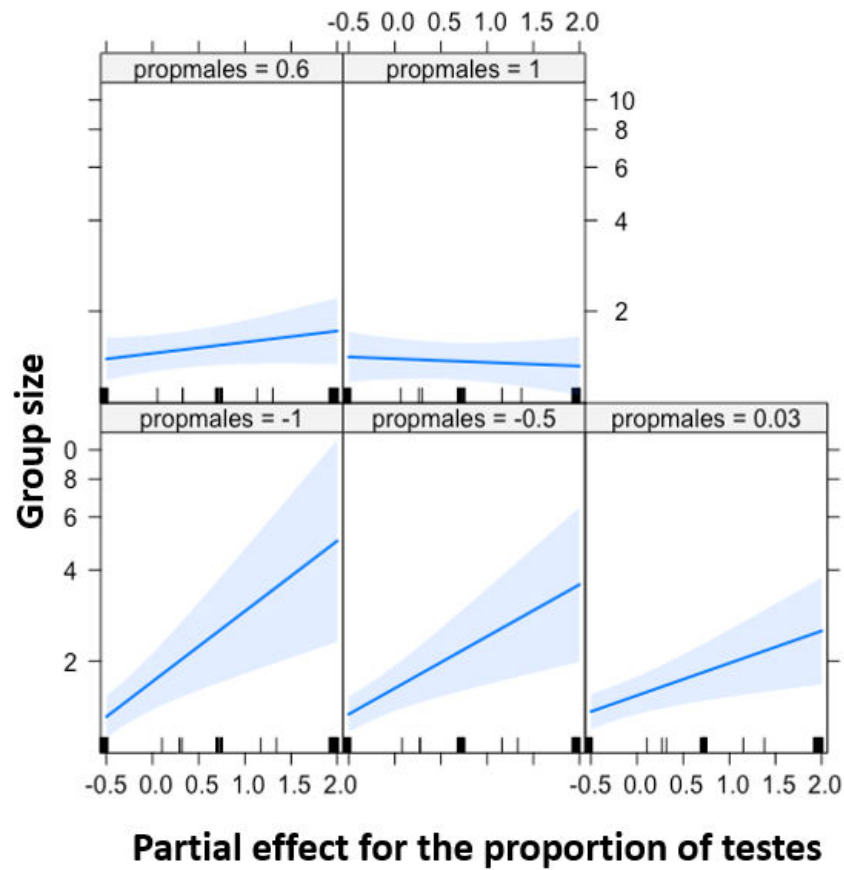
Figure 7: Effects plot of group size depending on the partial effect for the proportion of males and the partial effect for the proportion of males with testes within groups (i.e., Interaction proptestes:propmales, Table 2).

Table 2: Anova table of the variables affecting group size. Significant effects are printed in bold.

	df	χ2	P
all	1	3.100	0.078
propfam	**1**	**54.182**	**<0.001**
proptestes	**1**	**18.410**	**<0.001**
propmales	**1**	**8.227**	**0.004**
mast	**1**	**17.766**	**<0.001**
propfam:propmales	1	3.59	0.058
proptestes:propmales	**1**	**20.189**	**<0.001**
propmales:mast	1	3.069	0.08

It was further tested by using Monte Carlo Simulations and a Test of Equal or Given Proportions, whether the number of familiar animals per group occurred coincidentally or was statistically significant (details see Material and Methods). The analysis revealed that the number of familiar individuals per nest box (i.e., siblings or the mother) was significantly larger as expected by chance (χ^2 = 57.14, df = 1, p < 0.0001, Figure 8).

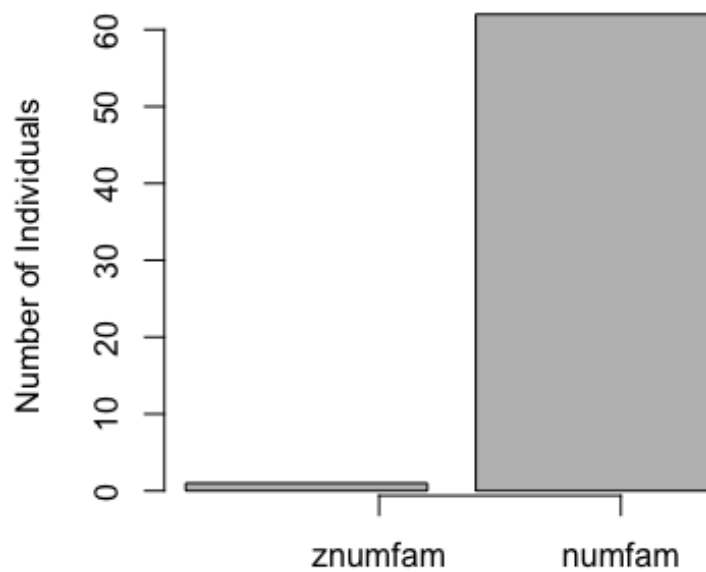Figure 8: Number of familiar animals observed (numfam) compared with the number of familiar animals expected by chance (znumfam).

4 Discussion

4.1 Demographic Parameters

The smaller numbers of captured dormice in mast failure years, compared to mass fructification years, can be explained by the skipping of reproduction and, therefore, a lack of juveniles in mast failure years. Generally, the number of yearlings and adults represent a relatively stable stock of individuals in populations of edible dormice, while the abundance of juveniles is causing considerable interannual population fluctuations triggered by food availability (Ruf et al. 2006; Weissensteiner 2012). Indeed, the number of captured animals in 2018 (n = 1118, Figure 3) is comparable to other mast years in this study area, such as 2016 (n = 1029) and 2013 (n = 1227, Bieber and Ruf, unpublished data). A greater fluctuation in captured dormice could be observed for the mast failure years of 2017 (n = 400, Figure 3), 2014 (n = 733), and 2012 (n = 269, Bieber and Ruf, unpublished data).

In the mast failure year of 2017, significantly more yearlings than adults were captured (Figure 3). A possible explanation for the variation of captured animals within mast failure years and the higher capture rate of yearlings might be the so-called summer dormancy, in which dormice conduct torpor in underground burrows during the summer months and can therefore not be captured in nest boxes (Bieber and Ruf 2009; Hoelzl et al. 2015). Torpor is a state of metabolic depression that reduces energy expenditure as well as water loss in cold and/or dry environments efficiently (Wyss 1932; Kayser 1961; Heldmaier and Elvert 2004) while minimizing the risk of predation (Bieber and Ruf 2009; Namekata and Geiser 2009; Fietz et al. 2010; Turbill et al. 2011). Consequently, prolonged hibernation may also occur during summer as an extension of the hibernation period and has been observed in dormice predominantly in non-reproductive years (Bieber and Ruf 2009; Hoelzl et al. 2015). After all, summer dormancy or prolonged hibernation is primarily found in heavier individuals with a good body condition, which may have been affected by the food abundance and reproductive effort in the previous year (Hoelzl et al. 2015). Therefore, only a part of the adult population can be found in nest boxes during the summer season, while others return to underground burrows already as early as in May (Hoelzl et al. 2015). Yearlings, however, which are still growing, are more dependent on the energy intake throughout the active season and are consequently more abundant than adults in mast failure years (Hoelzl et al. 2015). Thus, the results of the present study support these findings (Figure 3).

The observed earlier emergence of males from hibernation in 2017 and 2018 (Figure 4) has been reported as a typical pattern in edible dormice (Bieber 1998; Schlund et al. 2002; Krystufek 2003; Rotter 2008; Weissensteiner 2012; Weber et al. 2018). During this period,

testicular growth starts, while females are still hibernating (Storch 1978; Bieber 1998; Schlund et al. 2002). While a delayed onset of hibernation by females (Figure 4) was not significant for neither of the two examined years, the results display a significantly prolonged active season for juveniles in 2018 (Figure 3), as published previously (Bieber 1998; Schlund et al. 2002; Krystufek 2003; Weber et al. 2018). Further, studies about hibernating species such as common hamsters *(Cricetus cricetus)* hypothesize juveniles are compensating for their shorter active season and females for their energetic costs of reproductive effort by prolonging the pre-hibernation fattening period (Siutz et al. 2016). The here observed lack of a significant delayed onset of hibernation in females might be due to the smaller sampling size from solely two years, including a mast failure year without reproduction. Furthermore, beneficial environmental factors could have favored an early start of reproduction and a rapid compensation of reproduction costs, resulting in an early onset of hibernation in females. Nonetheless, the comparability of the above-described demographic results to the results of previous studies confirms the standard conditions of this study and allows to interpret results regarding group formation and group composition as a general pattern.

4.2 Influence of External and Internal Variables on Group Building and Group Size

The excessive availability of seeds in mast years has a significant influence on the hormone production in dormice, resulting in drastic behavioral changes compared to mast failure years (Fietz et al. 2010; Cornils et al. 2018). Only in reproductive years, a division of the active season into phases of gonadal growth, mating phase, gestation time, and raising of offspring are observable (Vietinghoff-Riesch 1960; Bieber 1998; Bieber et al. 2014). In mast failure years, the limitation of resources causes phenomenons such as the skipping of reproduction and summer dormancy, leading to higher survival rates (Bieber 1998; Ruf et al. 2006; Hoelzl et al. 2015). The larger possibility of survival in those years is most likely linked to the avoidance of predators due to summer dormancy but also to the evasion of high energy expenses resulting from the mating behavior and the rearing of the offspring (Bieber 1998; Ruf et al. 2006; Hoelzl et al. 2015). Furthermore, the particular age pattern within a population caused by juveniles born only in mast years and in consequence a high proportion of yearlings in the following year (often a mast failure year) leads to the assumption that mast effects might indirectly affect group building and group sizes, too (Vietinghoff-Riesch 1960; Fietz et al. 2010).
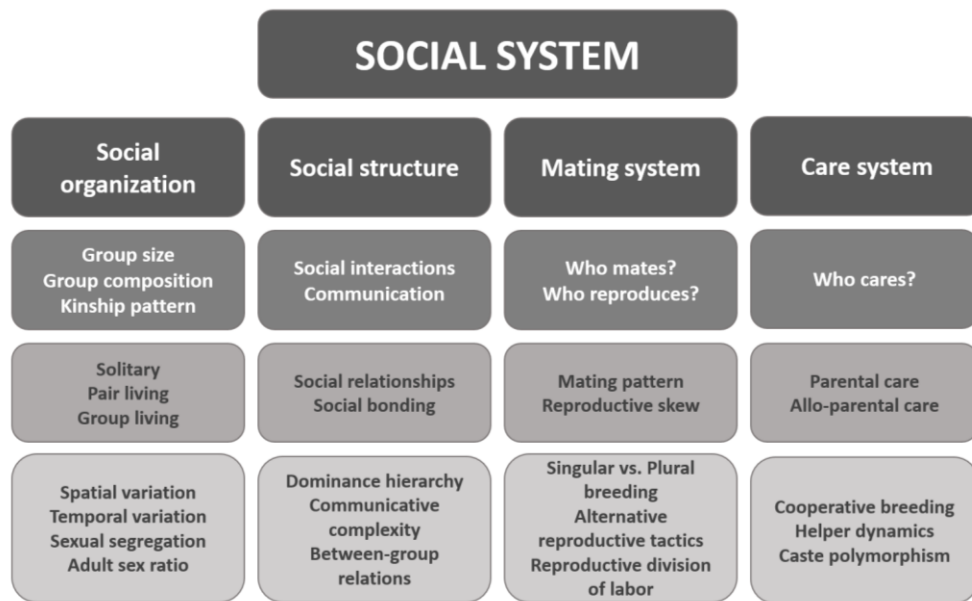
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Figure 9: Social System (modified from Kappeler 2019). First row: Four core components of a social system. Second row: Main variables or questions addressed by each component. Third row: key features of a social system that provide a general characterization of a given species. Fourth row: aspects of the above-mentioned key features.

By applying the categorization of the social system from Kappeler (2019), more in-depth insights into the sociality of dormice can be gained (Figure 9). Regarding the social structure, the lack of a stringent hierarchy and strictly defined territories favor the assumption of a rather sociable animal with peaceful conflict resolution strategies (Vietinghoff-Riesch 1960). There are very few reports of fatal fights between individuals; on the contrary, the opponents often share a nest box soon after their confrontation (Koenig 1960). Even though it has been observed that the home ranges of females do not overlap during the breeding period (Ściński and Borowski 2008) the small, generally loose territories outside of the mating season are characterized by extensive home range overlaps among males and females, resulting in a minimized conflict potential between individuals (Koenig 1960; Hoenel 1991; Juškaitis 2003; Jurczyszyn and Zgrabczyńska 2007; Ściński and Borowski 2008).

Interactions between individuals of the same species, e.g., vocal communications, are additional indications supporting the theory of dormice being social. While there are already various studies reporting about this trait in other dormice like hazel dormice (*Muscardinus avellanarius*), African woodland dormice (*Graphiurus murinus*), Savanna dormice (*Graphiurus parvus*, Hutterer and Peters 2001; Ancillotto et al. 2014; Ancillotto and Russo 2016) only little is known about its meaning in the edible dormouse (*Glis glis*, Vietinghoff-Riesch 1960; Koenig 1960; Jones-Walters and Corbet 1991). The family of Gliridae is known

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for its great variety of vocalization types and calls, ranging from audible noises such as squeaks, snuffling noises, churring, and cackling to ultrasonic vocalizations (Jones-Walters and Corbet 1991; Hutterer and Peters 2001; Ancillotto et al. 2014). With the latter noises, for example, edible dormice warn conspecifics from potential danger such as predators (Vietinghoff-Riesch 1960).

Furthermore, dormice communicate and recognize the familiarity of other individuals through traces of secretion, the so-called scent trails which are excreted by scent glands on feet and circumanal glands around the base of the tail (Vietinghoff-Riesch 1960; Koenig 1960; Morris 2004). Subsequently, another, more indirect form of communication amongst mammals is known as social grooming, in which individuals remove debris and ectoparasites from the fur of the grooming partner (Dunbar 2008). It is a trait widespread among a variety of mammals and does not solely serve a hygienic purpose (Kolb and Nonneman 1974; Kolb 1977; Lammers et al. 1988; Dunbar 2008). Moreover, it strengthens the bond between individuals and ensures to maintain and serve the relationships between them (Dunbar 2008). As already shown in other mammals (Taylor and Sussman 1985; Pastor-Nieto 2001; Schino and Aureli 2008), also dormice preferably conduct social grooming amongst close kin (Koenig 1960).

Unlike Vietinghoff-Riesch (1960) suggested, the mating system of the edible dormouse is not solely polygynous in which only males mate with several females. For years now, it was known to be promiscuous, since females can also copulate with different males (Kraus et al. 2008; Ściński and Borowski 2008). Furthermore, the assumption has been proven since Weber (2018) was able to show multiple paternity amongst juveniles in one litter. However, this type of mating system might be one justification for the results in the present study (Figure 7, Table 1 and Table 2). Males are presumed to claim territories during the mating time and might express rivalry towards other males due to their developed testes and therefore increased testosterone levels (Bieber and Ruf 2004; Ruf et al. 2006; Hau 2007; Fietz et al. 2010; Fietz 2012). Moreover, the proven philopatry shown by females might benefit males that can keep opponents out of their nest boxes, with privileged access to females during the mating period (Vietinghoff-Riesch 1960; Schlund 1996; Ruf et al. 2006; Sevianu and David 2012; Cornils et al. 2017). This explanation might also be applicable to mast failure years since a part of the male population developing testicles when resources are limited, might result in territorial behavior amongst males (Schlund et al. 2002; Bieber and Ruf 2004).

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In edible dormice, males are not involved in the care system and, consequently, the raising of the offspring (Koenig 1960). Only in captivity, it has been observed that males are helping females (Koenig 1960). However, communal nesting, the shared rearing, and often communal nursing of one or two litters has been described in dormice (Pilastro 1992; Hayes 2000). The frequency of this phenomenon varies from less than 5% of the total number of breeding females, up to 50%, (Pilastro 1992, 1994). Nonetheless, this phenomenon has been only observed once in the study year of 2018 and is probably related to the population density and the frequency of tree holes or nest boxes (Pilastro 1992, 1994). Pilastro (1992, 1994) reported close kinship to be an essential factor for communal nesting and proved relatedness to be positively related to reproductive success (Pilastro et al. 1996). This process of kin selection, by which traits are favored because of their beneficial effects on the fitness of relatives, displays the ability of kin recognition in dormice (West et al. 2007).

The social organization of dormice consists of loose groups which may change from one day to another, due to the animal's nocturnal habits and the lack of stringent territories (Vietinghoff-Riesch 1960; Čanády et al. 2016). Groups can consist of adults, juveniles, males, and females, while any composition of the variables above is possible (Vietinghoff-Riesch 1960). Based on the diffuse connection of groups, there do not seem to be between-group relations or separations (Vietinghoff-Riesch 1960). Besides forming groups during the active season, dormice have already been reported merging for hibernation as well, although parameters for this circumstance remain unclear to this day due to the lack of transparency of the burrows below ground level (Brehm 1918; Koenig 1960; Morris and Hoodless 1992; Trout et al. 2015).

If dormice solely aggregated to mate, larger groups and a higher probability of group composition would be expected in mast years, yet the opposite was observed in this study (Figure 5, Figure 6a, Table 1 and Table 2). One explanation for this phenomenon might be summer dormancy in mast failure years. Based on the findings that mostly heavier individuals conduct torpor during the active season, adults with little mass, males with palpable testes, and yearlings are forced to save energy throughout social thermoregulation (Jallageas and Assenmacher 1983; Fietz et al. 2010; Hoelzl et al. 2015). By implication, the negative correlation between temperature and group size in mast years (Figure 5 and Table 2) suggests that the population, consisting mostly of adults with sufficient energy reserves, can afford to avoid groups when temperatures are adequately high. Another influencing factor might be females, being found alone with their pubs in nest boxes when temperatures are high in summer, were counted as one individual (Figure 5 and Table 2).

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However, social components affecting huddling behavior such as allogrooming, can not be excluded. Early studies have already reported social grooming as an essential part of the life of edible dormice (Vietinghoff-Riesch 1960; Koenig 1960). Nonetheless, up to now, only little is known about the factors influencing huddling and whether an active decision process is involved when forming groups. In the present study, it could be shown that animals are more likely to be found with a related and familiar conspecific (Figure 6b) and that the familiarity of individuals within nest boxes is not coincidental (Figure 8). These findings indicate, on the one hand, kin recognition and on the other hand, a close kinship preference, as already seen in other species (Porter et al. 1981; Call et al. 1996; Takahashi 1997; Schradin et al. 2006; West et al. 2007). Studies have found that animals might connect familiarity with a reduced conflict potential and therefore, stress (Schradin et al. 2006).

4.3 Conclusion

The present study addressed the question of whether group building and group composition in edible dormice are solely caused by thermoregulation, or are affected by the familiarity of the individuals as well. Based on the gained results it has been proven that (i) external variables are influencing group building, (ii) external as well as internal variables are influencing group size, (iii) there is a higher probability of familiar or related animals sharing a nest box and (iiii) there is, therefore, a social component to their huddling behavior. These findings suggest that dormice do not form groups solely for mating purposes or thermoregulatory reasons. The discordant results of the influences of variables in mast and mast failure years show the importance of long term studies. Solely the presence of sufficient data over several years enables to counterbalance active seasons with exceptional results and to take the biology of animals with altering annual life cycles into account. Although this method is time and resource consuming, it helps to avoid false general conclusions and the understanding of the study subject, including their complex sociality. It is now up to further studies to pursue the discussion of the social classification of edible dormice and investigate to unveil further social traits in this cryptic living species.

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