



# Is promiscuity the key? Multiple paternity in the garden dormouse (*Eliomys quercinus*)

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## Abstract

Many mammals have a promiscuous mating system with multiple sired litters. Promiscuity can increase the genetic variability, reduce the risk of inbreeding, and increase the effective population size, and is therefore crucial for preventing genetic loss and maintaining adaptability. This is particularly true for small and threatened populations. The garden dormouse (*Eliomys quercinus*) is a threatened species, which exhibited a drastic decline over the last 20–30 years. The aim of this study was therefore to investigate the mating system of the garden dormouse in mountain forest habitat by parentage analyses using 5 polymorphic microsatellite markers combined with morphometric data and information about the nesting behavior. Genetic parentage analyses revealed that 64% (9 of 14) of the litters were sired by at least two males, suggesting that garden dormice have a promiscuous mating system. The genetic findings were further supported by indirect indicators of promiscuity, such as testes, that were nearly four times larger than predicted for a rodent of its body mass and only slight male biased sexual size dimorphism. The finding of a promiscuous mating system in garden dormice should be taken into account in future conservation efforts. Due to its habitat preferences and limited dispersal potential garden dormice are vulnerable to forest fragmentation. The connection of suitable habitats facilitates dispersal and promotes access to potential mating partners, which could be especially important for populations colonizing new habitats. Access to potential mates may also reduce inbreeding, loss of genetic variability which is crucial for populations viability and survival.

**Keywords** Microsatellites · Multiple mating · Conservation · Reproduction

## Introduction

Mating strategies in mammals can range from monogamy, polygamy to promiscuity. However, polygyny has long been thought to be the most common mating system (Clutton-Brock 1989). Over the last decades and with advances in molecular techniques, many mammalian species were recognized to be promiscuous, where both sexes mate with multiple partners during one reproductive event (Wolff and

Macdonald 2004). The evolution of different mating strategies depends on density, availability and distribution of key resources and potential mating partners, and may vary even within a species (Emlen and Oring 1977). In mammals multiple mating bears costs and benefits for both sexes. Both males and females incur negative consequences through multiple matings, such as increased energetic demand, risk of predation and especially infection with sexually transmitted diseases, and other pathogens and parasites (Huchard et al. 2011; Nunn et al. 2014). Polygynous males compete directly with other males and have a high risk of getting injured, whereas females can suffer through sexual coercion (Clutton-Brock and Parker 1995). However, males benefit from mating with multiple females as they can increase the number of juveniles sired and therefore enhance their reproductive success (Trivers 1972). Females can benefit directly from mating polyandrous by reducing the risk of male infanticide, as males may not be able to discriminate between own and unrelated juveniles (Wolff and Macdonald 2004; Klemme and Ylönen 2009; Auclair et al. 2014)

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and reduced costs of sexual harassment by males (“convenience polyandry”) (Boulton et al. 2018). Furthermore, polyandrous mating protects females from male infertility by ensuring that they receive an adequate amount of vital sperm, which can lead to increased litter sizes (Hoogland 1998; Briefer et al. 2013; Vasudeva et al. 2021). But there are also indirect (genetic) benefits for polyandrous females, which may arise by genetic bet-hedging or post-copulatory mate choice through either “good genes” or “genetic compatibility” (Yasui 1998; Jennions and Petrie 2000; Neff and Pitcher 2005). This can lead to higher offspring viability and offspring reproductive success (Fisher et al. 2006; Firman and Simmons 2012). Multiple mating also increases the level of heterozygosity and therefore genetic diversity in the offspring, as it was shown not only in mammals, (e.g. Brandt’s vole (*Lasiopodomys brandtii*, Huo et al. 2010), yellow ground squirrel (*Spermophilus fulvus*, Batova et al. 2021), wild boar (*Sus scrofa*) (Gayet et al. 2016)), but also in birds (e. g. common reed bunting (*Emberiza schoeniclus*, Suter et al. 2007), blue tit (*Cyanistes caeruleus*, Foerster et al. 2003), and reptiles (e.g. common European viper (*Vipera berus*) (Madsen et al. 2023)) and could lead to a higher fitness of the offspring (Suter et al. 2007). Multiple mating can also reduce the risk of inbreeding by decreasing the likelihood of having all offspring sired by one potentially closely related male (Stockley et al. 1997). Compared to other mating systems, promiscuity can increase the number of males successfully reproducing within a population (Nunney 1993; Sugg and Chesser 1994; Frankham 1995a) and therefore the effective population size ( $N_e$ ) of a given population.  $N_e$  refers to the size of an abstract population that loses genetic variability at the same rate as a real population (Wright 1931). A low  $N_e$  can lead to a rapid loss of genetic variability in future generations (Frankham 1995a).

Knowledge of a species’ mating systems can therefore help understand how the genetic variability of a population is maintained (Lande 1977). This is especially crucial for threatened species occurring in small isolated populations, as they are more susceptible to demographic and environmental stochasticity (Lande 1993; Stephens and Sutherland 2000) and have a higher risk of genetic drift and inbreeding, which can lead to a loss of genetic variability (Frankham 1998; Bijlsma and Loeschcke 2012). Low genetic variability can ultimately reduce the ability of populations to adapt to changing environmental conditions, decrease individual fitness, and is expected to increase the risk of population extinction (Hedrick and Kalinowski 2000; O’Grady et al. 2006; Palstra and Ruzzante 2008; Huisman et al. 2016; Hedrick and Garcia-Dorado 2016; Kardos et al. 2021).

The garden dormouse (*Eliomys quercinus*; Gliridae) is a threatened species that inhabits various habitats including orchards, vineyards, different types of forests and occurs also in cities, where human housings can provide nesting

sites. In Central Europe the main natural habitat is highly structured coniferous mixed forest, where rocks and boulders provide nesting sites and protection against predators (Bertolino et al. 2003; Bertolino 2017; Meinig and Büchner 2012; Mori et al. 2020). This small and nocturnal rodent is considered to be highly vulnerable to forest fragmentation due to its habitat preferences and limited dispersal potential (Bertolino et al. 1997; Sutherland et al. 2000). Being endemic to Europe, it was historically widespread from Portugal to the Ural (Storch 1978). However, over the last 20 to 30 years, the eastern populations have declined drastically, leading to the disappearance of the species from 50% of its former distribution area, especially in Central and Eastern Europe (Meinig und Büchner 2012; Bertolino 2017). Likely reasons for this decline include habitat destruction, limited availability of key resources like arthropods as important food resource and nesting sites and a reduced gene flow due to habitat fragmentation (Meinig and Büchner 2012). The International Union for Conservation of Nature (IUCN) has classified the garden dormouse as “near threatened” (Bertolino et al. 2008). Germany has a high degree of responsibility for the conservation of this species, as over 10% of the species range is located within the country. In 2020 the garden dormouse has been listed in the German Red List of endangered species as highly threatened (Meinig et al. 2020). The genetic mating system of the garden dormouse is currently unknown. The aim of this study was to describe the genetic mating system of the garden dormouse occurring in mountain forest habitat as a key information for future conservation measures.

In Germany, one of the last main distribution area of this species in its natural habitat is the Black Forest, Baden-Württemberg, where it occurs mainly in spruce (*Picea abies*) dominated forests. We conducted a capture-mark-recapture study at two study sites in the Black Forest National Park, taking morphometric measurements and tissue samples for genotyping with 5 polymorphic microsatellite markers (Hürner et al. 2009; Schoebel et al. 2013) for parentage analysis. Genetic data were complemented by observations of nesting behavior, information on relative testes size and sexual size dimorphism as indirect indicators of the role of sperm competition and direct intrasexual competition between males for receptive females (Ramm et al. 2005; Wolff 2007).

## Material and methods

### Study animal

Garden dormice have a head to body length of 10 to 17 cm with a tail length of 13 cm and a live expectancy up to 3–4 years in the wild. Body mass varies between 60 and 110 g

and can reach up to 130 g during the fattening period just before hibernation (Vaterlaus 1998; Schlund 2005). In comparison to hazel and edible dormice (*Muscardinus avellaniarius* and *Glis glis*), garden dormice are more ground-dwelling, using rock crevices and holes in the ground as daily resting and nesting sites and also forage mainly on the ground (Vaterlaus 1998; Bertolino et al. 2003). Their omnivorous diet consists of fruits, seeds and buds, with a preference for diet of animal origin, like arthropods (Kuipers et al. 2012; Büchner et al. 2022). The garden dormouse is a hibernator, however length and timing of the hibernation period depend on the geographical location. In Central Europe, dormice hibernate between October and April, whereas in the Mediterranean region they remain active throughout the winter. In Germany, the mating season begins immediately after emergence from hibernation in April/May (Schlund 2005), and after a gestation period of 23 days, litters averaging 4–6 young are born between the end of May and the beginning of July (Schlund 2005; Viñals et al. 2012). Second litters are rare in Central Europe. Females raise their young without their males and after 34–36 days juveniles feed on their own (Moreno and Collado 1989; Schlund 2005).

### Study sites

This study was conducted at two different study sites, Waldklassenzimmer (WK) and Ruhesteinloch (RL), located within 1 km of each other in the Black Forest National Park in south-western Baden-Württemberg, Germany. Study site RL (48°33'54.38"N, 8°13'17.88"E) covers an area of approximately 3.7 ha and extends over an elevation from 820 to 860 m above sea level on a steep, west-facing slope. 64 nest boxes (Schwegler 3SV, Schorndorf, Germany) were mounted on trees 1.5 m above ground, 30 m apart, at the nodes of a rectangular grid. The study site WK (48°33'39.14"N, 8°13'47.15"E) covers an area of approximately 4.7 ha and is located on a south-east-facing slope at an altitude of 900 to 930 m above sea level. Here, 60 nest boxes were installed in the same way as in RL. At both sites the vegetation consists predominantly of spruce, with blueberries (*Vaccinium myrtillus*, L.) and raspberries (*Rubus idaeus*, L.) in the understory.

### Capture-mark-recapture & body measurements

We monitored the nest boxes at all study sites during daytime from May to October at monthly intervals from 2018 (RL) and 2019 (WK) until 2021 (RL and WK). Dormice with a body mass above 50 g were individually marked using subcutaneously-implanted passive integrated transponders (Trovan, EURO I.D. Usling, Weilerswist, Germany). Individuals with a body mass below 50 g were individually marked with an ear marking (see 2.6 tissue sampling). For

each capture, we recorded sex and age (juvenile and adult). Juveniles are born within the respective study year, adults have hibernated at least once. We measured body mass to the nearest gram using a 100 g spring balance (Pesola, Baar, Switzerland; division: 2 g, accuracy: 99.7%). In addition, we measured tibia length, testis length and width of one testis to the nearest 0.1 mm using a sliding caliper. Tibia length is used as proxy for body size and as a determinant of the two age categories. In juveniles, tibia length was used to determine the age in days and subsequently the date of birth. Males were classified as reproductively active if testes were tangible. If so, morphometric measurements of one testis were used as proxy for the degree of reproductive activity (Moreno 1988; Bieber 1998). Females were classified as reproductively active, if they showed clear signs of gestation or lactation. The animals were returned into their nest boxes after the procedure.

### Sexual size dimorphism

To investigate the presence of sexual size dimorphism, we compared the tibia length of adult males and females. We used a linear mixed effect model with the function “lmer” from the package *lme4*, extended by the package *lmerTest* with Satterthwaite approximation for degrees of freedom (Bates et al. 2015; Kuznetsova et al. 2017), to explain the variation in the tibia length of all captured adult females and males. In addition, we included Julian day (day of sampling) as a covariate into the model, as yearlings still grow. Individual (ID) and year (2018–2021) were included as random factors. Analyses were conducted using RStudio Team (2021).

### Relative testes mass

The relative testes mass was used as an indirect indicator for sperm competition (Ramm et al. 2005). In rodents, testicular mass is in an allometric relationship with the body mass, with the function  $testes\ mass_{rodents} = 0.031\ body\ mass^{0.77}$  (Kenagy and Trombulak 1986). To compare observed and predicted testes mass in garden dormice, we calculated the predicted testes mass for the body mass observed in the field by using the above equation and compared it with the observed testes mass. Based on literature data, we assumed that 1 mg testis tissue corresponds to 1 mm<sup>3</sup> (Watson-Whitmyre and Stetson 1985; Sinha Hikim et al. 1988; Bailey et al. 1998). We calculated the volume of one testis (mm<sup>3</sup>) of reproductively active garden dormice by using the Hansen’s formula  $testis\ length(mm) \times testis\ width(mm)^2 \times 0.52$ . This has been shown to be the most accurate formula for estimating testis volume from caliper measurements (Peixoto et al. 2016). The volume of both testes (mm<sup>3</sup>) was converted into milligram and gram.

## Tissue sampling

From each first captured garden dormouse a tissue sample (ca. 1 × 2 mm) was collected from the ear for genotype analysis (permit: G-18-22 provided by the nature conservancy and the animal experiment department of the Regierungspräsidium Freiburg). Tissue samples were placed in 1.5 ml Eppendorf tubes with 70% ethanol. Samples were stored at – 20 °C until further analysis.

## Genetic analysis

For the genotype analysis DNA was extracted from the tissue samples using the Qiagen DNeasy® Blood & Tissue Kit. The extraction was performed according to the protocol included in the kit. 200 µl of template DNA were acquired from each tissue sample. For the genotype analysis five microsatellite markers: PZ3, PZ4, PZ6, PZ17, (Schoebel et al. 2013) and Gg8 (Hürner et al. 2009) were used. PCR amplification of each microsatellite marker was performed in 10 µl volume including 2 µl 5 × Green GoTaq® Reaction Buffer (Promega, Madison WI, US), 0.06 mM each dNTP (Promega), 0.05 µl GoTaq® G2 DNA Polymerase (5u/µl, Promega), 0.5 µM of each forward labeled Primer, 0.5 µM of each reverse primer (Supplementary Table S1), 1 µl of template DNA and 5,65 µl distilled water using Biometra TGradient 96 Thermocycler (Analytik Jena AG, Jena, Germany) or a Techne® Prime Thermocycler (Cole-Parmer, Stone, UK). PCR was conducted according to the protocols (Supplementary Table S2). Fragment length analysis of all five loci was performed using a capillary sequencer (ABI3730, Applied Biosystems) and a GS500LIZ size standard (Applied Biosystems). Allele size was determined and manually checked using GeneMapper (Applied Biosystems). If alleles could not be determined with certainty, the fragment length analysis was repeated. If alleles could not be determined with certainty even after repetition, the marker was marked as n. a. for the respective individual. The fragment length analyses, evaluation of the raw data and allele calling were performed by Seq-IT GmbH & Co. KG (Kaiserslautern, Germany).

## Characterization of microsatellite markers

For the allele frequency analyses only data from individuals captured as adults in the two study sites, were used. Allele numbers ( $k$ ) and frequencies, as well as observed ( $H_O$ ) and expected heterozygosity ( $H_E$ ) were determined for each marker. To determine if microsatellites could identify potential parents, we calculated the combined non-exclusion probability for the first parent (NE-1P), the second parent (NE2-P) and the parent pair (NE-PP). Additionally, we calculated the probabilities that two individuals are sharing the

same multilocus genotype (probability of identity, PI) and that related individuals share the same multilocus genotype ( $PI_{sib}$ ) (Waits et al. 2001). All analyses were performed using the software Cervus 3.0 (Marshall et al. 1998; Kalinowski et al. 2007).

## Parentage analysis

For parentage analyses, we considered only litters with at least three juveniles. At our study site, female garden dormice gave birth in ground holes and moved with their juveniles into the nest boxes afterwards (unpublished data), where they can be captured and sampled. Juveniles start leaving their nests at an age of 28–30 days and are weaned at an age of 34 days (Schlund 2005). In this study half of the sampled litters were captured before weaning. Thus, we cannot completely exclude that juveniles of an age above 34 days are found with unrelated juveniles within the same nest. To minimize the risk of considering older juveniles (after weaning) from different litters as sibs, we only regarded them to belong to the same litter, if they were found within the same nest box and were of the same age (with comparable development, tibia length and body mass). Some litters were recaptured several times until starting hibernation. To identify parentage of litters, we first assigned potential mothers to all juveniles of one litter. An adult female was assumed to be the mother of a litter, if she was found within the same or a neighboring nest box of the litter and could not be excluded from maternity by allelic mismatches of the markers analyzed. In two families (family 5 and 8), the females found in the nest box together with juveniles, were excluded from being the genetic mother of all juveniles due to a single allelic mismatch. These juveniles (two in family 5, three in family 8) were not considered to belong to the litter and were excluded from further analysis. In one case (family 13) two closely related females likely being mother and daughter, could genetically both not be excluded from being the genetic mother of a certain litter. However, one of these females was identified to be the genetic mother of family 6, and was therefore excluded as the potential mother of family 13. In a second step we assigned adult males to juveniles in litters with known genotyped mothers. Males were only considered as potential fathers if they did not show any mismatches with a juvenile-mother pair. Allele matching for each allele was performed using Cervus 3.0 software (Marshall et al. 1998; Kalinowski et al. 2007).

## Multiple paternity

Multiple paternity was detected indirectly by the number of alleles found in the juveniles of one litter. Siblings of a litter without a known genetic mother, were considered to be sired by more than one male if the combination of



the alleles could not be explained by only two parents, even when assuming that both passed two different alleles to the young. In one case (family 4) two juveniles were homozygous at one locus (PZ3) but with different alleles (122 and 124). In this case, one additional allele (118) occurring within the litter, indicated multiple paternity. Litters with a known genetic mother were considered to be sired by more than one male if they had at least three different alleles for a certain marker, besides those of the mother.

## Results

### Allele numbers and frequencies

We genotyped 32 adult garden dormice (16 females and 16 males) from both study sites. The number of different alleles found in the five loci analyzed varied between three and eight (Table 1). Observed multilocus heterozygosity was lower (0.481) than expected heterozygosity (0.617). The combined non-exclusion probability was 0.159 for the first, 0.042 for the second and 0.005 for the parent pair. The probability of two unrelated adult garden dormice sharing the same genotype was 0.000074 and the probability of two related adult garden dormice sharing the same genotype was 0.025 (Table 1).

### Maternity analyses

We genotyped 54 juveniles belonging to 14 different families, with litter sizes varying between three and five juveniles, note that litters with two juveniles were not considered. In 9 of these families (64%) and for 37 juveniles, the genetic mother could be determined based on her genotype combined with nesting behavior (Table 2, Supplementary Table S3).

**Table 1** Characteristics of the five microsatellite markers for 32 adult garden dormice (16 females and 16 males)

Locus	k	N	H <sub>o</sub>	H <sub>E</sub>	PIC	NE-1P	NE-2P	NE-PP	PI	PI <sub>sib</sub>
GG8	5	31	0.581	0.506	0.426	0.873	0.755	0.62	0.324	0.582
PZ3	7	32	0.625	0.824	0.789	0.54	0.363	0.179	0.058	0.359
PZ4	7	31	0.29	0.819	0.781	0.554	0.376	0.193	0.063	0.363
PZ6	8	32	0.75	0.785	0.738	0.615	0.437	0.252	0.086	0.385
PZ17	3	31	0.161	0.153	0.143	0.989	0.926	0.864	0.729	0.857
Multilocus			0.4814	0.617	0.575	0.159	0.042	0.005	$7.4 \times 10^{-5}$	0.025

Number of alleles (k), number of individuals analyzed (N), observed heterozygosity (H<sub>o</sub>), expected heterozygosity (H<sub>E</sub>), polymorphic information content (PIC), non-exclusion probability for the first parent (NE-1P), the second parent (NE-2P) and the parent pair (NE-PP), probability of identity for unrelated (PI) and related (PI<sub>sib</sub>) individuals, for each locus separately and for all loci combined

**Table 2** Families, study site, study year, mother, litter size and the number of males that sired juveniles of one family

Family	Study site	Study year	Mother	Litter size	Minimum number of fathers
1	RL	2018	74c-27c1	4	1
2	RL	2018	74c-3875	3	1
3	WK	2019	Unknown	4	1
4	WK	2019	Unknown	3	2
5	WK	2020	74e-df7e	3	2
6	RL	2020	74d-ef91	5	1
7	WK	2020	Unknown	3	1
8	RL	2018	74c-27c1	5	2
9	RL	2018	Unknown	4	2
10	RL	2019	74c-3875	5	2
11	RL	2019	Unknown	3	2
12	RL	2020	74b-f3dd	3	2
13	RL	2020	74c-3875	4	2
14	RL	2021	74b-f3dd	5	2

### Paternity analyses

In 27% of the juveniles (10 out of 37), with known mothers, we found between 1 and 5 adult males that could not be excluded from being the genetic father by mismatches. In 2020 we found one male (74b-e19a) which was the potential father of two juveniles of family 12 and of one juvenile in family 13, revealing that this male mated with at least two different females within the same year. In the remaining 27 juveniles all adult males were excluded from being the genetic father by at least one mismatch with the mother-juvenile pair.

### Multiple paternity

In 64% (9 out of 14) of the families, juveniles of one litter were sired by at least two different males. Female 74b-f3dd gave birth in 2020 (family 12) and in 2021 (family 14). In both years her juveniles were sired by more than one male.

Female 74c-3875 gave birth every year from 2018 to 2020 (families: 2, 10, 13), with her juveniles being sired by at least two males in both 2019 and 2020. In 2018, one of the two litters of female 74c-27c1 was sired by at least two males. Multiple paternity was detected in both study sites, in RL multiple paternity occurred in 70% (7 out of 10) of the families analyzed, in WK 50% of the litters were sired by multiple males (2 out of 4, Table 2, Supplementary Table S3).

### Sexual size dimorphism

Adult males had a tibia length of 33.5 mm (SE  $\pm$  0.4 mm,  $n=29$ ,  $N=20$ ), which was slightly but significantly larger than the tibia length of adult females 32.5 mm (SE  $\pm$  0.6 mm,  $n=65$ ,  $N=16$ , Table 3).

### Relative testes size

Male garden dormice with tangible testes ( $n=11$ ) had a mean body mass of 60.7 g (SD  $\pm$  7.2 g) with a mean testis length of 14.3 mm (SD  $\pm$  2.4 mm) and mean testis width of 6.3 mm (SD  $\pm$  1.3 mm). Based on the equation given above, the expected testes mass for a rodent with a body mass of 60.7 g is 0.15 g. Garden dormice males of this study had a median testes volume of 0.59 cm<sup>3</sup> ( $Q_{25}=0.42$  cm<sup>3</sup>,  $Q_{75}=0.64$  cm<sup>3</sup>), which corresponds to a testes mass of 0.59 g. Thus, observed testes mass is nearly four times above the expected testes mass for a rodent with a body mass of 60.7 g.

## Discussion

The knowledge of the mating system of a threatened species provides important information for the implementation of conservation measures (Sigg et al. 2005; DeMay et al. 2016; Nardelli et al. 2020; Madsen et al. 2023). In the studied garden dormouse population, we identified the genetic mother in 64% of the litters and in 27% of these mother juvenile pairs we were able to assign the potential fathers. 64% of the litters (9 out of 14) were sired by at least two males. Rates of multiple paternity differed between the

two study sites, but as both study sites are located in close proximity (1 km apart) we assume that these differences are due to limited sample sizes. With our marker set the non-exclusion probability of the first parent is comparatively high and the probability of closely related individuals sharing the same multilocus genotype is above the recommended value of 0.01 (Waits et al. 2001). Nevertheless, we are confident that our microsatellite marker set, combined with behavioral observations of the nesting behavior of potential mothers with their litters, suffices to determine paternity in this population. Although we were only able to show in one case that a male reproduced with more than one female within a reproductive period, we strongly suggest that both sexes generally mate with several partners and have a promiscuous mating system as our genetic findings were further supported by indirect indicators of promiscuity.

In promiscuous species, males do not compete directly for receptive females, but through sperm competition (Firman and Simmons 2010). Accordingly, these species are expected to lack sexual size dimorphism and should have relatively large testes (Heske and Ostfeld 1990). Thus, the relative testes mass of males can be used as a proxy for the mating system, with monogamous or extremely polygynous species having comparatively small testes. Here males monopolize receptive females and sperm competition does not play a role. In promiscuous or polygynous species with strong sperm competition, testes are large relative to their body mass (Kenagy and Trombulak 1986). Typical for a promiscuous species, garden dormouse males have testes that are almost four times larger than expected for a rodent of its body mass, suggesting that sperm competition is important for male reproductive success (Ramm et al. 2005). Also matching expectations for a promiscuous species, garden dormice showed a weak sexual size dimorphism, with males being only slightly larger than the females. Previous studies of their ranging behavior also suggested that males use large home ranges overlapping with those of several females in order to gain access to them when they are in estrus (Vaterlaus 1998; Bertolino et al. 2003; Wolff 2007). A promiscuous mating system would not be surprising in garden dormice, as it has been found in other dormouse species like in edible (Weber et al. 2018; Moska et al. 2021) and hazel dormice (Naim et al. 2011), and is generally common in other rodent species, like wood mice (*Apodemus sylvaticus*, Bartmann and Gerlach 2001), yellow necked mice (*A. flavicollis*), Ural field mice (*A. uralensis*), striped field mice (*A. agrarius*, Bryja et al. 2008), Brandt's vole (*Lasiopodomys brandtii*, Huo et al. 2010), and North American red squirrel (*Tamiasciurus hudsonicus*, Lane et al. 2008). Compared to the edible dormouse with rates of multiple paternity between 70 and 100% (Weber et al. 2018; Moska et al. 2021) and the hazel dormouse with 94 and 100% multiple paternity

**Table 3** Results of the linear mixed effect model explaining the variance in the tibia length of adult garden dormice ( $n=31$ ,  $N=16$ )

	Estimate	SE	df	t value	p
(Intercept)	32.54	0.60	50.15	53.85	<0.001***
Julian day	0.01	0.002	71.36	4.26	<0.001***
Sex <sub>male</sub>	0.96	0.42	31.83	2.31	<0.05*

Reference level are females. Variance of random effect (ID) is 1.21, Variance of random effect (year) is 0.2, residual variance is 0.38,  $R^2_m=0.12$ ,  $R^2_c=0.81$

\*Refers to p value < 0.05, \*\*\* refers to p value < 0.001

(Naim et al. 2011), garden dormice of this study showed a lower rate of multiple paternity (64%). However, we assume that the proportion of multiple paternity in this garden dormouse population is underestimated, because we analysed only paternities of litters with at least three juveniles and we further detected multiple paternity only indirectly by counting alleles and not by identifying individual males as genetic fathers (Burton 2002), and we assumed that both parents were heterozygous if they were unknown. Furthermore, we did not perform observational studies of male mating attempts and therefore could not exclude mechanism of postcopulatory sexual selection (Ramm et al. 2005). We were able to identify the genetic father in only 26% of those juveniles with known mothers. The low proportion of identified fathers could be explained by a low capture probability due to them preferring to use natural nesting sites instead of nest boxes or having home ranges outside of our study site. It has been shown that population density can positively influence the rate of multiple paternity, due to higher mate encounter rates (Bryja et al. 2008; Dean et al. 2006). Therefore, we cannot exclude an effect of the population density on the comparatively low level of multiple paternity in our garden dormouse population compared to those found in other dormouse populations (Naim et al. 2011; Weber et al. 2018; Moska et al. 2021).

The maintenance of genetic variability was shown to be strongly influenced by the mating system in different taxonomic groups (e. g. Cohas et al. 2008; Lewis et al. 2020; Madsen et al. 2023). In promiscuous and polyandrous species, females avoid inbreeding by mating with multiple, potentially unrelated males (Stockley et al. 1997). Litters sired by multiple fathers also show a higher level of heterozygosity (Foerster et al. 2003; Rafajlović et al. 2013; Batova et al. 2021) increasing the offspring's individual genetic diversity and potentially its fitness (Suter et al. 2007; Huo et al. 2010). Additionally it can increase  $N_e$  and thus counteract the loss of genetic variability (Frankham 1995a). The main natural habitat of garden dormice in Germany are forested areas (Schlund 2005), which are highly fragmented, with nearly 98% of the fragments being smaller than 1 km<sup>2</sup> (Mann et al. 2023). For small mammals like the garden dormouse even roads can act as barriers, as has been shown for mice (*Apodemus sylvaticus*, Ascensão et al. 2016; *A. flavicollis*, Rico et al. 2007), bank voles (*Myodes glareolus*, Rico et al. 2007), common shrew (*Sorex araneus*, Rico et al. 2007) and edible dormice (*G. glis*, Fietz et al. 2014). In a radio tracking study conducted at the same study sites, we observed that even forest trails (3 to 4 m width) pose a barrier for garden dormice (unpublished data), dividing the habitat into smaller patches. This can have a significant impact on mating opportunities and consequently on genetic variability

and population persistence (reviewed by Banks et al. 2007; Giuntini and Pedruzzi 2022).

Based on our genetic findings and morphometrics, we suggest that garden dormice mate promiscuously. Forest fragmentation may limit the accessibility to potential mating partners, reducing their genetic variability and chance of survival (Banks et al. 2005). In order to find susceptible females, male garden dormice roam through large home ranges during mating (Vaterlaus 1998, unpublished data). Forest fragmentation can prevent both sexes from finding potential mating partners and therefore reduce their mating success (Lane et al. 2011; Anthonysamy et al. 2014). In populations occurring in small isolated patches with low population sizes the level of multiple paternity can be lowered, as was shown for agile antechinus (*Antechinus agilis*) inhabiting small habitat fragments (Banks et al. 2005). This can reduce the fertilization rate and increase the risk of sperm incompatibility, ultimately reducing reproductive success (Zeh and Zeh 1997; Hoogland 1998). All of this may also apply to the garden dormouse. Additionally, a lower rate of multiple paternity could decrease genetic variability within garden dormice siblings, as the level of heterozygosity in a litter is positively linked to the number of fathers (Rafajlović et al. 2013; Taylor et al. 2014). Those offspring can be assumed to have a lower fitness, as genetic variability is positively correlated with fitness (Chapman et al. 2009; DeWoody et al. 2021).

In mammals, females are often the philopatric sex (Greenwood 1980), which can also be assumed for garden dormouse, as we frequently recaptured juvenile females as adults within the same study site and found one female frequently nesting together with her mother (ID: 74d-ef91, 74c-3875). In mammals, males often disperse, reducing kin competition and the risk of inbreeding (Li and Kokko 2019). However, impeded dispersal of juveniles through habitat fragmentation could lead to an increased relatedness among garden dormice within a forest patch, as was shown for the closely related hazel dormouse (Bani et al. 2017). In cases where no kin avoidance mechanisms exist, this would increase the risk of inbreeding depression and genetic drift (Banks et al. 2005; Walker et al. 2008). In addition to fitness benefits for males and females, promiscuity is known to increase  $N_e$  (Sugg and Chesser 1994). However, if inbreeding is increased due to lower levels of multiple paternity and limited dispersal abilities, the effective population size decreases (Sugg and Chesser 1994; Taylor et al. 2014). This could lead to higher genetic drift and fixation of deleterious genes in this population, which consequently influences survival (Palstra and Ruzzante 2008; Charlesworth 2009).

Many rodent species show a high plasticity in their mating system (Waterman 2008), depending on resource availability, population density and fragmentation (McEachern et al. 2009; Maher and Burger 2011). Thus,

the promiscuous mating system in the garden dormouse population of the Black Forest may represent an adaptive behavioral response which buffers the discussed negative effects of habitat fragmentation on genetic variability (Lange et al. 2013; Lewis et al. 2020). Thus, the relatively high rate of multiple paternity may also be a consequence of forest fragmentation. For example, Fietz et al. (2014) showed that edible dormice inhabiting forest fragments did not have a lower genetic variability than those inhabiting continuous forest. This could be a consequence of the high level of multiple paternity in this species, as was shown by Weber et al. (2018) and Moska et al. (2021).

Whether the level of multiple paternity observed in the studied garden dormouse population is an adaptive response to forest fragmentation, or whether forest fragmentation reduces the occurrence of multiple paternity, cannot be answered by this study. Nevertheless, we assume that the promiscuous mating system in garden dormice is important for maintaining genetic variability, reducing the risk of inbreeding and increasing the  $N_e$  of populations and therefore their adaptability to environmental changes (Frankham 1995b, 2005; Palstra and Ruzzante 2008; Kardos et al. 2021). Although multiple mating may be sufficient to maintain genetic variability, as was shown for *Vipera berus* on a small isolated island where multiple and non-random mating maintained genetic variability after a severe bottleneck (Madsen et al. 2023), suitable garden dormice habitats should provide high functional connectivity to reduce the loss of genetic variability and thus the adaptive potential to environmental change, which is crucial for population viability and persistence (Frankham 1995b; Hedrick and Kalinowski 2000; Palstra and Ruzzante 2008). As connecting suitable habitats facilitates dispersal and promotes access to potential mating partners, which may be particularly important for populations colonizing new habitats (Power and Holman 2014; Lewis et al. 2020), connecting habitats represents a key conservation measure for the garden dormouse. The results of our study should also be considered in conservation breeding programs, and in translocation and reintroduction programs of garden dormice, in order to maintain the genetic variability of these populations (Gregory et al. 2012; DeMay et al. 2016).

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**Data availability** The dataset used in the current study is available from the corresponding author on request.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interest to disclose.

**Ethical approval** This work was conducted under license from the nature conservancy and the animal experiment department of the Regierungspräsidium Freiburg (G-18–22) and permit given by the Black Forest National Park.

**Informed consent** All authors have read, commented on and approved the manuscript.

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