
Twenty-four-year investigation of the reproductive biology of *Glis glis* in England (Rodentia: Gliridae)

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Abstract. Nest boxes were used to monitor a population of edible dormice (*Glis glis*) for 24 years. Details were recorded of reproductive condition, age and co-habitation by ca. 10,000 tagged individuals. Age at first breeding, periodic failure to breed, ‘absenteeism’ among adults, changing litter size with growth of young, survival rates and lifetime reproductive output were documented. The proportion of communal breeders and their kinship was examined as well as the occurrence of breeding by subadults. Life strategy and potential benefits of seasonal and annual behaviour are discussed.

Key words. Dormice, Gliridae, introduced species, longevity, reproduction, litter size, kinship, life strategy, hibernation, ‘absenteeism’.

INTRODUCTION

The edible dormouse *Glis glis* (Linnaeus, 1766) was introduced to Great Britain in 1902, with damage to forestry interests and nuisance within houses becoming evident by the 1950s (MORRIS 1997). A significant increase in distribution and population size has occurred since then (TROUT & MOGG 2017, TROUT et al. in press), along with an increasing need for population control measures. Apart from distribution surveys and assessments of forestry damage, few studies of this species have been made in Britain, yet understanding population dynamics, population density, reproduction and survival rates is essential for scientifically based control measures and for quantifying possible effects of climate change. They hibernate, with an active period normally lasting about five months (with seven months in hibernation), but research elsewhere may not be fully relevant as Britain lies outside the natural distribution of this species in Europe. A population study was therefore initiated in 1995. Basic information regarding numbers, reproduction and survival rates among individual animals was recorded from October 1995 until the end of 2018, a total of 24 seasons. The use of nest boxes in the present study enabled samples of tagged animals to be monitored regularly, providing an opportunity to investigate aspects of social behaviour, such as communal nesting and the aggregation of litters to form creches.

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STUDY AREA, MATERIALS AND METHODS

The study site, Hockeridge Wood, lies about 60 km north-west of central London, 2 km from Berkhamsted in Hertfordshire (51°45'N, 0°40'W). It is deciduous woodland, mainly stands of beech *Fagus sylvatica*, with some softwood species present, especially spruce *Picea abies* and Scots pine *Pinus sylvestris*. Wooden nest boxes were attached to tree trunks about 3 m above the ground, in lines, and approximately 20 m apart. Initially there were 145, covering about 20% of the site, with more added in 2008 (TROUT et al. 2015). The 220 nest boxes then covered about a third of the wood at a density of ca. 6.7 per hectare.

Nest boxes were checked once each month during the season of *Glis* activity until 2008 and twice per month thereafter. Monthly inspections ceased each year when all the animals were likely to have left the nest boxes and retired to their hibernacula, usually by November. Capture and release were licensed under the provisions of the Wildlife and Countryside Act 1981.

Beech trees periodically produce a heavy crop of flowers, then fruits, referred to as “mast” (HILTON & PACKHAM 2003) and it soon became clear that masting events played a key role in reproductive activity (MORRIS & MORRIS 2010). A record was kept of “masting years”, when the beech flowering was conspicuously abundant, contrasting with years when there were few fruits on the beech trees or none at all. The term “breeding year”, as used here, refers to years in which many new-born young were present in the nest boxes. In “non-breeding years” there were very few or none at all. Additionally, on average, only a third of adults known to be alive are found in boxes in non-flowering years as opposed to 90% in breeding years (TROUT et al. 2015).

Each animal was recorded and assigned an age category based on the following criteria: **Pink newborn**: hairless with eyes closed, weight <20g; **nestling**: suckling, dependent individual in the presence of siblings and/or its mother; **juvenile**: individual young of the year, regardless of weight, that was found alone or with others of similar size, apparently independent of their mother; **subadult**: animal that was born the previous year; **adult**: animal that was born more than one year previously; **litter** refers to a group of nestlings.

Nestlings weighing <20 g in August were assumed to have been born that month. They were counted and then weighed, either collectively or separately, depending on size. Animals of adequate size were marked individually using 12 mm by 2 mm diameter microchips (‘PIT tags’ – AVID/Labtrac UK) and, by the end of 2018, the capture database comprised more than 25,000 records representing ca. 10,000 individual *Glis*.

Adult female breeding condition was noted, based upon external indications such as presence of a sperm plug, visibly pregnant, signs of recent birthing, prominent nipples evidently lactating or post lactating. Each animal was assigned a likely birth date within the database using a set of algorithms based on a ‘weight vs. age’ analysis of animals of known age and month of first marking. Using these rules, a month and year of birth of each *Glis* was assigned retrospectively and applied in a 24-year calendar-of-captures spreadsheet. The number of litters produced during the known lifetime of females was collated.

Instances of communal breeding were identified where several adult females were found together in a single box (at various stages of breeding: pregnant; lactating; post lactation) with at least one live young. There were also cases where nestlings occurred together in groups of noticeably different body mass, indicating that they were unlikely to be siblings. From 2008 until 2018, fortnightly nest box checks were made and most young were microchipped well before they left the nest. This provided samples of tagged nestlings that were individually identifiable and could be associated with particular tagged females to explore whether communally breeding adults were related.

Information on nestling population trends over time (e.g. number of newborns, number of litters, litter sizes, nestling weight) were extracted using pivot tables. Generalized linear models (GLMs) were used to analyse monthly and annual variations in nestling population trends using the statistical software R version 4.2 (R Core Team 2022). Non-normal residual error distribution and over dispersion were tested for using the R packages ‘AER’ and ‘DHARMA’ (VER HOEF & BOVENG 2007). Any over-dispersion was accounted for using GLMs with quasi-poisson or negative binomial errors. When measuring changes in death rate (where the response variable is a percentage), a GLM with quasi-binomial errors was used to account for over dispersion.

RESULTS

There were 2,676 individually tagged adult females recorded during the years 1995–2018, with 10,451 captures of females, with many being found in several years. There were 1,277 breeding events recorded. Breeding did not take place every year (Fig. 1).

In 10 of the years, beech trees produced conspicuously abundant mast and many females bred. In six of the years, masting was less abundant and fewer females bred. Masting failed in eight of the years and there was no evidence of breeding (except 1 litter in 2017). Masting sometimes occurred in successive years but non-masting was always followed by a masting year.

Overall, a minimum of 45% of known adult females, captured at least once in breeding years, appeared to have given birth. The proportion participating in breeding in a given year ranged from 8% in 2006 to 71% in 2002. In eight very good breeding years the proportion was 50% or more (but including 2009 when over 1,000 adult females were recorded).

Breeding females apparently gave birth to between one and five litters in their lifetime (Table 1).

The majority (70.3%) appear to have bred only once, but this also reflects the decreasing numbers that survive long enough to breed multiple times. Just over half of all litters produced were born to multiple breeders, with 12% producing 4 or 5 litters in their lifetime. Overall, 87% of litters are newborn in August, 12% in September and 1% in October (686, 96, and 6 litters with ‘pink newborns’ respectively). Late-born litters are unlikely to survive the winter. The mean litter size at birth, or soon after, was 6.6 (SE=0.35), and did not change significantly over the study period.

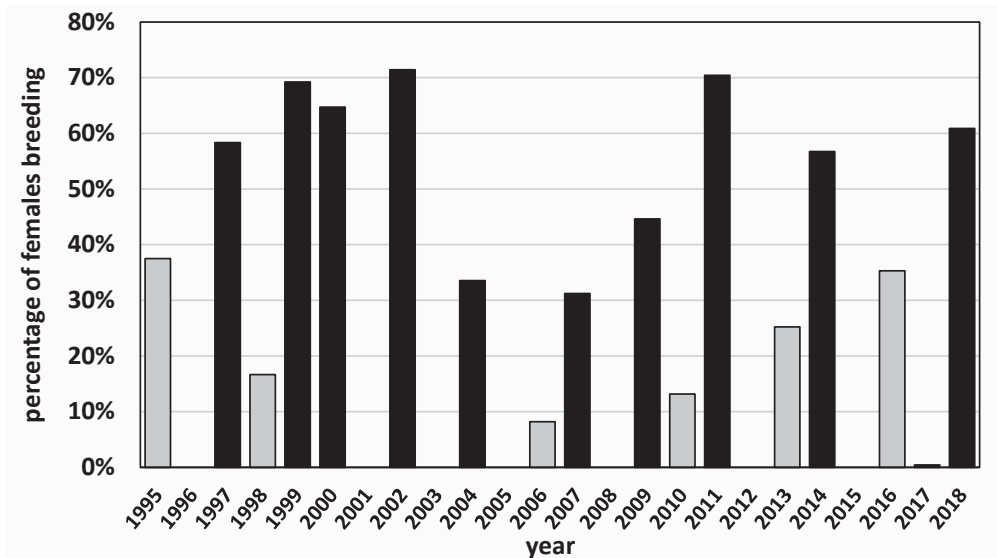


Fig. 1. The proportion of breeding females in each year of full (black bars), partial (pale bars) and no beech flowering. (NB in 2009 over 1,000 adult females were recorded, although only 45% of them were breeding.)

Table 1. The number of litters per breeding female observed over their known lifetime

lifetime number of litters born	No. of breeding females monitored	% producing that litter size	total number of litters of that size born	% of all litters
1	692	70.3	692	47.5
2	171	17.4	342	23.5
3	79	8.0	237	16.3
4	30	3.0	120	8.2
5	13	1.3	65	4.5
total	985	100	1456	100

The number of adult females encountered in the nest boxes gradually increased throughout the study period (Fig. 2), both in breeding and non-breeding years, reflecting a steady overall increase in population size.

For non-breeding years the number recorded was substantially lower than in the preceding and succeeding breeding years, confirming (as reported in our previous studies) an occurrence of temporary ‘absenteeism’, where animals are not found during a year and may be presumed dead, but are known to be alive because they re-appear in subsequent years.

During the study period, the annual number of litters has increased significantly ($t=4.49$, $p=0.00061$, $R^2=0.72$), Fig. 3, reflecting an increasing *Glis* population at the study site as reported

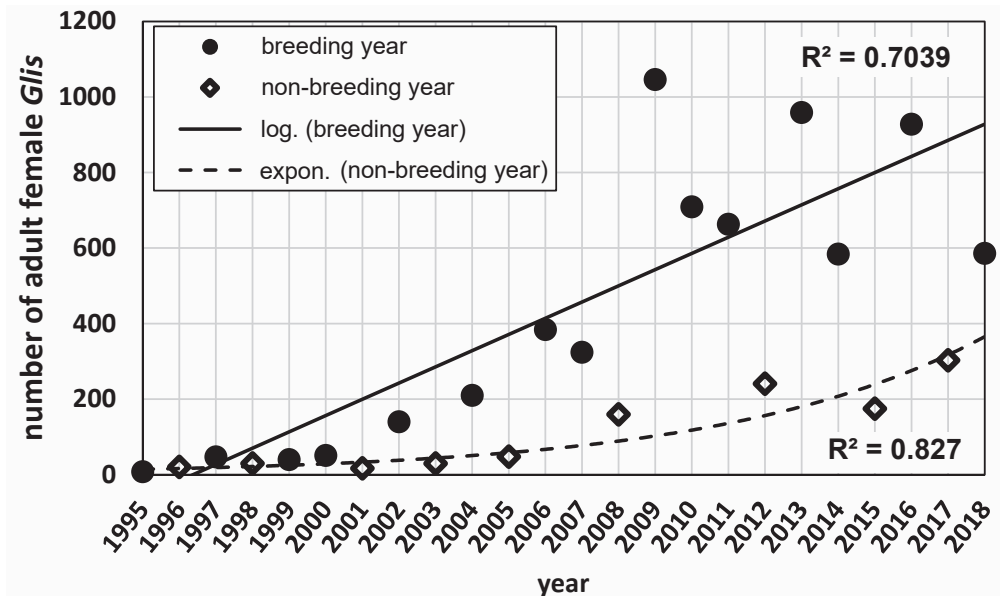


Fig. 2. The numbers of adult females recorded in breeding years and non-breeding years.

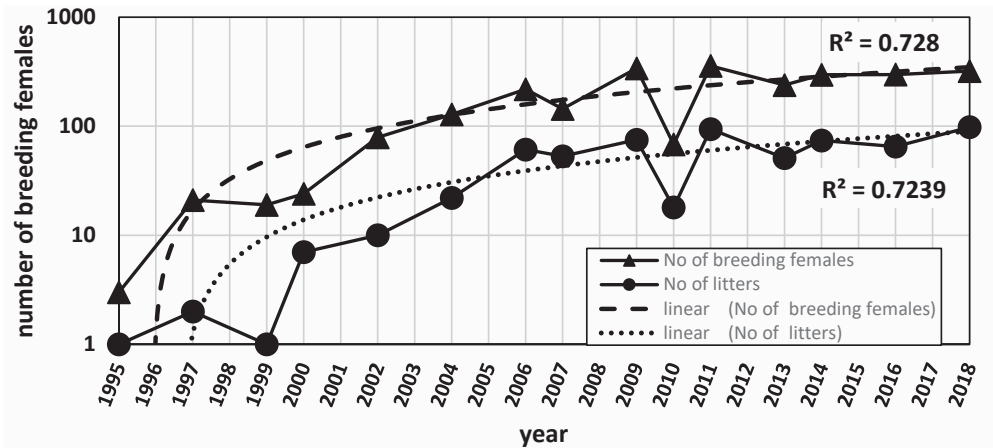


Fig. 3. Change in numbers of breeding females and of litters found during the study (15 breeding years only).

by TROUT et al. (in press). Similarly, there was also a significant increase in the annual number of newborns ($t=4.45$, $p=0.00065$, $R^2=0.64$; Fig. 4).

Litter size and growth of nestlings

As expected, there was an increase in the average weight (g) of nestlings (i.e. those marked animals still in their original nests with siblings and/or mother present), reflecting the actual growth of known individuals that were followed over the 3 months from birth (Table 2).

The average monthly weights of those individuals followed over August, September and October increased significantly. Between August and October, the mean weight of nestlings increased nearly five-fold in about 60 days, an average weight gain of more than 1 g per day. Overall, the combined 3-month average nestling weights rose significantly through the study period ($z=2.1$, $p=0.035$, $R^2=0.2$). However, as the nestlings grew larger, the recorded litter size (Table 2) simultaneously decreased significantly throughout the same period, reflecting death of nestlings or dispersal as they left the nest. The rate at which litter size declined in these autumn months decreased over the whole study period, but this trend was not statistically significant ($z=-0.112$, $p=0.91$).

Table 2. Mean weight (g) and litter size of tagged nestlings recorded for 3 months

	August	September	October
sample size	1085	1076	335
mean weight (g)	17.29	47.41	85.20
standard error	2.10	4.10	5.50
litter size	6.60	5.41	4.29
standard error	0.36	0.29	0.23

Communal breeding and kinship

Adult males were only found associating with females early in the season (May–June). By early July, nest boxes were predominantly occupied by females. Adult males were never found sharing a nest box with a heavily pregnant female or with a litter of nestlings. A total of 2,653 instances of breeding were recorded in our nest boxes with some communal breeding evident (Table 3).

Single females were present in 89.5% of breeding locations, but up to four females in breeding condition were sometimes found co-habiting in a nest box. Communal breeding was observed in 10.4% of nest boxes and 21.7% of breeding females were involved in communal breeding.

The unique microchip numbers enabled a search of the database to determine whether the individual females involved in communal breeding were related to each other ('kin'). The data included those where the co-habiting adults were pregnant or nestlings were present. Each recorded communal breeding event was scrutinised for evidence of kinship, for example by being mother and known daughter or previously being found as offspring of one mother and microchipped in the same nest box at the same time. Categories were identified as 'definitely related,' 'very likely related', 'definitely not related', or 'indeterminate' (where kinship could not be verified e.g. because litters from unrelated mothers had been marked, but nestlings could not be allocated to an individual mother).

There were 790 valid lines of data indicating communal breeding occurrence where the microchip history was known. There were 226 cases where communal breeding events involved 'definite' directly related individuals. A further 70 cases were 'very likely' close relatives. The largest group, 120 records, were associated mother and their daughter(s), including three breeding females with their granddaughters. There were 72 records of sisters breeding together,

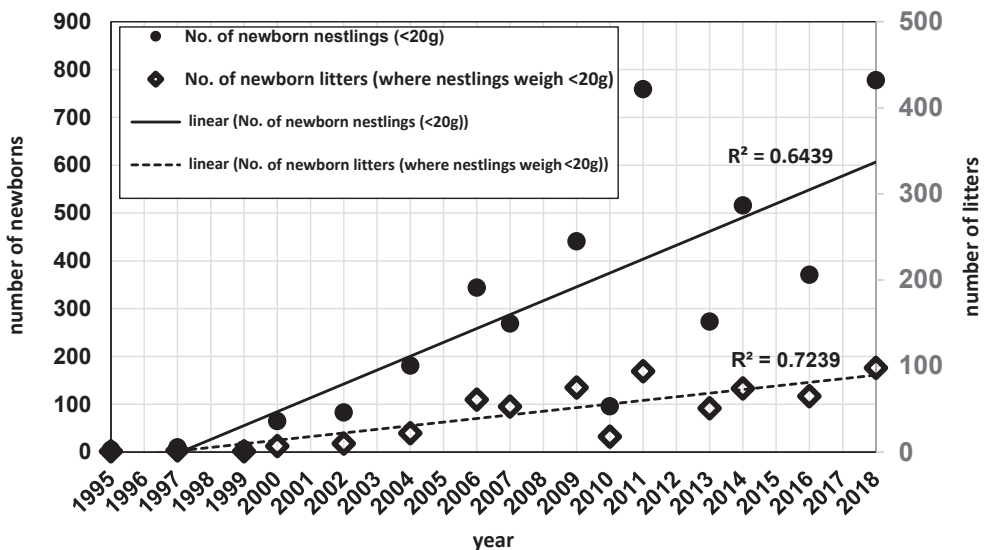


Fig. 4. The annual number of newborns (animals weighing <20 g) and the annual number of litters containing newborns over the course of the study (1995–2018).

Table 3. The occurrence of communal breeding

group size	No. of groups recorded	No. of adult females involved
1	2,136	2,136
2	229	458
3	17	51
4	2	8
total communal	248	517

(including 2 siblings that were 13 years old). On 104 occasions, a lactating mother was recorded, accompanied by a known sister or daughter that appeared to be pregnant or have young of her own. Altogether, there were 296 instances of communal breeding recorded, involving known kin and 268 cases where communally nesting mothers were definitely not related. In 29% of cases, relationship could not be determined, usually because one of the females was unmarked or where several litters were present (in one case 19 nestlings) and parenthood was not possible to determine. Thus of 564 cases where breeding females shared a nest box, 52.5% involved kinship and 47.5% did not.

Without DNA analyses (outside the scope of our study) we cannot determine kinship or breeding outcomes for males.

Subadult female breeding

Subadult breeding involves young females that have survived their first hibernation and become pregnant in their second calendar year. Because periodic breeding failure occurs in this species (Fig. 1), breeding in the year following birth (i.e. after one hibernation) only happens when breeding in the population as a whole occurs in two successive years. As shown in Fig. 1, successive breeding years occurred in 1999/**2000**; 2006/**2007**; 2009/**2010** (and **2011** making a third successive year); 2013/**2014**.

Evidence was sought of breeding, or lack of it, from those microchipped nestlings and juveniles that were also captured in the summer that followed their first hibernation. An example of subadult breeding was a juvenile marked in early October 1999 at 52 g and recorded as lactating with nestlings in early September 2000. Individuals that were not captured in a succeeding year were ignored for this analysis.

Of 4,599 juvenile females marked in the relevant years, many were not seen in the subsequent breeding year, even though some were known to be alive. The number of subadults recorded in the summer after their first hibernation was 1,752 (38% of those tagged). Of these, 1,722 were not recorded as showing any evidence of breeding. The 30 individuals with positive evidence of breeding comprised five pregnant individuals, 23 with litters, and two post lactation. Thus, only 1.7% of subadult individuals were shown to have bred after their first hibernation, whilst 98.3% did not.

Survival and longevity

The weight/date algorithm applied to the first capture date created the birth month for all animals. The calendar of captures spreadsheet also recorded the last known date of capture

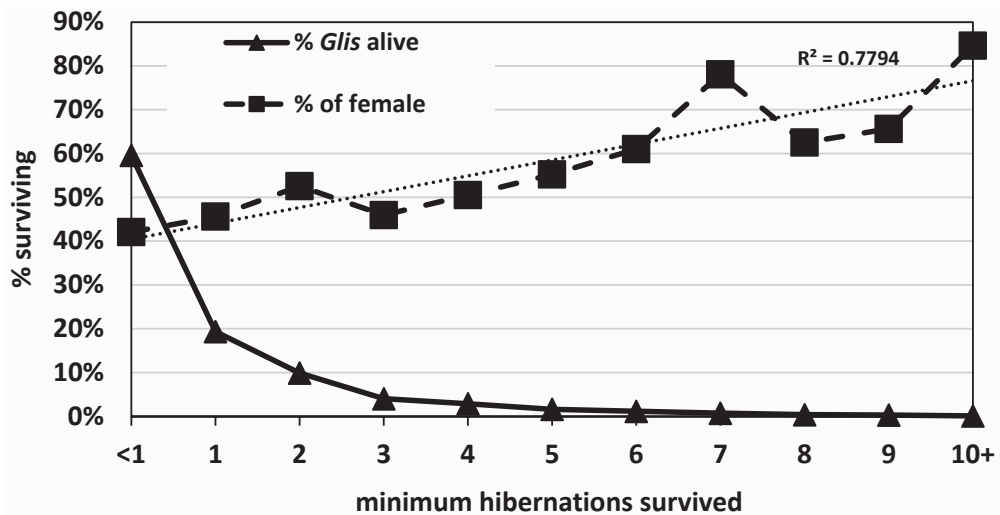


Fig. 5. Overall survival rates, based on the number of hibernations survived, and the proportion of survivors that were female.

and the difference was the known survival from birth. These are minima, especially for older animals because the algorithm potentially underestimates the age of old adults captured for the first time. The age/weight criteria used could not estimate an earlier birth year than before the previous non-breeding year. Eleven percent of all *Glis* were at least six years/hibernations old (Fig. 5) and the oldest had survived 13 hibernations.

Females were more likely to survive than males. From 4 years of age, females predominated and from 6–9 years they formed more than 60% of the survivors. At 10–14 years females represented 85–100% of survivors.

DISCUSSION

Females in our population of *Glis glis* produced only one litter per year, mainly in August. This, and other basic features of reproduction, confirm the general pattern described by MORRIS & MORRIS (2010) for a sample of ca. 1,000 individuals compared to the current 10,000. This includes periodic failure to breed at all (usually in alternate years, with exceptions, Fig. 1). Comparable data from several European populations are described by LEBL et al. (2011). Within a wide range, on average 45% of all females reproduced in tree masting years, whereas in non-masting years almost none (only 5) bred. Litter size at birth was ca. 6.5, declining with the age of the young, until they left the nest, mainly in October.

Mothers will occasionally respond to disturbance by taking their newborns to another place and this possibly contributes to the reduction in number of litters counted, from 1,085 in August to 1,076 in September, but does not explain the decline in average number of nestlings as they grow larger. Dispersal will only account for reduced numbers in October as juveniles do not appear to become independent until they weigh more than about 65 g (MORRIS & MORRIS

2010). Progressive reduction in the average litter size during the first three months of life may also reflect cannibalism, contributing to the unusually rapid rate of growth among nestlings as speculated by MORRIS & MORRIS (2010). Predators will usually take the whole litter.

Thus, since periodic breeding failure occurs, females often do not breed until their third calendar year, following a second hibernation. Consequently, those producing 4 or 5 litters are very long-term survivors, but they contribute a significant proportion of the production of young, with 29% of all litters being from females producing 3, 4 or 5 litters over their lifetime. Our data suggest that, for a very dense population, there is a high mortality rate during the first autumn and winter.

Given that only a single litter is born per year, and not until the third calendar year, with periodic failure to breed at all, it is hard to see how the population could increase, locally or nationally, to the extent demonstrated here, except for the longevity that we and others have confirmed. PILASTRO et al. (2003) and KRYŠTUFEK (2010) report individual *Glis* surviving over 5, and up to 9 years after their first hibernation (some breeding females here surviving at least 10 hibernations). *Glis* thus appears to behave as a classic k-selected species, a life strategy not normally associated with rodents. Perhaps this was originally a strong selection factor when adapting to the periodic occurrence of non-flowering years among key tree species.

Overall, 10% of breeding in nest boxes comprised communal breeding, involving just over 20 percent of breeding females. This is similar to other studies (MOSKA et al. 2021, PILASTRO et al. 1996). The challenge to establish whether or not co-habiting females were related rested on our microchipping history being adequate. Thirty percent of cases had to be excluded. For those where the relationship could be established, half were and half were not closely related 'kin', a pattern suggested independently by PILASTRO et al. (1996).

Multiple litters occurring in one nest box could be a response to insufficient alternative refuges being available, but at our study site there was always a surplus of nest boxes and at least half of them remained empty even in breeding years. This prompts speculation that communal breeding confers some advantage to the individuals involved and thus to the species as a whole. The return of the same animals to the same nest boxes year after year appears to be normal in this species and implies a significant degree of social behaviour. Might the litters gain some survival advantage by sharing body warmth or perhaps benefit from a junior female learning from a mother? Maybe the presence of another lactating female offers an opportunity to share surplus milk, helping to achieve a rapid rate of growth among nestlings. These could be useful traits where the parents are related but HAYES (2000) suggested this was a disadvantage in 'large communal nesting of rodents' where most would not be closely related. The examination of our data for kinship enlightens the situation, but our results indicate only half were closely related. It could be concluded that, of those *Glis* choosing to breed communally, the relatedness of the adults was not important and any potential advantage did not include kinship as the principal driving force.

About 60% of the marked nestlings and juveniles were not recaptured in an immediately following breeding year, either because they died, emigrated, or simply were not found in a nest box on the days we visited. However, the large numbers of subadults that were encountered confirms that breeding in a breeding year after their first hibernation can and does take place but involves fewer than 2% of subadult females, a level unlikely to have a significant effect on the population dynamics.

Glis appears to have evolved a life strategy termed 'absenteeism' by MORRIS & MORRIS (2010). In non-breeding years, on average two thirds of adults known to be alive do not appear in nest

boxes but subsequently re-appear in the following season (TROUT et al. 2015). This compares with about 90% of adults recorded using the nest boxes in breeding years, even if they do not breed. Dormouse trappers in Slovenia suggest that in non-breeding years some animals remain in hibernation in caves for the whole season and the following winter (KRYŠTUFEK 2010). Opting out of a mast-failure year by hibernating for 18–20 months seems unlikely, but old edible dormice do become extremely fat prior to hibernation so extended hibernation might be feasible. If (experienced) adults emerged from hibernation and became active for the summer period in non-masting years they would compete for food with the subadults they reared the previous year. This would compromise their own previous breeding success and much of the population might be at risk of starvation. However, if the adults do not come out in those years (we do not find them in nest boxes during the whole season) to compete for food with active animals it reduces pressure on food supplies enabling more subadults to survive and hibernate until the next tree masting year. TROUT et al. (2015) showed that both males and females were largely absent in non-breeding years but reappeared in their natal nest box the following year. It appears that over-wintered adult dormice anticipate the forthcoming mast crop, perhaps in response to springtime availability of fruit buds of beech or other trees. It seems adult animals may then return to hibernation or summer torpor (RUF & BIEBER 2020), ‘opting out’ of being part of the active population in non-masting years and relying on substantial fat reserves to survive. Whilst a number of rodent species hibernate overwinter, optional absenteeism for a summer season and foregoing reproduction, followed by a second hibernation period, appears unique to this species.

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