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Socio-spatial organization in a local population of the forest dormouse *Dryomys nitedula*, with a review of these relations in other dormouse species

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Abstract: The socio-spatial organization in a local population of the forest dormouse *Dryomys nitedula* situated in Lithuania was studied using the capture-mark-recapture (CMR) method in a nestbox grid. Adult *D. nitedula* are sedentary and have permanent home ranges which are the basis of the socio-spatial organization of their populations. Average home range size per activity season was two times larger in adult males than in females (2.6 ha and 1.3 ha, respectively). On average, 53% and 44% of the area of the ranges of males and females, respectively overlapped with the ranges of neighboring individuals. Intersexual overlap of ranges was higher than intrasexual overlap. Males shared their home range with a larger number of other individuals than females (3.6 and 1.5 individuals, respectively). Adult dormice partly shifted their home ranges in consecutive years. During the course of the entire activity season, single individuals of both sexes (72.9%) were found most frequently in nestboxes, while females with litters of young (12.6%) and groups consisting of two or more dormice (14.5%) were much rarer. Pairs consisting of an adult male and female were found during the mating season, while groups of different composition were recorded most often when juveniles became independent.

Keywords: dormice; home range; social relations; spatial structure; territoriality.

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Introduction

In comparison to most other small mammals of similar size, dormice (Gliridae) are characterized by their mostly arboreal lifestyle, hibernation, unusual longevity and low reproductive rate (Morris 2011). Among all dormouse species, the hazel dormouse *Muscardinus avellanarius* L. and the fat dormouse *Glis glis* L. are the best studied (reviews in Kryštufek 2010, Juškaitis 2014), while the remaining species have attracted less attention to date. Although the forest dormouse *Dryomys nitedula* Pallas has the largest distributional range of the dormice, stretching from Switzerland in the west to Mongolia and China in the east, it is rare in Europe and is included in Annex IV of the Habitats and Species Directive of the European Union (Batsaikhan et al. 2008).

Only a few aspects of the socio-spatial organization of *Dryomys nitedula* populations have been studied previously. Radio-tracking studies of *D. nitedula* have been carried out in Poland and Latvia, but very limited numbers of dormice were investigated (Ściński and Borowski 2006, Pilāts et al. 2012). Additionally, some data on the social relations of *D. nitedula* have been obtained during studies using nestboxes (Golodushko and Padutov 1961, Angermann 1963, Nowakowski 2001). Socio-spatial organization in populations of some other dormouse species has been investigated more comprehensively, for example in the fat dormouse (e.g. Lozan et al. 1990, Pilastro 1992, Jurczyszyn and Zgrabczyńska 2007, Ściński and Borowski 2008, Koppmann-Rumpf et al. 2012), hazel dormouse (e.g. Likhachev 1967a,b, Morris et al. 1990, Bright and Morris 1991, 1992, Juškaitis 2014), garden dormouse *Eliomys quercinus* L. (Bertolino et al. 1997, 2001, 2003, Vaterlaus-Schlegel 1997) and woodland dormouse *Graphiurus murinus* Desmarest (Madikiza et al. 2011). Also some data exists on spatial organization in spectacled dormouse *Graphiurus ocularis* Smith (Van Hensbergen and Channing 1989) and Japanese dormouse *Glirulus japonicus* Schinz (Shibata et al. 2004).

Lithuania is situated in the very north-western corner of the large distributional range of *Dryomys nitedula* (Batsaikhan et al. 2008). Only two populations of this species are known in Lithuania, and they are both situated in large forest tracts. Studies supported by Fauna and Flora International in 2001–2002 revealed that the population of *D. nitedula* in one of these forest tracts can be considered a metapopulation, i.e. a system of local populations living in suitable habitat patches which interact with one another via individuals moving among these local populations (Hanski and Gilpin 1991). The local populations of *D. nitedula* occur in patches of mixed forest stands which are surrounded by stands of pure Scots pine *Pinus sylvestris* L. The latter are not suitable for permanent residence by the dormice, but are possibly crossed by dispersing juveniles (Juškaitis et al. 2012, Juškaitis 2015).

The aims of the present study were to:

1. reveal the spatial structure of the local population of *Dryomys nitedula*, i.e. estimate the size of home ranges per activity season, their shifts between years and the extent of home range overlap within and between sexes;
2. evaluate social relations among individuals of different sex and age during the activity season.

Materials and methods

Study area

The study site was situated in the southern part of the large Kazlų Rūda forest tract (area 58,700 ha) in Kaunas district, central Lithuania (54°58′N, 23°30′E). This part of the forest consisted of a mosaic of forest stands differing in terms of main tree species dominance. The majority of the study site was occupied by Scots pine dominated stands with Norway spruce *Picea abies* (L.) Karst and the birches *Betula pendula* Roth and *B. pubescens* Ehrh. The remaining parts of the site were characterized by birch dominated stands with aspen *Populus tremula* L., Norway spruce and Scots pine, Norway spruce dominated stands with birches and Scots pine, and black alder *Alnus glutinosa* (L.) Gaertn. dominated stands. Most of the forest stands were about 60 years old. Norway spruce, aged at approximately 40 years, grew in the subcanopy of most of these forest stands. Solitary pedunculate oak *Quercus robur* L. and small-leaved lime *Tilia cordata* Mill. trees also grew in the area. Rowan *Sorbus aucuparia* L. and glossy buckthorn *Frangula alnus* Mill. were the main understorey species, while hazel *Corylus avellana* L. was absent. For more detailed description of the study site see Juškaitis et al. (2012).

Methods

A pilot study on the *Dryomys nitedula* population was carried out in the period 1999–2000 by controlling 20 wooden bird nestboxes which were put up in a line along the edge of a forest compartment and forest road. In April 2001, 63 ordinary wooden bird nestboxes were put up in a grid pattern, each at a distance of 30–50 m from each other. The old nestboxes arranged in a line were removed in early August 2001. In spring 2003, the nestbox grid was expanded to 70 boxes spaced over an area of 13.5 ha (see Figure 1). The study area with the nestbox grid was delineated by a treeless belt situated over a gas pipeline to the east, an overgrowing clear-cut area to the west, a forest road to the north and a pure Scots pine stand to the south. The internal dimensions of nestboxes used were 12×12×23 cm and the entrance hole diameter was 35 mm. Most nestboxes were put up in Norway spruce trees at a height of 3 m.

All dormice caught in the nestboxes were marked with aluminium rings (inner diameter 3.0 mm, height 3.0 mm). The rings were placed on the right hind leg above the ankle. During the entire study period, 124 individuals were marked with rings, and the total number of times that dormice were handled was 570. All the animals caught were aged, sexed and weighed using a pair of scales or 100 g spring balances (Pesola AG, Baar, Switzerland) with accuracies to 0.1 g and 0.5 g, respectively. Dormice were considered adults if they had survived at least one hibernation. Nestboxes were controlled regularly during

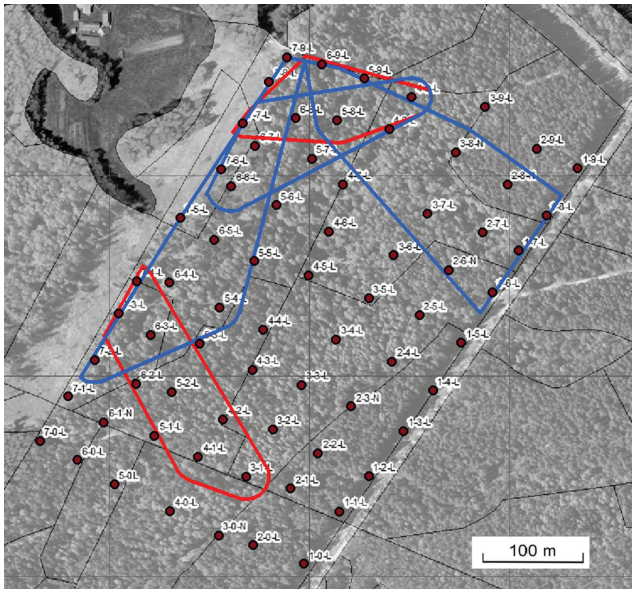

Figure 1: Example of home ranges of *Dryomys nitedula* males (blue polygons) and females (red polygons) at the study site in 2013.

the entire dormouse activity period from late April until early September. During May–August, nestboxes were controlled twice a month in 2001–2003 and 2010–2014, but once or twice a month in 1999–2000 and 2004–2009.

The size of the nestbox-derived home range of the dormice was determined by the minimum convex polygon method (MCP; Samuel and Fuller 1994), which was slightly modified for these studies. Using the MCP method, the outermost occupied nestboxes are generally considered to be the border points of the dormouse ranges, though dormice also use some areas around those nestboxes (Bright and Morris 1991). For this reason, a buffer zone representing half the distance to the nearest unused nestbox was added around each MCP range (Brooks et al. 2012). The nestbox-derived home range of each animal was calculated from at least six captures during one activity season. Over the study period, a total of 12 male and 12 female home ranges were calculated. For these 24 ranges, overlap was calculated as the percentage of the area of the home range of the target individual that was shared with neighboring individuals irrespective of the number of their captures. The number of individuals whose home ranges were overlapped by the range of the target dormouse was another indicator of spatial interactions. Shifts in the position of individual home ranges between years were evaluated according to the percentage of overlap, as well as to the distance between the centers of home ranges in two consecutive years.

Social relations among *Dryomys nitedula* individuals were evaluated according to the frequency of sharing of nestboxes during the entire activity season. Proportions of solitary dormice found, females with litters of young and groups consisting of two or more individuals were evaluated. Spatial data (i.e. home range size, overlap, centers of home ranges) were analysed using the ArcGis 10.2.2 software (ESRI 2014), and statistical analysis was done using the Statistica for Windows 7.0 software (StatSoft 2004). Differences between males and females for home range characteristics were assessed through the Mann-Whitney U-test. Average distances between two consecutive recapture locations for different time intervals (2 weeks, 4 weeks and 6 or more weeks) were compared using ANOVA. Results are presented as mean±SD.

Results

Home range size, overlap and fidelity

Adult *Dryomys nitedula* are sedentary and have permanent home ranges (Figure 1). The average home range size per activity season in adult males (2.6±1.4 ha, range 0.6–5.4 ha, n=12) was two times larger than that of adult females (1.3±1.0 ha, range 0.2–3.5 ha, n=12) (U=32, p=0.023). Males were significantly more mobile than females: the average distance between two consecutive recapture locations was 115±105 m (range 0–409 m, n=106) in males, while it was only 75±58 m (range 0–223, n=119) in females (U=5248, p=0.029). These distances did not depend on the time between the two recaptures in either males or females (ANOVA $F_{2,102}$=0.02, p=0.98 and $F_{2,116}$=2.24, p=0.11, respectively).

Home ranges of individual dormice overlapped with the ranges of other individuals (Figure 1). On average, 52.9±26.1% (range 7.4–98.5%, n=12) of the area of male ranges and 43.8±44.5% (range 0–100%, n=12) of the area of female ranges overlapped with the ranges of other individuals, but the difference between sexes was not significant in this respect (U=60, p=0.506). Males shared their home ranges with a larger number of other individuals (3.6±2.4, range 1–9, n=12) than females (1.5±1.6, range 0–5, n=12) (U=29, p=0.012). Home range overlap was larger between individuals of different sexes than between same-sex individuals (Table 1).

In two consecutive years, adult *Dryomys nitedula* showed site fidelity, though their home ranges did partially shift (Figure 2). The average distance between their home range centers was 70±52 m (range 22–139 m, n=5) in males and 41±13 m (range 16–64 m, n=10) in females. In a given year, on average, males used 65.7±29.8% (range 22.8–88.6%, n=5) of the area of the home range they used in the previous year, while females used 58.2±18.2% (range 39.9–96.6%, n=10).

Female no. 86254, born in 2001, was recorded in the area of the study site over six consecutive seasons. After the first hibernation in 2002, she had the largest home range (2.07 ha). In the following years, the size of her home range decreased by half and varied between 1.02 and 1.24 ha. The configuration and position of her home ranges somewhat changed over the years, but the average

Table 1: Home range overlap in *Dryomys nitedula* males (n=12) and females (n=12) at the study site in Lithuania.

Interaction	Average home range overlap according to	
	% Area (range)	No. of individuals (range)
Males with males	26.5±18.8 (0–71.3)	1.7±1.0 (0–3)
Males with females	43.2±27.2 (0–98.5)	1.9±1.7 (0–6)
Females with females	11.5±28.5 (0–100)	0.5±0.9 (0–3)
Females with males	33.9±42.3 (0–100)	1.0±1.0 (0–3)

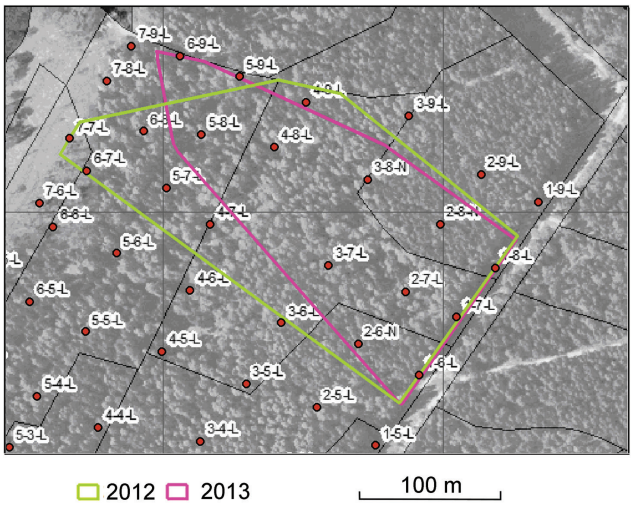

Figure 2: Example of home range shift of *Dryomys nitedula* male no. 74F07 in 2013 in comparison to 2012.

distance between the home range centers was only 35±12 m (range 16–49 m, n=5) (Figure 3).

Social relations among individuals

Over the course the entire activity season, dormice found in nestboxes were mostly single individuals of either sex. Females with litters of young and groups consisting of two or more dormice were much rarer (Table 2). During the activity season, the proportions of these classes changed (Figure 4). Single dormice accounted for more than 80% of all records in April–May, but this proportion decreased in June and July, when females with litters of young were present in nestboxes. In August, the proportion of single dormice increased again.

Table 2: Nestbox sharing by *Dryomys nitedula* at the study site in Lithuania during April–September in 1999–2014.

Dormice found in one nestbox	n	%
Single dormouse	306	72.9
Female with a litter of young	53	12.6
Adult male and adult female	17	4.0
Two adult females	6	1.4
Three and more dormice (at least two adults)	14	3.3
Adult dormouse and independent juveniles	15	3.6
Several independent juveniles	9	2.1
Total	420	100

Among cases when two or more dormice were found together in the same nestbox, pairs consisting of adult male and adult female were most frequent. Two adult females or two adult females together with one or two juveniles were found in six and five cases, respectively. In one case, two females "exchanged" their young: female no. 86212 was found together with one of her marked juveniles and two juveniles of female no. 86230 in a nestbox previously used by the latter female. At the same time, female no. 86230 was found with three marked juveniles of female no. 86212 in another nestbox.

Nestbox sharing purely by adult males was recorded only once when a 5-year-old male was found together with two young overwintered males in the same nestbox on 12 May 2013. Excluding females with litters, the largest

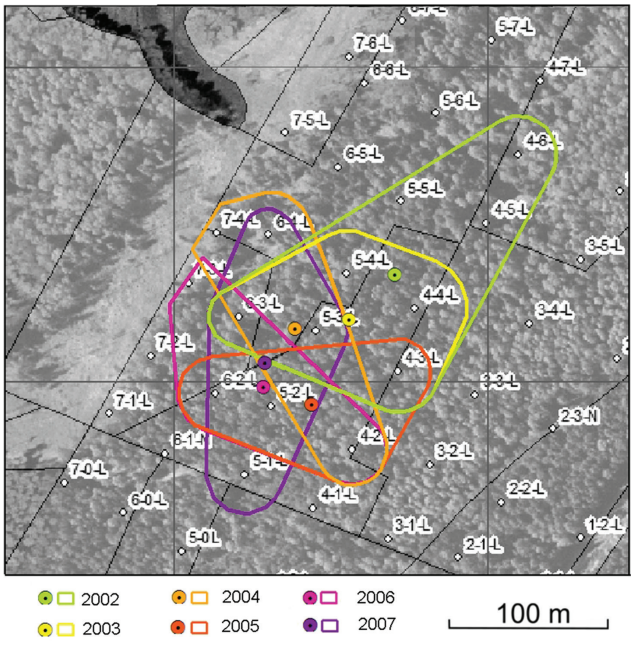

Figure 3: Shifts of the home ranges and range centers of *Dryomys nitedula* female no. 82654 in 2002–2007.

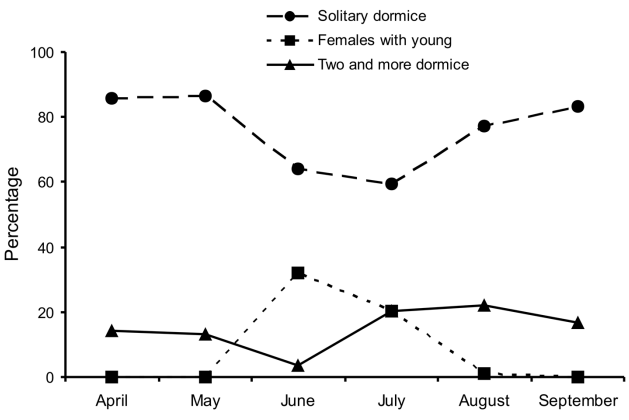

Figure 4: Dynamics of the proportions of single individuals and different groups of *Dryomys nitedula* found in nestboxes during the activity season.

dormouse groups found in a single nestbox during our studies consisted of five individuals of different sex and age (two cases). Dormice tend to stay in groups even after disturbance. For example, four adult dormice (two males and two females) were found together on 11 May 2001, and immediately after nestbox inspection, three of them moved to a neighboring nestbox situated 15 m away. In two more cases (two adult females and one juvenile female, plus an adult female and young female), the dormice moved together to other nestboxes in the daytime.

Discussion

Home ranges derived from capture-mark-recapture (CMR) studies using live traps or nestboxes are usually smaller than home ranges estimated using radio-tracking (Ribble et al. 2002, Ściński and Borowski 2006, Lira and Fernandez 2009, Brooks et al. 2012). In CMR studies, animals are not followed all the time, but the records are made only when they are found in live traps or nestboxes during routine controls. Using live traps, the movements of animals are interrupted by successive recaptures. In nestbox studies, animals chose nestboxes voluntarily and the outermost nestboxes in which they are found are considered to be border points of their home ranges. In reality however, animals also use some areas beyond these nestboxes (Bright and Morris 1991), and this circumstance thus results in an underestimation of home range size. The adding of a buffer zone around each home range representing half the distance to the next unused nestbox (Brooks et al. 2012, present study) should compensate this underestimation of nestbox-derived home range size.

As in many other animal species, the home ranges of adult individuals are the basis of socio-spatial organization in the population of *Dryomys nitedula*. According to the results of our nestbox study and radio-tracking studies carried out in Poland and Latvia (Ściński and Borowski 2006, Pilāts et al. 2012), the home ranges of males are larger than that of females. In both above-mentioned radio-tracking studies, the sizes of the home ranges of the two males were similar (4.19 ha in Poland and 3.41 ha in Latvia), while the sizes of the home ranges of the four females were different (0.73 ha and 0.75 ha in Poland, but 2.91 ha and 4.54 ha in Latvia). In comparison with these results, the average nestbox-derived home range sizes estimated for Lithuania (2.6 ha in males and 1.3 ha in females) were smaller than in the earlier studies for males and of an intermediate position for females. These differences in estimated home range sizes could be explained by habitat quality and food availability in the particular years, but also by different study methods and very small sample sizes in Poland and Latvia.

Overlap of individual home ranges with ranges of several neighboring dormice is typical for *Dryomys nitedula*. In six *D. nitedula* radio-tracked in Latvia, individual home ranges overlapped on average with the ranges of 4.0 individuals (Pilāts et al. 2012). In Lithuania, overlap was slightly less: on average, individual male home ranges overlapped with the ranges of 3.6 other individuals, while females on average only overlapped with 1.5 individuals. Overall, intersexual overlap of home ranges was higher than that of intrasexual overlap. Such a spatial structure of *Dryomys nitedula* populations with larger home ranges of more mobile males partially overlapping smaller home ranges of more sedentary females creates favorable conditions for reproduction. This has also been found in hazel dormouse populations (Juškaitis 2014).

Results of nestbox inspections over the course of entire activity seasons have demonstrated that *Dryomys nitedula* are mainly solitary living rodents (Golodushko and Padutov 1961, Angermann 1963, Nowakowski 2001, present study). Pairs consisting of adult males and adult females are found during the mating season and females with litters in early summer. Groups of different composition are found most often when juveniles become independent (approximately from mid-July). The largest group recorded consisted of seven dormice (two adult males, one adult female, one juvenile male and three juvenile females) (Angermann 1963). Although intrasexual overlap of home ranges has been recorded in both males and females, cohabiting of two or three adult males in the same nestbox has been found only in a few exceptional cases (Golodushko and Padutov 1961, Angermann 1963, present study). Records of two adult females in the same nestbox however are more frequent (present study). Cohabitation of two adult females in the same shelter without communal nesting is a specific feature of *D. nitedula* in comparison to other dormouse species (see below).

A similar socio-spatial organization is typical of populations of the hazel dormouse (Juškaitis 2014). Both males and females have home ranges that partly overlap, but usually dormice of the same sex are antagonistic to their neighbors and they are not found together in the same nestbox. In overlapping parts of home ranges, nestboxes can be used by neighboring individuals of the same sex as daily resting sites, but at different times. It seems that inside their home ranges, hazel dormice have territories. For example, Morris (2011) reported that "occasionally rival males can be seen by red torchlight facing up to each other at their territory boundaries, flicking their tails aggressively just as squirrels do". Aggressive encounters were also observed in captivity, and no reproductively active males were found together in

nestboxes (Likhachev 1967a, Morris et al. 1990, Woods 1997, Juškaitis 2014). In one exceptional case, a freshly-killed adult male was found inside a nestbox also occupied by another male that had an overlapping home range. Cohabitation of adult hazel dormice of the same sex can be regarded as the exception and is recorded only before the beginning of breeding season (Juškaitis 2014).

In all dormouse species so far investigated, the home ranges of males were larger than the ranges of females (e.g. Van Hensbergen and Channing 1989, Vaterlaus-Schlegel 1997, Shibata et al. 2004, Ściński and Borowski 2006, 2008, Madikiza et al. 2011, Juškaitis 2014). In all cases, dormouse ranges overlapped and the home ranges of males generally overlapped with a larger number of ranges of other individuals than those of females. However, there were pronounced differences among dormouse species regarding the territoriality of individuals. According to Burt (1943), the "territory is the protected part of the home range". In populations of the hazel dormouse and the forest dormouse, both males and females have territories, at least during the breeding season, when individuals of the same sex do not usually share daily resting sites (Golodushko and Padutov 1961, Angermann 1963, Likhachev 1967a, Juškaitis 2014, present study).

In populations of the fat dormouse however, only females are usually territorial and non-territorial males can be found together in the same nestboxes in groups of two to eight individuals during the mating season (e.g. Fietz et al. 2010, Koppmann-Rumpf et al. 2012, Sevianu and David 2012). However, also close-kin breeding females (usually a mother-daughter pair) can occasionally share the same nest and communally nurse their young. This phenomenon was rather frequent in northern Italy (Pilastro 1992, Marin and Pilastro 1994) and isolated cases were recorded in Romania (Sevianu and David 2012). It was not observed during studies in Poland however, where the population density in the study areas was probably not high enough to limit the space available for reproducing females (Jurczyszyn and Zgrabczyńska 2007, Ściński and Borowski 2008).

In populations of the woodland dormouse, both males and females were shown to be non-territorial during the breeding season (Madikiza et al. 2011). High food and nesting site availability seems to have allowed the spatial clumping in females. Only very limited areas of the female home ranges were really exclusive. This observation was paralleled by a high degree of nestbox sharing and communal nesting in putative related females.

Thus, according to differences in territoriality during the breeding season, dormouse species can be roughly divided into two groups:

1. Both males and females are territorial and sharing of nestboxes during the breeding season between adult individuals of the same sex does not occur (hazel dormouse) or is very rare (forest dormouse);
2. Males are non-territorial and aggregate around females, which can be territorial (fat dormouse) or not (woodland dormouse). Adult males can be found in groups sharing nestboxes during the mating season and communal nesting in close-kin breeding females is also possible.

Data on the socio-spatial organization of other dormouse species are scarce in comparison to that on the four species reviewed above. Results of the studies by Bertolino et al. (1997, 2001) on socio-spatial organization in populations of the garden dormouse strongly suggest that female dormice are territorial during the gestation and lactation periods. However, male and female home ranges overlapped during the mating season. No sign of territorial defense was noted, but it is not clear whether garden dormice share daily resting sites during mating period. Male Japanese dormice rested in or around multiple female ranges during the mating season, suggesting a polygynous or promiscuous mating system (Shibata et al. 2004). Spectacled dormice defend territories, occupied by individuals or pairs, using aggressive behavior. According to Van Hensbergen and Channing (1989), the main social unit in this species consists of an adult pair with the young of the year, but these observations are based on a very small sample size. Further studies on territoriality and social relations are necessary to clarify the socio-spatial organization of the populations in these and other dormouse species.

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