



# Spatial dynamics of a hazel dormouse (*Muscardinus avellanarius*) population at different densities

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## Abstract

The dynamics of socio-spatial organisation are little investigated in dormice (Gliridae), a specific group among small mammals. During 2007–2017, 668 adult individuals were captured in a hazel dormouse (*Muscardinus avellanarius*) population in Lithuania, with the home ranges calculated for 134 males and 62 females. Over the study period, the abundance of the population gradually declined, and it was categorised into three groups: (1) high (1.2–1.4 adults/ha), (2) medium (0.9–1.0 adults/ha) and (3) low (0.4–0.7 adults/ha). When population abundance changed from high to low, the average sizes of home ranges increased from  $1.4 \pm 0.6$  to  $2.1 \pm 1.2$  ha in males and from  $0.8 \pm 0.5$  to  $1.1 \pm 0.4$  ha in females, while the total overlap of home ranges decreased from  $57 \pm 28$  to  $35 \pm 23\%$  in males and from  $77 \pm 27$  to  $44 \pm 32\%$  in females. Home ranges of marked individuals changed in consecutive years. In males, the average displacement of the centres of the home ranges was  $58 \pm 21$  m,  $75 \pm 52$  m and  $73 \pm 39$  m at high, medium and low densities, respectively. The dynamics of the spatial relations in the investigated hazel dormouse population are consistent with the general tendency of home ranges to increase when population density decreases. However, the spatial organisation of population is more stable and potentially less related to the dynamics of food resources in comparison with other forest-dwelling small mammals.

**Keywords** Gliridae · Home range · Population dynamics · Small mammals

## Introduction

There are many patterns of social organisation in animals which range along a spectrum from extremely non-social species to extremely gregarious species (McBride 1964). Even morphologically similar small mammal species are extremely variable in their behaviour and social organisation (Ostfeld 1990). Among forest-dwelling small mammals (voles, mice, dormice), the home ranges of adult individuals are the basis of socio-spatial organisation in their populations. Males usually have home ranges larger than those of females, with the overlap of ranges also larger in males than in females, whereby females often have relatively exclusive home ranges (e.g.

Bondrup-Nielsen and Karlsson 1985; Wolton 1985; Mazurkiewicz and Rajska-Jurgiel 1998; Grün and Bujalska 2000). As population densities increase, home ranges become smaller and their overlap increases (e.g. Wolf 1993; Bogdziewicz et al. 2016; Efford et al. 2016). For example, both bank voles (*Myodes glareolus*) and yellow-necked mice (*Apodemus flavicollis*) hold larger home ranges in years of low density and smaller in years of high density (Mazurkiewicz and Rajska-Jurgiel 1998; Casula et al. 2019).

However, many studies have reported that home range sizes also correlate negatively with food availability, but problematically food availability and population density are positively correlated with each other. Experimental manipulation of population density and food availability has shown that an increased food availability and decreased population density independently affect the size of the home range size of female individuals of African-striped mice (*Rhabdomys pumilio*) (Schoepf et al. 2015). However, separating the effects of density from other factors is difficult in natural populations, as different factors covary in space and time (Schoepf et al. 2015; Bogdziewicz et al. 2016; Efford et al. 2016). The amount of shelter available (e.g. hollow trees, nestboxes, dense vegetal

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cover) may have an influence on socio-spatial organisation of small mammal populations (Mazurkiewicz 1994; Juškaitis 2005; Madikiza et al. 2011). Animal space use patterns may also be affected by the interspecific density of individuals of sympatric species competing for resources (Wolf 1985; Eccard and Ylönen 2003; Casula et al. 2019).

Dormice (Gliridae) form a specific group among small mammals. They are characterised by mostly arboreal lifestyle, hibernation, unusual longevity and low reproductive rates (Holden-Musser et al. 2016). The socio-spatial organisation of populations has been investigated among some dormouse species, e.g. forest dormouse (*Dryomys nitedula*) (review in Juškaitis and Keturka 2017), hazel dormouse (*Muscardinus avellanarius*) (review in Juškaitis 2014), edible dormouse (*Glis glis*) (Jurczyszyn and Zgrabczyńska 2007; Ściński and Borowski 2008), garden dormouse (*Eliomys quercinus*) (Bertolino et al. 1997, 2001) and woodland dormouse (*Graphiurus murinus*) (Madikiza et al. 2011).

In the studies indicated above, great variability has been found in the spatial relations of different dormouse species. The size, overlap and exclusivity of the home ranges of males and females, as well as the sharing of shelters during the breeding season, can be very different in separate dormouse species (Juškaitis and Keturka 2017). However, it is unclear how these spatial relations depend on dormouse population density. To date, only a few studies have been carried out in which the same authors using the same methods have estimated dormouse home range sizes, travelled distances and overlap of home ranges at different population densities (Jurczyszyn and Zgrabczyńska 2007; Ściński and Borowski 2008; Seviānu and David 2012). All these studies were carried out in edible dormouse populations. Home range sizes of the hazel dormouse have been estimated in several populations differing in their densities, but both the population densities and home range sizes were estimated using different methods (review in Juškaitis 2014). For this reason, the results obtained in these studies cannot be directly compared with each other.

The hazel dormouse is considered a threatened species, listed in Annex IV of the Habitats and Species Directive of the European Union. In many European countries, the hazel dormouse is also included on national Red Lists (see review in Juškaitis 2014). Despite a high level of species protection and widespread conservation measures, an ongoing decline in dormouse abundance has been recorded in the UK (Goodwin et al. 2017). Considerable efforts are also made in order to protect dormouse populations in Germany, Denmark, the Netherlands and the Flanders (Holden-Musser et al. 2016). In this context, it is important to know what happens to the spatial structure of a dormouse population when it is declining.

A long-term study of a hazel dormouse population has been carried out in Lithuania (Juškaitis 2014 and unpublished). The density of this population was rather stable for many years, but

it has started to decrease from 2011. During the 2007–2017 period, the abundance of the investigated hazel dormouse population was more than halved: from an average 1.2 adults/ha to an average of 0.5 adults/ha. Such a decrease in population density has provided the opportunity to investigate how spatial relations in hazel dormice depend on population abundance. Of particular note, overlap of home ranges and changes of home range localization over two consecutive years were estimated for the first time in the hazel dormouse population. The aim of the present study was to analyse spatial relations in the hazel dormouse population at different levels of population abundance and to compare them with other forest-dwelling small mammals.

## Materials and methods

### Study species

The hazel dormouse is a small rodent of the family Gliridae. Distributed mainly across Europe, they occur in deciduous or mixed forests with a well-developed understorey. They are nocturnal and forage for flowers, fruits, seeds and insects. Dormice hibernate during winter and also exhibit short daily torpor bouts during their active season. Females produce normally one or two litters per season, with litters of 3–5 juveniles being most frequent. Young-of-the-year females can breed when population density is low. A long-lived mammal in comparison with other rodents of similar size, the life span of the hazel dormouse is up to 6 years in the wild. Adult dormice are sedentary and have fixed home ranges, which can overlap partially. The average population density is only 1–2 adults/ha in large areas with different habitats, but it may reach up to 10–16 adults/ha in most favourable habitats. The abundance dynamics of dormouse populations is comparatively “smooth” without sudden changes (Juškaitis 2014).

### Study area

Investigations into the hazel dormouse population were carried out in Šakiai district (55° 03' N, 23° 04' E), south-western Lithuania. The dormouse study site covered an area of 60 ha within a large mixed deciduous-coniferous forest tract of about 3000 ha dominated by Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*). The other main tree species growing in the area of the study site were black alder (*Alnus glutinosa*), grey alder (*Alnus incana*), ash (*Fraxinus excelsior*), aspen (*Populus tremula*), small-leaved lime (*Tilia cordata*) and pedunculate oak (*Quercus robur*). Hazel (*Corylus avellana*), glossy buckthorn (*Frangula alnus*), bird cherry (*Padus avium*), rowan (*Sorbus aucuparia*) and dwarf honeysuckle (*Lonicera xylosteum*) were the main species in the understorey. Over most of the study site, the forest

was middle-aged (about 60–70 years old). Different forest management operations, including clear felling, were carried out by foresters. The area of the study site was delimited by forest edge to the east, by a stream and meadow belt to the south, by a forest road to the west and by a border nestbox line to the north.

## Study methods

Long-term investigations into the hazel dormouse population were carried out from 1999 to 2018, but only data from the period 2007–2017 were used in the present study, this being when dormouse home ranges were estimated annually. Standard wooden nestboxes intended for small hole-nesting birds, e.g. great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*), were used for the studies of the hazel dormouse population. The internal dimensions of the boxes were 12 × 12 × 23 cm with an entrance hole diameter of 35 mm. The boxes were put up at a height of 3–4 m with the entrance facing outwards. In the study site, 272 nestboxes were placed in a grid system at 50 m intervals between boxes. The nestbox density was four boxes per hectare.

The nestboxes were checked during daytime twice a month from April until October. All dormice caught were marked with aluminium rings with individual numbers (inner diameter—2.5 mm, height—3.0 mm). The rings were placed on the right hind leg over the ankle. All animals were weighed using KERN 60 g spring balances with accuracy to 0.5 g, and their sex and age were determined. During the entire study period, 668 adult individuals were captured, and the total number of times that adult dormice were handled was 2708. Dormice were considered adults if they had survived at least one hibernation. Unmarked young-of-the-year individuals were distinguished from adults by their lower body weight, greyer fur colouration and narrower tail (Juškaitis 2014).

The enumeration method or the minimum-number-alive (MNA) method (Krebs 1999) was used for the estimation of the number of adult dormice living in the area of the study site in spring after hibernation. Adult individuals which were not recorded in spring, but were found during any subsequent nestbox inspection, were included in the calculations of the MNA in spring. The spring density of population was calculated by dividing the MNA in spring by the effective trapping area (Flowerdew 1976; Krebs 1999). The trapping area of the whole study site was considered to be 68 ha. It was calculated by adding a 50-m boundary strip to the sides of the area containing nestboxes, except when this area was delimited by forest edge. Spring densities of the same hazel dormouse population were estimated using program MARK for the period 2001–2006 (Bieber et al. 2012). Spearman rank correlation between population densities in May, estimated using program MARK, and population densities, estimated using

MNA in spring, was very high and statistically significant ( $r_s = 0.94$ ,  $p = 0.005$ ).

Population densities in spring varied between 0.4 and 1.4 adults/ha during the study period. The values of the population densities were not distributed evenly, classed into three groups: (1) high abundance (1.2–1.4 adults/ha in 2007, 2008 and 2010), (2) medium abundance (0.9–1.0 adults/ha in 2009, 2011, 2012 and 2014) and (3) low abundance (0.4–0.7 adults/ha in 2013, 2015, 2016 and 2017). Dormouse recapture rate was very similar in high, medium and low abundance years:  $4.1 \pm 2.9$  ( $n = 257$ ),  $4.0 \pm 2.9$  ( $n = 266$ ) and  $4.1 \pm 2.6$  ( $n = 145$ ), respectively. In addition, we also used raw values of population densities for analysis of dependence of home range size ( $n = 196$ ), average distance between two consecutive recapture locations ( $n = 1994$ ) and overlap of the home range with the ranges of other individuals ( $n = 196$ ). The normality of the distribution of the abovementioned parameters was tested using the Kolmogorov-Smirnov test.

The size of the nestbox-derived home ranges of the dormice was determined by the minimum convex polygon method (MCP; Mohr 1947; Hayne 1949), 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 boundary strip representing half the distance to the nearest unused nestbox was added around each MCP range (Hayne 1949; Brooks et al. 2012). The nestbox-derived home range of each animal was calculated from at least six captures during one activity season, as was done in previous analogous studies (Juškaitis 1997, 2005, 2014; Juškaitis and Keturka 2017). The total number of captures used to calculate the home ranges varied from six to 14, averaging  $8.2 \pm 2.2$  ( $n = 196$ ). Over the study period, a total of 134 male and 62 female home ranges were calculated. For these 196 ranges, overlap was calculated as the percentage of the area of the home range of the target individual that was shared with neighbouring individuals irrespective of the number of their captures. For 32 males and 6 females, the home range sizes were estimated over two consecutive years. Shifts in the positions of individual home ranges between years were evaluated according to the percentage of overlap, as well as to the distance between the centres of the home ranges in the two consecutive years.

Results are presented as mean  $\pm$  SD. The minimum significance level was  $p = 0.05$ . As population densities were non-normally distributed, non-parametric Kruskal-Wallis  $H$  test was applied to investigate the difference in spatial relation characteristics between years with different population densities. For ungrouped density data, we used correlation and linear regression analysis. Male-female differences between spatial relation characteristics were assessed through the Mann-Whitney  $U$  test, using all within-year values. Calculations were done with Statistica for Windows, ver. 6.0 software

(Statistica 2019). Spatial data (i.e. home range size, home range overlap, distance between centres of home ranges) were analysed using the ArcGis 10.5 software (ESRI 2019).

## Results

During 2007–2017, the abundance of the investigated hazel dormouse population decreased by 60%: from an average  $1.2 \pm 0.2$  adults/ha in 2007–2010 to an average of  $0.5 \pm 0.1$  adults/ha in 2015–2017 (Fig. 1). Space use by adult hazel dormice was different at high and low population densities. At low population density, the home ranges of the adult dormice were larger, and a large part of the study site was not used by dormice at all (Fig. 2).

During the entire study period, the average home range size per activity season was about two times larger in adult males ( $1.7 \pm 0.9$  ha,  $n = 134$ ) than in adult females ( $0.9 \pm 0.5$  ha,  $n = 62$ ) (Mann-Whitney,  $Z = 6.45$ ,  $p < 0.001$ ). A negative correlation between average home range size and population density was found in males ( $r = -0.31$ ,  $p < 0.001$ , Fig. 3a) and in females ( $r = -0.26$ ,  $p < 0.05$ , Fig. 3b). Average home range size differences were significant between density groups (Kruskal-Wallis  $H_{2,134} = 10.96$ ,  $p < 0.01$  in males,  $H_{2,62} = 6.70$ ,  $p < 0.05$  in females). When the population abundance changed from high to low, the average size of home ranges increased from  $1.4 \pm 0.6$  ha ( $n = 52$ ) to  $2.1 \pm 1.2$  ha ( $n = 30$ ) in males and from  $0.8 \pm 0.5$  ha ( $n = 25$ ) to  $1.1 \pm 0.4$  ha ( $n = 12$ ) in females (Mann-Whitney,  $Z = 3.40$ ,  $p < 0.001$  and  $Z = 2.55$ ,  $p = 0.011$ , respectively) (Fig. 3).

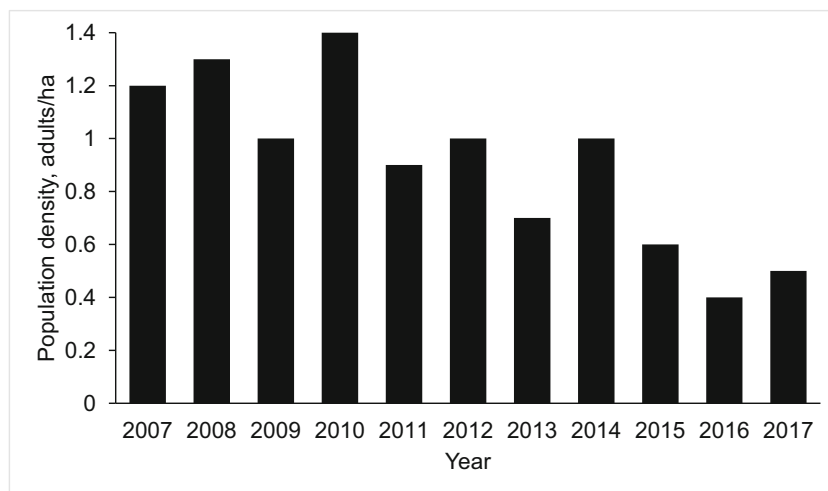
Males were significantly more mobile than females: the average distance between two consecutive recapture locations was  $54 \pm 55$  m ( $n = 1276$ ) in males and  $29 \pm 36$  m ( $n = 718$ ) in females over the entire study period (Mann-Whitney,  $Z = 9.42$ ,  $p < 0.001$ ). A weak, though significant, negative correlation between the average distance between two consecutive

recapture locations and population density was characteristic to both males ( $r = -0.07$ ,  $p = 0.011$ , Fig. 4a) and females ( $r = -0.16$ ,  $p < 0.001$ , Fig. 4b). Distances between recaptures significantly differed between density groups (Kruskal-Wallis  $H_{2,1276} = 10.00$ ,  $p = 0.007$  in males,  $H_{2,718} = 18.29$ ,  $p < 0.001$  in females). At high and average population densities, the average distances between two consecutive recapture locations were very similar both in the case of males (Kruskal-Wallis post hoc,  $p = 1.0$ ) and in females ( $p = 0.45$ ), but these distances increased at low population density in both sexes (Mann-Whitney,  $Z = 3.00$ ,  $p = 0.002$  and  $Z = 3.96$ ,  $p < 0.001$ , respectively) (Fig. 4). This difference was related to the differing proportions of individuals recaptured in the same nestboxes. At high and average population densities, 40.8% and 40.9% respectively of consecutive recaptures of males were in the same nestboxes, while this figure was only 31.6% at low population density. In females, the proportions of consecutive recaptures in the same nestboxes were 61.8%, 55.4% and 39.0% at the respective population densities.

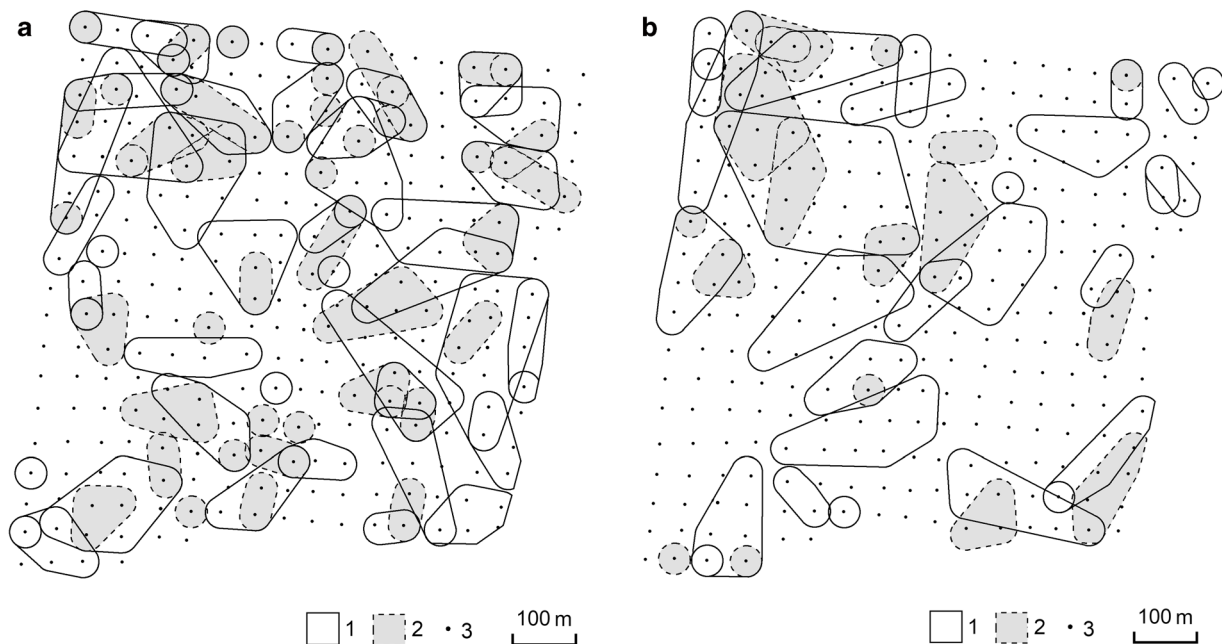
The home ranges of individual dormice overlapped partly with the ranges of other individuals (Fig. 2). On average,  $46 \pm 28\%$  ( $n = 134$ ) of the area of male ranges and  $61 \pm 32\%$  ( $n = 62$ ) of the area of female ranges overlapped with the ranges of other individuals, and this overlap was larger in females (Mann-Whitney,  $Z = 3.22$ ,  $p = 0.0012$ ). Males shared their home ranges with a larger number of other individuals ( $2.7 \pm 1.7$ ,  $n = 134$ ) than females ( $1.8 \pm 1.0$ ,  $n = 62$ ) ( $Z = 3.12$ ,  $p = 0.0013$ ). In overlapping parts of the home ranges, the same nestboxes were used by two or even three individuals, but at different times, i.e. two adult individuals of the same sex were never found together in the same nestbox.

An increase of home range overlap at higher population densities was observed in males ( $r = 0.34$ ,  $p < 0.001$ , Fig. 5a) and even more so in females ( $r = 0.44$ ,  $p < 0.001$ , Fig. 5b). Home range overlap significantly differed between density groups in males (Kruskal-Wallis  $H_{2,134} = 14.01$ ,  $p < 0.001$ )

**Fig. 1** Dynamics of the hazel dormouse population density at the study site in Lithuania in 2007–2017







**Fig. 2** Home ranges of adult hazel dormice at the study site. **a** At population density 1.4 adults/ha in 2010. **b** At population density 0.7 adults/ha in 2013. 1—home range of male, 2—home range of female, 3—nestbox

and in females ( $H_{2,62} = 18.29$ ,  $p = 0.001$ ). In males, the total overlap of home ranges decreased from  $57 \pm 28\%$  ( $n = 52$ ) in high-density years to  $35 \pm 23\%$  ( $n = 30$ ) in low-density years, and in females, from  $77 \pm 27\%$  ( $n = 25$ ) to  $44 \pm 32\%$  ( $n = 12$ ) (Mann-Whitney,  $Z = 3.41$ ,  $p < 0.001$  and  $Z = 3.03$ ,  $p = 0.002$ , respectively) (Fig. 5).

In subsequent years, localization of home ranges of marked individuals changed, though the new home ranges semi-overlapped with the previous home ranges. There was no difference between sexes in the extent of between-year home range overlap. On average,  $54 \pm 25\%$  ( $n = 32$ ) of the area of male ranges and  $68 \pm 31\%$  ( $n = 6$ ) of the area of female ranges overlapped with the area used in the previous year (Mann-Whitney,  $Z = 0.90$ ,  $p = 0.37$ ). The average distance between centres of home ranges used in two consecutive years was  $68 \pm 39$  m ( $n = 32$ ) in males and  $43 \pm 19$  m ( $n = 6$ ) in females ( $Z = 1.66$ ,  $p = 0.096$ ). In males, the average displacement of the home range centre was  $58 \pm 21$  m ( $n = 12$ ),  $75 \pm 52$  m ( $n = 15$ ) and  $73 \pm 39$  m ( $n = 5$ ) at high, medium and low densities, respectively. However, despite the large increase in displacement values at medium and low densities, the difference was not statistically significant between the density groups (Kruskal-Wallis  $H_{2,38} = 0.41$ ,  $p = 0.815$ ). The sample sizes were too small for analogous comparison in females.

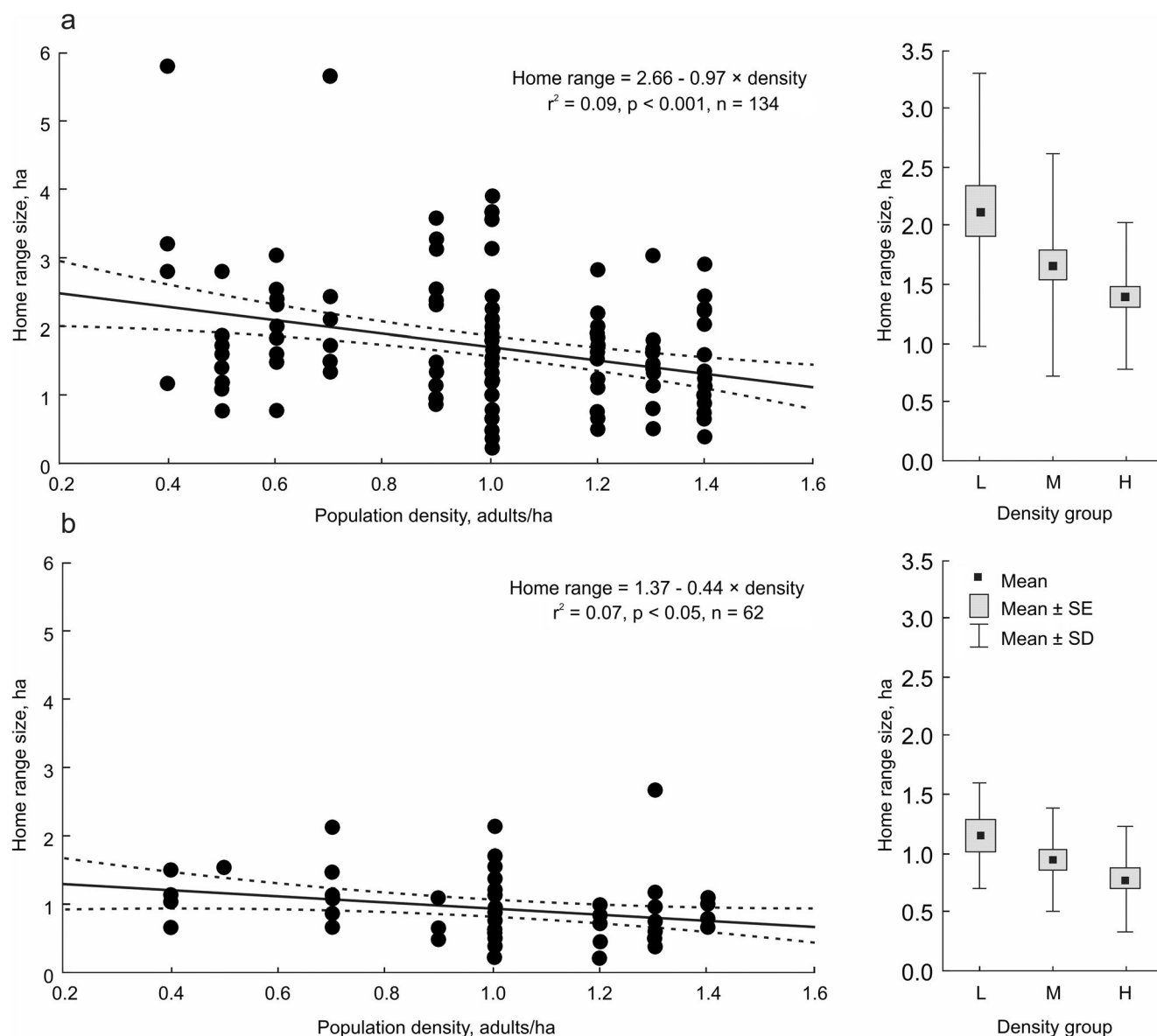
## Discussion

Dynamics of spatial relations in the investigated hazel dormouse population matched the overall trend typical for

forest-dwelling small mammals, i.e. when the population density decreased, the home range sizes and distances between recaptures increased, while the home range overlap decreased. However, the spatial organisation of the hazel dormouse population was more stable and possibly less dependent on the availability of specific food resources than was observed in other forest-dwelling small mammals, especially in that of edible dormice and yellow-necked mice.

In the edible dormouse population in Białowieża forest, the home range size in males was significantly larger at high population density in 2002 (the hornbeam mast year) than at lower population density in 2001 (the oak mast year), which was probably due to the lower energy value of hornbeam mast. Additionally, males shared their home ranges with more males in 2002 than 2001. However, it is possible that a change of food resources between the years influenced the spatial behaviour of the male edible dormice more than the changes in population density (Ściński and Borowski 2008). For the edible dormouse, which can skip reproduction in non-mast years, spatial relations may be different in breeding and non-breeding years: home ranges, especially in males, were indeed greater in mast years with reproduction (Ruf et al. 2006; Jurczyszyn and Zgrabczyńska 2007). In a yellow-necked mouse population in the Italian Alps, home range size increased, but home ranges also overlapped more, when population density decreased from high to relatively low values, and food availability was also lower (Stradiotto et al. 2009).

The feeding preferences of the hazel dormice were also studied in the investigated population over 5 years (2010–2014). This study showed that, living in a habitat with

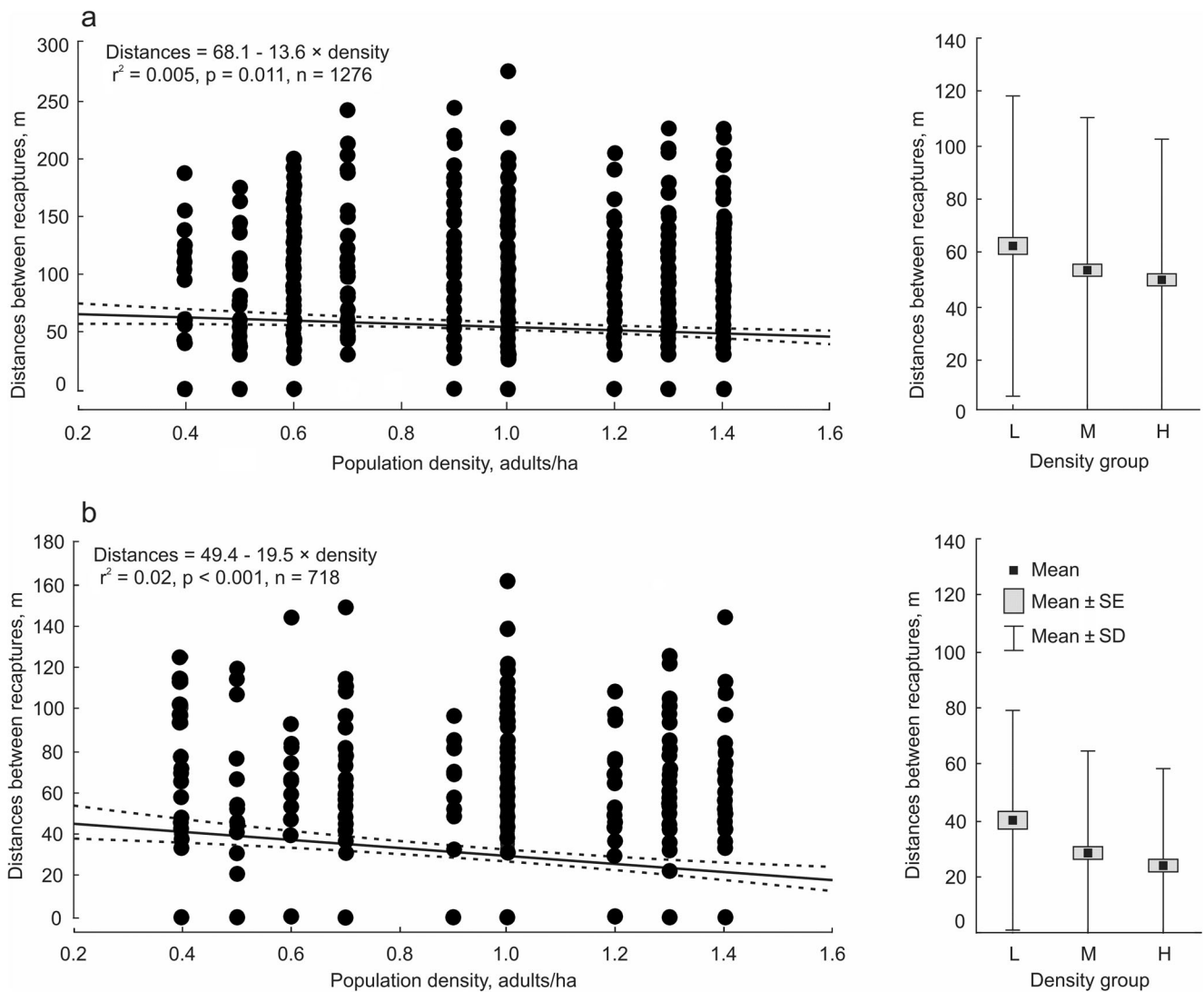


**Fig. 3** Home range size of hazel dormouse males (**a**) and females (**b**) at different population densities (L low, M medium, H high) at the study site in Lithuania. Dotted line shows 95% confidence interval of regression line

irregular fruiting of the main food plants, the hazel dormice are adapted to feed on varying food sources in the course of activity season and can switch from one food source to another in different years (Juškaitis et al. 2016). A statistically significant negative correlation was found between average home range size of hazel dormouse males and population density, but not between home range size and the proportions of main food items (fruits of glossy buckthorn, oak acorns, hazel nuts or birch seeds) in the diets of the hazel dormice in autumn (R. Juškaitis, unpublished). Gatter and Schütt (1999) indicated that the abundance of hazel dormice by nestbox occupancy was relatively constant in some regions for 13 years and was not related to mast crops of beech and oak, while at the same time, the abundance of the edible dormouse

fluctuated considerably. Yellow-necked mice also response to increased food availability: they reproduce in spring-summer every year, but they also can reproduce in autumn in years with a good crop of oak acorns. The abundance of mice reaches its peak in the year following an oak mast year (e.g. Pucek et al. 1993; Stenseth et al. 2002; Suchomel and Heroldova 2007).

An abundance of secure closed nest sites has evident influence on the spatial relations of hazel dormouse. Although woven ball-shaped nests in thick tangles of shrubs are considered to be typical natural nests for these dormice, they occupy artificial nestboxes willingly (review in Juškaitis 2014). When the density of nestboxes was increased from 4 to 16 boxes per hectare, dormouse abundance increased 3–4fold, and



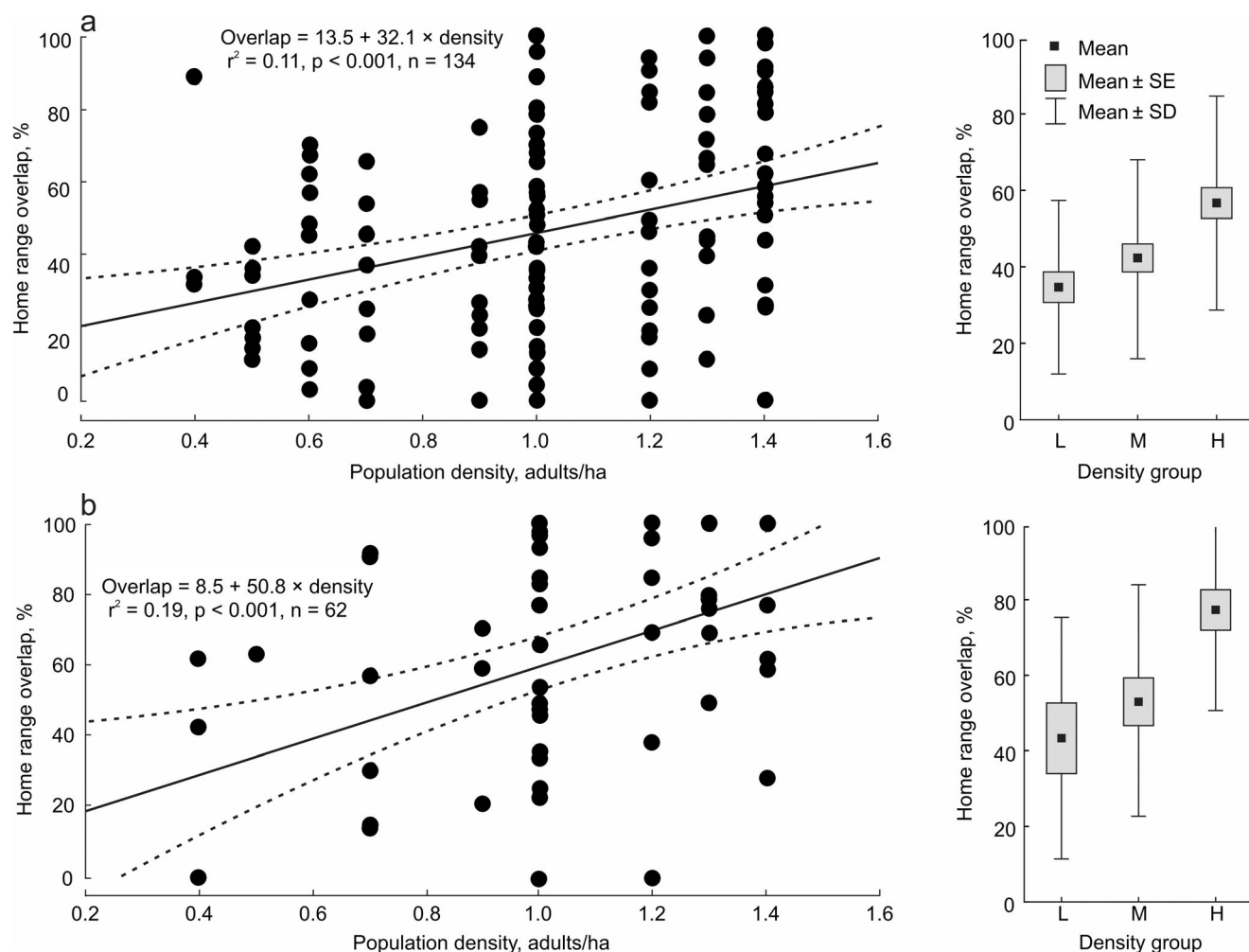
**Fig. 4** Distances moved by hazel dormouse males (**a**) and females (**b**) between consecutive recapture places at different population densities (L low, M medium, H high) at the study site in Lithuania. Dotted line shows 95% confidence interval of regression line

average home range size decreased by approximately half both in males and females (Juškaitis 2005, 2014). In this case, hazel dormice were able to find enough food even in twofold smaller home ranges, while at the same time, they used twofold larger home ranges in the same habitat with lower nestbox density. This experiment confirms the possible independence of spatial relations from food resources in hazel dormice.

The home ranges of marked hazel dormouse individuals changed over consecutive years. However, the average displacement of the centres of the home ranges was similar at different population densities in males. Even at low density when large areas were not used by dormice at all (Fig. 2b), adult dormice remained sedentary and did not shift their ranges significantly further. By contrast, most bank voles and yellow-necked mice shifted their home ranges by significantly larger distances in low-density years, with the

proportion of individuals abandoning their home ranges also larger in the low-density years (Mazurkiewicz and Rajska-Jurgiel 1998). Increased movement of yellow-necked mice was affected by resource availability: a permanent movement away from the study grid was more frequent when seed production was low (Stradiotto et al. 2009).

The pattern of spatial distribution shown by yellow-necked mice in large forest areas with a high diversity of tree-stands is related to the productivity and spatial distribution of forest trees with heavy seeds (mainly oak and hazel). In separate years, mice used to occupy nestboxes in those forest plots where a heavy seed crop was present (Juškaitis 2002). In contrast, hazel dormice stay in their home ranges irrespective of changes in the fruiting of different food plants. Radio-tracking has shown that dormice have small home ranges, about 0.3 ha over 8 days, but they use about 1 ha annually with different



**Fig. 5** Overlap of home ranges of hazel dormouse males (**a**) and females (**b**) with the ranges of other individuals at different population densities (L low, M medium, H high) at the study site in Lithuania. Dotted line shows 95% confidence interval of regression line

parts exploited seasonally according to food availability (Bright and Morris 1996; Morris 2011).

At higher population densities, the home ranges of hazel dormice may be smaller due to aggressive contacts with neighbours. According to Morris (2011), rival males can occasionally be seen by red torchlight facing up to each other at their territory boundaries, flicking their tails aggressively just as squirrels do. At lower population density, home ranges can be extended due to decreased pressure of neighbours. In the current study, dormice extended their home ranges significantly at low population density, but to a limited degree. At low population density, changes in species behaviour ensure hazel dormouse reproduction, with all adult females that survived until June breeding. As is important that males and females are able to encounter each other for mating, both males and females become more mobile at low population density and, as a result, were less frequently recaptured in the same nestboxes.

What would happen if dormouse population abundance continued to decline? It seems that this would depend on forest size. It is possible that in large forest tracts, dormice would

concentrate in the most favourable forest areas as happened in another hazel dormouse population that was investigated in 1988 when the population broke up into several territorial groups. The average population density was low and large areas of the study site were not used by dormice at all, but dormouse density in the territorial groups was sufficient for successful reproduction (R. Juškaitis, unpublished). However, for hazel dormouse populations living in small forests, further declines in population abundance could be fatal.

Despite the general tendency of home ranges to increase when population densities decrease, every forest-dwelling small mammal species has some peculiarities in their dynamics of spatial relations. Some, such as edible dormice and yellow-necked mice, depend very much on the availability and distribution of food resources. Meanwhile, the spatial relations of hazel dormice are more stable than compared with other forest-dwelling small mammals.

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