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Late summer and autumn swarming of bats at Sikspārņu caves in Gauja National Park

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Abstract

Late summer and autumn swarming of bats at underground hibernacula has so far been poorly investigated in the north-eastern part of Europe. This study was conducted at Sikspārņu caves in Gauja National Park in 2005 to 2007 with the main aim to determine the species composition of swarming bats and the swarming phenology for different species. Mist-nettings of swarming bats were performed once per fortnight from the end of June until the beginning of November. Altogether 3,448 bats of seven species were caught of which *Myotis daubentonii* and *M. brandtii* were the most numerous. For all species adult males predominated initially, but numbers of adult females and subadult individuals increased as the season progressed. The capture-mark-recapture method revealed an individual-specific trend of visitations by adult males of *M. daubentonii* in subsequent swarming seasons. Migration between different swarming and hibernation sites located at 5- to 21-km distances were also recorded.

Key words: autumn swarming, bats, Gauja National Park, *Myotis brandtii*, *Myotis daubentonii*.

Introduction

At the end of summer and in autumn bats gather at underground sites in great numbers and perform a peculiar flying behaviour, which involves circling inside or outside the hibernaculum, chasing each other and emitting various social calls (Fenton 1969; Thomas et al. 1979; Kretzschmar, Heinz 1995). This behaviour was first reported from North America in the 1960s and was termed autumn 'swarming' (Davis 1964). The most popular hypotheses regarding this behaviour are: (i) assessing hibernacula, (ii) show the location of hibernacula to offspring (Fenton 1969) and (iii) mating activities, hence facilitating the gene flow and preventing inbreeding (Kerth et al. 2003; Veith et al. 2004; Rivers et al. 2005). In the Baltics this phenomenon has been reported previously (Liiva, Masing 1987; V. Vintulis, unpublished data), but so far it has remained without further examination.

Sikspārņu (Bat) caves were discovered in the 1980s and a colony of about 150 hibernating *Myotis dasycneme* was found at this site (Busha 1986). Since then census of hibernating bats at these caves has been conducted every year.

The main aim of this study was to describe changes in the species composition, sex and age structure of the bats during the autumn swarming period (further referred to as swarming season) to obtain basic knowledge about this phenomenon. Capture-mark-recapture method was used to check for possible migration between swarming sites and hibernacula and to analyze visitation tendencies for recaptured individuals within the same season and in consecutive seasons.

Materials and methods

The Sikspārņu caves are located in Gauja National Park near the town of Cēsis (57° 19', 25° 21'). Altogether six dolomite caves and holes have been discovered in this area. The largest of them – Lielā Sikspārņu cave (ca. 60 m in length) – was chosen as a study site for this research (Fig. 1). Seven bat species are known to hibernate in these caves regularly: *Myotis daubentonii* (Kuhl), *M. dasycneme* (Boie), *M. brandtii* (Eversmann, 1845), *M. mystacinus* (Kuhl), *M. nattereri* (Kuhl), *Eptesicus nilssonii* (Keyserling & Blasius) and *Plecotus auritus* (Linnaeus).

The study was conducted in 2005 to 2007. Swarming bats were mist-netted from the end of June until the beginning of November. During this period bat nettings (n = 6 in 2005, n = 7 in 2006, n = 8 in 2007) were performed only once per fortnight (usually twice per month) to minimize disturbance. Weather conditions varied during the netting events. We avoided only nights with strong wind and heavy rain, when nettings were not performed. The main entrance of the cave was covered by a mist-net for the entire night (Kunz, Kurta 1988), and two nearby entrances were closed by polythene, branches, and leaves. Captured bats were identified to species, sexed, aged and banded with numbered wing bands. We used aluminum bird rings, which were specially adapted for the bats (for *M. dasycneme* the ring diameter was 4.5 mm, but for other species – 3.0 mm). There were two classes of age (adults and subadults) used for age estimation according to degree of ossification and form of the metacarpal-phalageal joints (Anthony 1988). The bats were released after banding at the site of capture. Bat nettings using the same approach were additionally performed at two sandstone caves in the Gauja National Park at 8- and 21-km

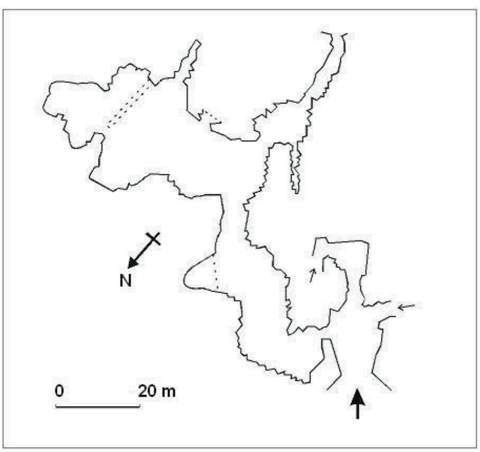

Fig. 1. Schematic plan of the Lielā Sikspārņu cave adapted from Eniņš (2004) (the main entrance and two other entrances covered in netting events are showen by arrows).

distances from the study site.

To compare species composition of bats in swarming and hibernation seasons at the Sikspārņu caves data from the annual hibernating bat census were used. In 2005 to 2007 census was conducted once every year in December or January. Hibernating bats were identified to species, except *M. brandtii* and *M. mystacinus*, which were pooled in one group '*M. brandtii*/*mystacinus*' (the accurate determination of these sibling species is impossible without disturbing their torpor). There are many deep and immense crevices in these caves, hence the actual number of hibernating bats might be considerably larger than recorded. Since 1992 all the important hibernacula in Gauja National Park as well as in other parts of Latvia have been surveyed every winter (V. Vintulis, unpublished data), and in the framework of this survey, search was made for bats with wing bands to check for possible migration between sites.

During most of the study period the presence of a roaming cat was noticed at the study site. This cat had adapted itself to catch and kill bats in the narrowest paths of the cave. The corpses and remains of the bats as well as the wing bands found were collected in every netting event. Dead recoveries were taken into account only in tests where the exact time of recapture was not required.

To compare the species composition between swarming and hibernation seasons Pearson's chi-squared goodness-of-fit test was used. This test was also performed in sex and age structure analysis and to compare the number of recoveries within one swarming season and consecutive swarming seasons, respectively. Spearman's rank correlation analysis was used to test the relationship of visitation timing in consecutive swarming seasons for individual bats if the sample size was greater than 15.

Results

During the swarming seasons altogether 3,448 individual bats of seven species were caught. The same species were found both in swarming and hibernation seasons, but their proportions differed between seasons (Table 1). In comparison with the swarming

Table 1. Number of bats found during hibernation seasons and caught during swarming seasons at the Lielā Sikspārņu cave in 2005 to 2007 (recaptures are not included)

Species	Hibernation seasons	Swarming seasons
M. daubentonii	23 (12.4 %)	1601 (46.4 %)
M. dasycneme	43 (23.1 %)	387 (11.2 %)
M. brandtii	–	973 (28.2 %)
M. mystacinus	–	141 (4.1 %)
M. brandtii/*mystacinus*	76 (40.9 %)	–
M. nattereri	5 (2.7 %)	289 (8.4 %)
Myotis sp.	12 (6.5 %)	–
E. nilssonii	3 (1.6 %)	36 (1.0 %)
P. auritus	15 (8.1 %)	21 (0.6 %)
Not identified	9 (4.8 %)	–
Total	186 (100 %)	3448 (100 %)

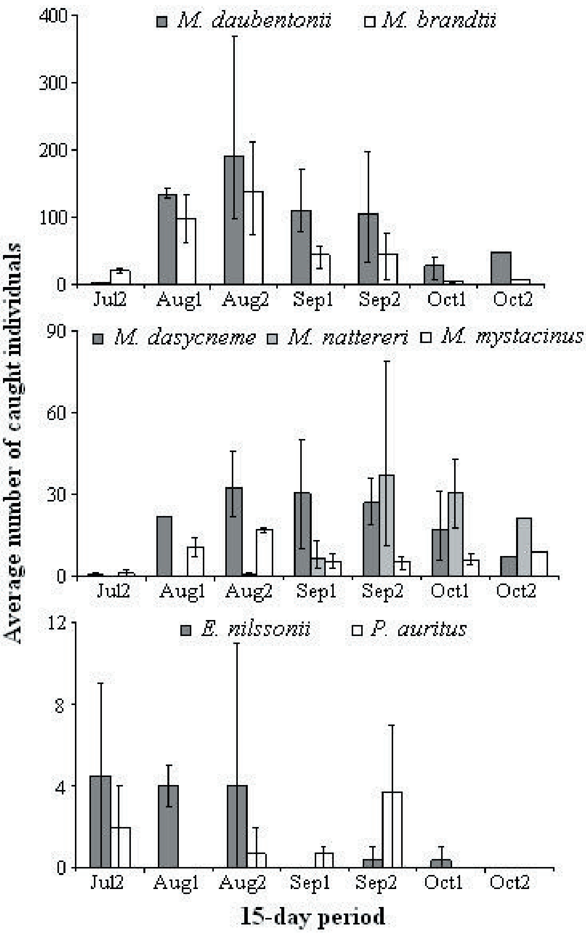

Fig. 2. Seasonal changes in mean, minimum and maximum number of caught bats during swarming seasons at the Lielā Sikspārņu cave in 2005 to 2007.

seasons, in the hibernation seasons *M. dasycneme* (χ^2 = 25.77, d.f. = 2, p < 0.001) and *M. brandtii*/*mystacinus* (χ^2 = 6.15, d.f. = 2, p < 0.05) were observed significantly more than expected, while *M. daubentonii* were found significantly less often than expected (χ^2 = 48.91, d.f. = 2, p < 0.001).

For most species the greatest swarming activity was observed at the end of August and in September. Temporal distribution of swarming activity differed among species (Fig. 2). For *M. brandtii* and *M. mystacinus* the greatest swarming activity was observed at the end of August. *M. daubentonii* reached its peak activity at the end of August and in September. For *M. dasycneme* a clear maximum was not observed; the swarming activity for this species was high at the end of August and in September. *M. nattereri* was the last species to begin swarming with peak activity at the end of September and beginning of October. The greatest activity of *E. nilssonii* was observed at the end of July and in August, reaching its peak at the end of August. Later this species rarely visited the study site. The majority of *P.*

Table 2. Number of all autumn swarming captures at the Lielā Sikspārņu cave in 2005 to 2007 (recaptures are not included). The male dominance between adults and subadults tested by Pearson's chi-squared goodness-of-fit test (* – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$)

Sex and age group	*M. daubentonii*	*M. dasycneme*	*M. brandtii*	*M. mystacinus*	*M. nattereri*	*E. nilssonii*	*P. auritus*
Ad. males	654 (40.8 %)***	152 (39.3 %)***	357 (36.7 %)***	62 (44.0 %)*	142 (49.1%)**	14 (38.9 %)	12 (57.1 %)
Ad. females	379 (23.7 %)	86 (22.2 %)	202 (20.8 %)	37 (26.2 %)	93 (32.2%)	7 (19.4 %)	6 (28.6 %)
Total ad.	1027 (64.5 %)	238 (61.5 %)	559 (57.5 %)	99 (70.2 %)	235 81.3%)	21 (58.3 %)	18 (85.7 %)
Subad. males	330 (20.6 %)***	94 (24.3 %)***	216 (22.2 %)	21 (14.9 %)	23 (8.0%)	6 (16.7 %)	2 (9.5 %)
Subad. females	229 (14.3 %)	49 (12.7 %)	183 (18.8 %)	21 (14.9 %)	25 (8.7%)	7 (19.4 %)	1 (4.8 %)
Total subad.	559 (34.9 %)	143 (37.0 %)	399 (41.0 %)	42 (29.8 %)	48 (16.6%)	13 (36.1 %)	3 (14.3 %)
Indet. males	4 (0.2 %)	4 (1.0 %)	7 (0.7 %)	0	3 (1.0%)	0	0
Indet. females	3 (0.2 %)	2 (0.5 %)	8 (0.8 %)	0	1 (0.3%)	0	0
Indet. sex	2 (0.1 %)	0	0	0	2 (0.7%)	2 (5.6 %)	0
Total indet.	9 (0.6 %)	6 (1.6 %)	15 (1.5 %)	0	6 (2.1%)	2 (5.6 %)	0

Table 3. Number of recaptures in different years during swarming seasons at the Lieā Sikspārņu cave in 2005 to 2007 (dead recoveries included)

Year of banding	Year(s) of recapture	*M. daubentonii*	*M. dasycneme*	*M. brandtii*	*M. mytacinus*	*M. nattereri*	Total
2005	2005	8 (8.3 %)	4 (10.5 %)	4 (12.9 %)	0	2 (16.7 %)	18 (10.1 %)
2005	2006	26 (27.1 %)	15 (39.5 %)	14 (45.2 %)	1 (50 %)	2 (16.7 %)	58 (32.4 %)
2005	2006, 2007	1 (1.0 %)	1 (2.6 %)	0	0	1 (8.3 %)	3 (1.7 %)
2005	2007	7 (7.3 %)	4 (10.5 %)	2 (6.5 %)	0	7 (58.3 %)	20 (11.2 %)
2006	2006	13 (13.5 %)	2 (5.3 %)	3 (9.7 %)	1 (50 %)	0	19 (10.6 %)
2006	2007	31 (32.3 %)	8 (21.1 %)	6 (19.4 %)	0	0	45 (25.1 %)
2007	2007	10 (10.4 %)	4 (10.5 %)	2 (6.5 %)	0	0	16 (8.9 %)
Total		96 (100 %)	38 (100 %)	31 (100 %)	2 (100 %)	12 (100 %)	179 (100 %)

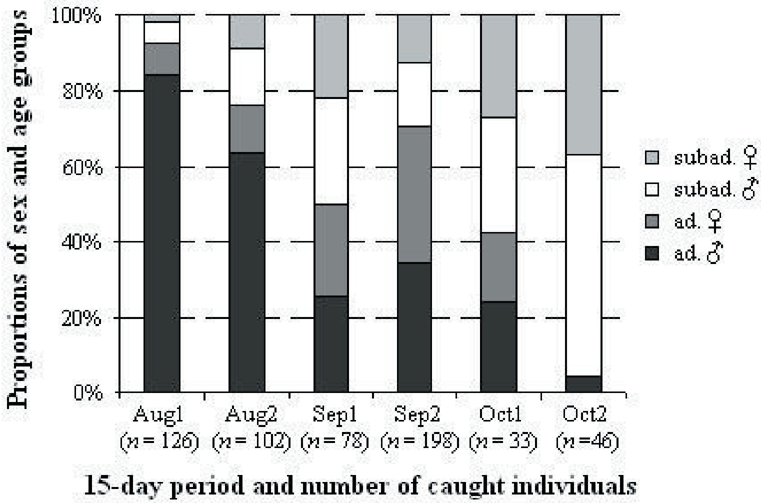

Fig. 3. Dynamics of particular sex and age groups of *M. daubentonii* netted at the Lielā Sikspārņu Cave in 2007 (recaptures are included).

auritus individuals were caught at the end of July and at the end of September.

The sex and age structure of caught individuals is shown on Table 2. Among adults significantly more males than females were observed for all *Myotis* species, but this difference was not significant for *E. nilssonii* (χ^2 = 2.38, d.f. = 1, p = 0.12) and *P. auritus* (χ^2 = 2.06, d.f. = 1, p = 0.15). The difference in numbers of subadult males and subadult females was not significant except for *M. daubentonii* (χ^2 = 18.25, d.f. = 1, p < 0.001) and *M. dasycneme* (χ^2 = 14.17, d.f. = 1, p < 0.001) – in these cases subadult males predominated. Temporal changes in sex and age structure during the swarming season, however, were common for all species. At the beginning of swarming the dominant group was formed by adult males, but the proportion of the adult females and subadult individuals increased as the season progressed (Fig. 3).

In this study 3,285 individual bats were banded. Only *Myotis* species were recaptured (Table 3). The total number of recaptured individuals, including dead recoveries, was 177 (5.4 %). There were significantly more cases where bats were recaptured in consecutive swarming seasons rather than in the same season (χ^2 = 31.35, d.f. = 3, p < 0.001, the sample size for *M. mystacinus* was too small to include in this test). Spearman's rank correlation analysis revealed a significant relationship of visitation timing in consecutive swarming seasons for *M. daubentonii* adult males (r = 0.97, d.f. = 27, p < 0.001). For other species and sex-age groups this test was not performed due to small sample sizes.

Three bats were recaptured outside the banding sites (Fig. 4). One swarming *M. nattereri* subadult male was first caught and banded at an artificial sandstone cave ca. 21 km southwest of the study site, but later in the same year recaptured at the study site. At the same sandstone cave a lactating *M. mystacinus* female was recaptured, which was banded at the Lielā Sikspārņu cave in the previous year. Another *M. nattereri* adult male banded at the study site was found hibernating in a sandstone cave ca. 5 km northeast of the study site.

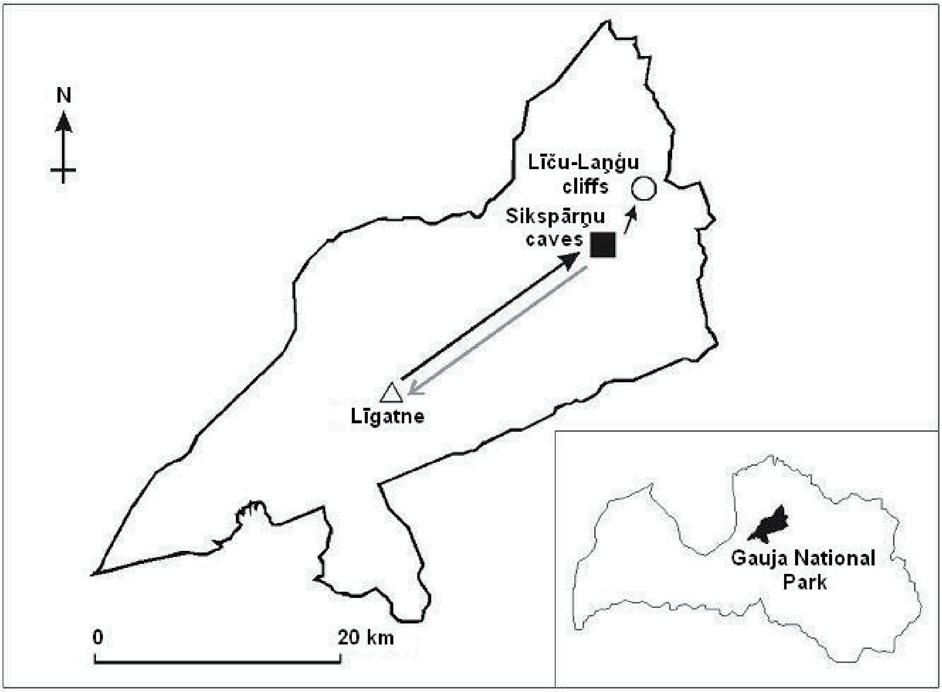

Fig. 4. Discovered bat movements among the Lielā Sikspārņu cave and other swarming (△) and hibernation (○) sites. Movements of *M. nattereri* are showed by black arrows, but the gray arrow represents *M. mystacinus* (see details in the text).

Discussion

In this study swarming behaviour was recorded for seven bat species, which all usually hibernate in underground sites. This supports the general opinion that autumn swarming behaviour is characteristic to those bat species using underground sites for hibernation (Fenton 1969; Kretzschmar, Heinz 1995; Parsons et al. 2003a). Therefore, swarming can be distinguished from another behaviour of bats at the end of summer called 'invasions' (Sachteleben 1991), which usually involves subadult and inexperienced individuals of *Pipistrellus* species, which accidentally enter buildings.

The differences in the species composition of the bats during the swarming and hibernation seasons can be explained by different habitat selection of species regarding hibernation in deep and large crevices (Furmankiewicz, Górniak 2002). For example, *M. dasycneme* are more likely to hibernate in bigger crevices than smaller species. Hence the proportions of this species observed in hibernation seasons may appear greater than they really are.

In this study the greatest swarming activity for most species was observed at the end of August and in September. Other studies performed in Czech Republic (Berková, Zukal 2006), Denmark (Degn et al. 1995), Germany (Harrje 1994), Great Britain (Parsons et al. 2003b; Rivers et al. 2006) and Poland (Furmankiewicz, Górniak 2002) suggest that the autumn swarming phenology in Latvia does not differ much from other parts of Europe.

The temporal distribution of swarming activity was species-specific. For example, *M. brandtii* and *M. mystacinus* had their activity peak in August, *M. daubentonii* – at the end of August and in September, and *M. nattereri* at the end of September and in October. It is known that these species leave their hibernacula in spring in the opposite order (Degn 1987; Parsons et al. 2003a). Parsons et al. (2003a) associate these observations with the foraging strategies of these species. *M. nattereri* is a gleaning species, which is able to capture prey from surfaces. Therefore, this species might be active for a longer period in the year than *M. daubentonii* and *M. brandtii*, which are specialized in catching flying insects. Moreover, *M. brandtii* and *M. mystacinus* are considerably smaller in size than other *Myotis* species. Hence their early swarming and start of hibernation could be related to thermoregulation as they have a large body surface-to-volume ratio (Ransome 1990).

In previous studies the visits of *E. nilssonii* at underground sites during the swarming seasons were considered occasional (Furmankiewicz, Górniak 2002; Karlsson et al. 2002). This study and other research in Latvia (J. Šuba, unpublished data) confirm that the swarming behaviour is characteristic of this species. For *Myotis* species it is known that their swarming activity overlaps with the start of hibernation (Fenton 1969; Harrje 1994; Trappmann 2005). In contrast, *E. nilssonii* actively swarm in August and up to the beginning of November they visit underground sites rarely.

Overall the proportions of different sex and age groups among the caught individuals tended to be species-specific, yet the temporal changes of the sex and age structure were common for all species. At the beginning of the swarming season the study site was mostly visited by adult males, but at the end of the season subadult individuals of both sexes predominated. Fenton (1969) suggests that swarming behavior could be related to the information transfer from adults to subadults, indicating the location of the hibernacula. Adult males may emerge earlier than females due to their idleness during the summer while females are rearing their offspring (Parsons et al. 2003a).

There were significantly more cases when bats were recaptured in consecutive swarming seasons than in the same season. An exhausting behaviour like swarming would considerably inhibit the fat deposition for the winter if performed continuously. Therefore, bats are expected to visit the swarming sites only once or a few times per season. The analysis of recaptured *M. daubentonii* adult males in consecutive swarming seasons shows that these bats tended to visit the swarming site at the same time every year. Similar results have been obtained in other studies (e.g. Fenton 1969; Parsons et al. 2003a).

The maximum distance of the diurnal roosts or hibernacula to swarming sites can be from 20 up to 60 km (Parsons, Jones 2003, Rivers et al. 2006). Capture-mark-recapture and radio-tracking studies indicate that bats from different summer roosts visit a common swarming site, which may also function as a hibernaculum, though migrations to other hibernacula have also been recorded (Fenton 1969; Parsons et al. 2003a; Parsons, Jones 2003; Rivers et al. 2006). There are two opinions about the swarming sites per se. There is evidence that bats show a great fidelity to a particular swarming site and do not visit other swarming sites (Parsons et al. 2003a; Parsons, Jones 2003), however, migration between different swarming sites have been recorded (Rivers et al. 2006). Bat migration found in this study indicate that two distant caves may serve as swarming sites for the same individuals.

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Sikspārņu vēlās vasaras un rudens spietošana Gaujas nacionālā parka Sikspārņu alās

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Kopsavilkums

Rakstā aplūkota Eiropas ziemeļaustrumu daļā maz pētīta tēma – sikspārņu „spietošana” pie ziemošanas mītnēm vasaras beigās un rudenī. Pētījums veikts Sikspārņu alās (Gaujas nacionālajā parkā) no 2005. līdz 2007. gadam, un tā galvenais mērķis bija noskaidrot spietojošo sikspārņu sugu sastāvu un to spietošanas fenoloģiju. No jūnija beigām līdz novembra sākumam reizi divās nedēļās veikta spietojošo sikspārņu ķeršana un gredzenošana. Pavisam pētījuma periodā noķerti 3448 sikspārņi no septiņām sugām. Visām sugām spietošanas sezonas sākumā domināja pieaugušie tēviņi, bet sezonas laikā ievērojami palielinājās pieaugušo mātīšu un nepieaugušo īpatņu īpatsvars. Pieaugušajiem ūdeņu naktssikspārņa tēviņiem konstatēta individuāla spietošanas laika izvēles tendence dažādās spietošanas sezonās. Konstatētas arī atsevišķu īpatņu pārvietošanās starp dažādām spietošanas un ziemošanas mītnēm piecu līdz divdesmit viena kilometra attālumā.