



Distribution of Daubenton´s bat
(*Myotis Daubentonii*)
-why are males and females spatially segregated?

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Abstract

Sexual segregation in Daubenton's bat, *Myotis daubentonii*, which males and females separated into different geographic areas, has earlier been documented in areas with differences in altitude and thereby climate. This study provides evidence for segregation also in an area with only small differences in altitude and climate. Sites with both males and females were found, as well as sites with only males. The results indicates that male sites often are located at creeks in agricultural landscapes, while sites with both males and females often are located in or close to a park, nearby a large lake. Different hypotheses which might explain the results are discussed.

Keywords

Sexual segregation, spatial segregation, sex distribution, competition, climate, altitude, water area, parks.

Introduction

Sexual segregation is common among vertebrates. Mammals have been in focus for studies of the subject, especially ungulates (Bowyer 2004), such as Rocky mountain mule dears (Main & Coblentz 1996) and elephants (Shannon et al. 2008). Several hypotheses

about segregation in ungulates has been developed, and can be separated into two types, habitat segregation and social segregation, described in detail by Ruckstuhl (2007). The hypotheses suggested to explain habitat segregation are predation risk hypothesis, forage selection/gastro centric hypothesis and scramble competition hypothesis (Main & Coblentz 1990, Main et al. 1996, Ruckstuhl 2007). The proposed hypotheses for social segregation are social-preference, activity budget hypothesis, aggressiveness hypothesis, and oddity effect hypothesis (Main et al. 1996, Ruckstuhl & Neuhaus 2000, Weckerly et al. 2004, Ruckstuhl 2007). Some of the hypotheses have temporal or seasonal restrictions (Ruckstuhl 2007).

One order of vertebrates where sexual segregation occurs is bats (Chiroptera), where segregation has been found in several of the species in temperate zones. In general, females form nursery roosts during reproductive season, such as *Myotis capaccini* (Papadatou et al. 2008) and *Vespertilio murinus* (Safi et al. 2007), while males live solitary or in small groups nearby. However, in some cases females and males also are separated into different habitats and areas. Females of several species, e.g. *Myotis lucifugus* and *Eptesicus fuscus*, have been found more common on lower than on higher elevations during lactating and pregnancy period compared to males, explained by different energy demands among males and females (Barkley 1991, Grindahl et al. 1999, Cryan et al. 2000).

An example of a bat species where males and females are separated into different areas is Daubentons bat, *Myotis daubentonii* (Chiroptera: Vespertilionidae). It forages over water, preferring smooth or slowly running water, probably since rapid water would interfere with their echolocation too much (Rydell et al. 1999). It is specialized in

catching insects at the watersurface by gaffing (Jones & Rayner 1988, Kalko & Schnitzler 1989) and feeds mainly on prey from the family Chironomidae, but also from other Diptera families and taxa of insects (Beck 1995, Vaughan 1997). At rivers they choose sections that have trees on both sides and smooth water surface, which coincide with high density of insects (Warren et al. 2000). In Daubenton's bat females are slightly larger than males (Jones & Kokurewicz 1994), as well as in many other species of vespertilionids (Myers 1978). Females form nursery roosts during lactating and pregnancy period, while males live solitary or in small groups (Encarnacao et al. 2005, Dietz and Kalko 2006). The females increase the daily ingested energy during pregnancy (Encarnacao & Dietz 2006).

Earlier studies show that males and females roost at different altitude, with females only roosting at lower altitudes which are climatically favourable (Russo 2002, Encarnacao et al. 2005). While both males and females can be found at low altitudes, females are not found at higher altitudes; the effect of altitude depends on the latitude, from 900-950 m a.s.l. as limit for females at 41°N, to 100-150 m a.s.l. at 54°N (Russo 2002). Further on more females are found in lowland where the water surface area is large compared to upland (Encarnacao 2005, Senior et al. 2005, Dietz et al. 2006). The landscape surrounding nursery roosts is more covered with water and coppices than the landscape surrounding male roosts (Encarnacao et al. 2005). Since males and females are geographically separated during lactating and pregnancy period Daubenton's bat is an appropriate species for studies of sexual segregation.

Sexual segregation both in *M. daubentonii* and other species of bats have been studied in areas with more or less altitude differences, and thereby differences in climate and

insect density and the hypotheses that have been tested are about competition and differences in habitat requirements and nutrition requirements. The explanation proposed is that male bats are able to roost and forage in habitats with lower insect densities and less favourable climate than breeding females do, since females have an increased energy demand during pregnancy and lactating period and need to stay homoeothermic, while males have less energy demand and can use daily torpor to cope with poorer conditions (Barkley 1991, Cryan et al. 2000, Russo 2002, Encarnacao et al 2005). This is confirmed by that the males at higher altitudes have a lower BCI (body condition index, quota between body mass and forearm length) than males at lower altitude (Russo 2002), as well as males in poorer upstream areas have a lower BCI compared to males roosting in richer downstream areas (Senior et al. 2005). Males in upstreams areas spent more time out of the roost than downstream males and used more distant foraging sites, suggesting that upstreams males work harder for food in a poor habitat (Senior et al. 2005). Senior et al. (2005) also, after genetic analysis, suggested that males in downstream areas, i.e. same areas as females, have better fitness than upstream males, claiming that this shows that competition between males is the driving force for sexual segregation, also claiming that the segregation was not based on age. They also recorded that at swarming site sex distribution was 80/20 males/females and the explanation for this might be that females that already have mated successfully will not need to go to the swarming site, or they can swarm less time, and by that save energy when going directly to the hibernation site (Senior et al. 2005). Dietz et al. (2006) found males and females in the same roosts during the period of pregnancy and lactating and they refer to this as mating roosts.

Previously suggested hypotheses for Daubenton's bats in the subject are that differences in nutritional requirements between the sexes during lactating and pregnancy period may lead to intra-specific competition if both sexes feed in the same foraging area (Dietz et al. 2006). The competition might be indirect by exploitation or direct by resource defence and lead to segregation (Russo 2002). Some males are excluded by other males or females, resulting in increased mating success for the males staying in the same areas as females (Senior et al. 2005).

All the studies of the intraspecific distribution of Daubenton's bat have shown that there is segregation. However, all of them have been carried out in areas with altitude or temperature differences, none have been done in a lowland landscape with homogenous climate. The purpose of this study was to investigate how males and females of Daubenton's bat were distributed in a landscape without differences in altitude or temperature, and based on that discuss the following hypotheses:

- 1: Males and females are separated in space because of different demands on habitat qualities in terms of vegetation structure, presence of water and spatial and temporal distribution of insects
- 2: Males and females are separated in space because of inter- and/or intraspecific competition

If this is true it was predicted that there would be male and female sites and that males and females would be found in different habitats.

Material and methods

The study area

The study area was located in the county of Uppland, Sweden (59°N, 17°E, Fig. 1). Uppland is a flat landscape with only small differences in altitude, and the highest point is 118 m a.s.l. The temperature is therefore not affected by differences in altitude, instead it is the distance to the Baltic sea that controls the temperature in this area. During July, the average temperature is about 16°C (Anon. 2005). The difference in altitude between the study sites is at most 25 m (5-30 m a.s.l.).

Capture and marking

During 18 nights from 1 of July until 27 of July 2008, Daubenton's bats were captured at their foraging sites with mist nets located over small creeks, lakes and ponds. When the catching place was a creek the net was set from a bridge or nearby a bridge. The net was set 0-60 minutes after sunset and during 20-180 minutes depending on the bat activity and the numbers of captures. The time between first and last bat captures were between eight minutes and one hour and eight minutes. As soon as a bat flew into the net it was taken out, the capture time was recorded and sex and age (juvenile or adult) were identified. With exception of two catching occasions (Marielund and once at Skebobruk) the bat was banded with a steel ring with a reflex band glued to it. Then the bat was released. The places for capture were chosen from what seemed to be an appropriate hunting habitat or places where Daubenton's bat was known to be foraging from previous observations.

Also data from trapping with mist net during 2003 and 2004 were used.

Other species

Species besides *M. daubentonii* were registered using ultra sonic detector (Pettersson Electronic) every time a site was visited. Also other species caught in the mist net were registered.

Landscape analysis

For landscape analysis of the home range of bats ArcGIS 9.2 was applied. The area of different habitats (water, crop fields, coniferous and mixed forest, deciduous forest, parkways, densely populated area and clear-cuts) were measured in a zone of 1 km (in total about 314 ha) surrounding the sites where the bats were caught. This was based on the assumption that the most important foraging area was visited in the beginning of the night and that this area was located near the home range centre. This assumption is supported by results from radiotracking (de Jong, pers. com.). Also the distance from the foraging site to the nearest lake at a size of at least 10 ha was measured.

The home ranges were separated into male and mixed home ranges, depending on if there were only males or a mixture of males and females at the foraging site where they were caught, and the area of different habitats in male and mixed home ranges was compared.

Statistics

Mann-Whitney U-test was applied to test for differences in habitats between male and mixed sites, and was calculated in Microsoft Excel 95. Chi² test, calculated in Excel 95 combined with power analysis using GPower 3.0, was applied to test sex distribution between sites. Logistic regression was implemented, using Statistica 6.0, to test for connection between presence of females at a site and area of or distance to a certain habitat. To test for difference in the number of bat species between sites with only males and sites with both males and females, 2-sample t-test was applied, using Minitab 15.

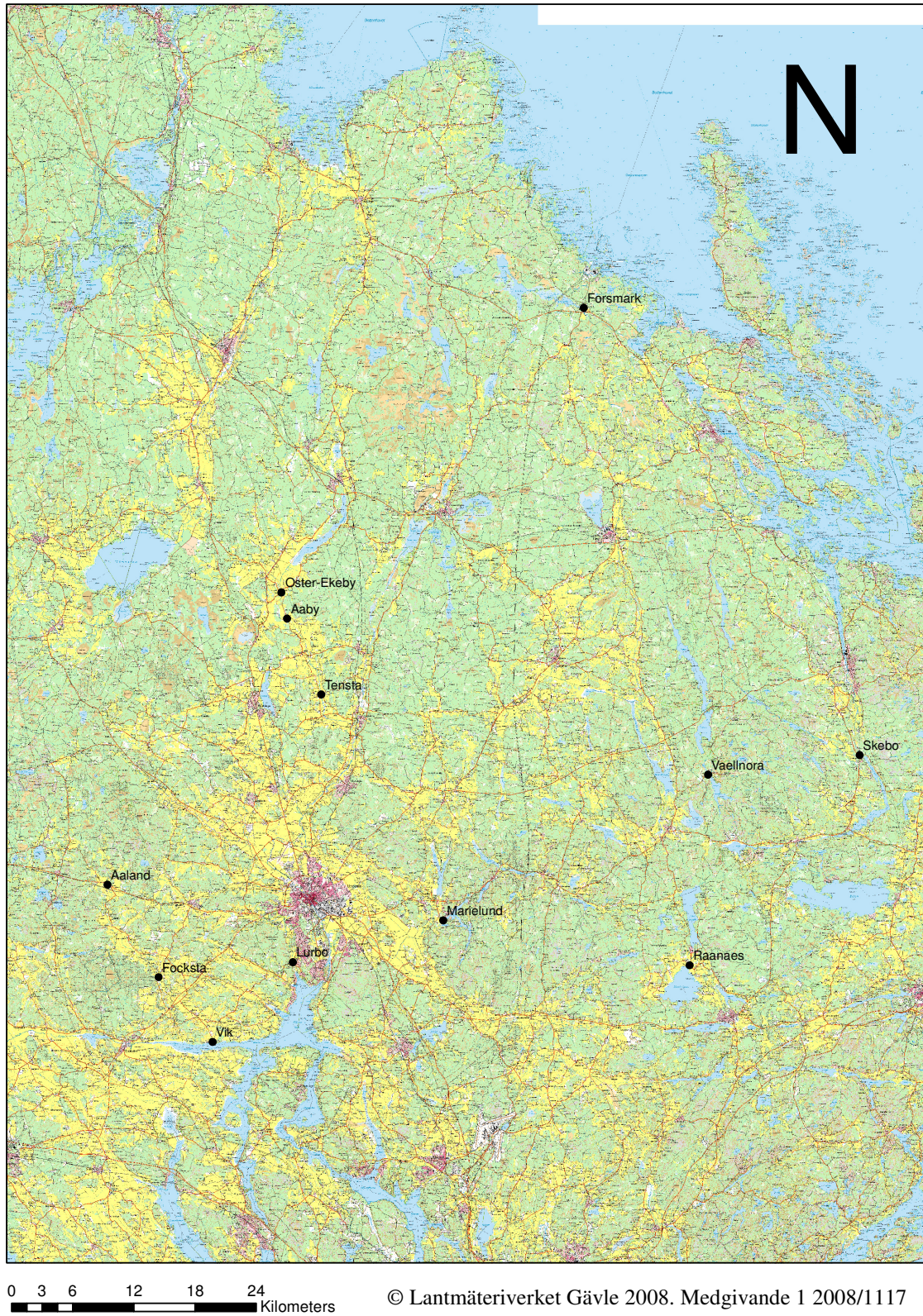


Fig. 1: The study area with all the sites and the Baltic sea in the north east.

Results

In total 12 sites were studied and 117 bats (64 males and 53 females) were caught (Table 1, Fig. 1).

Table 1. Total number of bats captured at different sites

Site	Year	Females	Males	Total
Focksta	2003	0	6	6
Focksta	2008	0	4	4
Forsmark	2004	1	0	1
Forsmark	2008	3	2	5
Lurbo	2003	0	5	5
Lurbo	2008	0	1	1
Marielund	2004	0	4	4
Marielund	2007	0	2	2
Marielund	2008	0	2	2
Rånäs	2003	3	5	8
Skebobruk	2007	5	0	5
Skebobruk	2008	28	2*	30
Tensta	2008	0	7	7
Vik	1987	1	0	1
Vik	2004	5	0	5
Vik	2005	1	0	1
Vik	2008	2	2	4
Vällnora	2008	0	3	3
Åby	2008	1	9	10
Ålands kyrka	2008	0	6	6
Öster Ekeby	2003	2	3	5
Öster Ekeby	2006	1	1	2
Total		53	63	98

*Of which one juvenile

Sex distribution at foraging sites

At the site Åby there were significantly more males than females ($n = 10$, $\chi^2 = 4.900$, d.f. = 1, $p < 0.05$, power 0.7156) and at Skedbo there were significantly more females than males ($n = 11$, $\chi^2 = 5.818$, d.f. = 1, $p < 0.05$, power 0.7745). For the rest of the sites there were too little data for statistical analysis, due of the risk of pseudoreplications,

because bats only were marked during 2008. There were though indications of differences in the sexual distribution by some sites with both males and females and others with only males (Table 1).

Sex distribution in relation to habitats

Four of the six sites where only males were found were at creeks in home ranges with only small water surfaces. Also the site Åby, with a majority of males, were at a creek with only a small proportion of water in the home range. Four of the sites where females were found were near parks or in parks with large water areas nearby.

According to Mann-Whitney U-test there were no significant differences between sites with only males (n=6) and sites with a mixture of males and females (n=6) (Table 3a and b). The logistic regression analysis did not show any relation between presence of females and area or length of different habitats in the home range; neither were there any relation with the distance to a lake and the presence of females at a site (Fig. 2).

Table 3a. Sex distribution at different sites

Site	Males or mixed
Focksta	Males
Forsmark	Mixed
Lurbo	Males
Marielund	Males
Rånäs	Mixed
Skebobruk	Mixed
Tensta	Males
Vik	Mixed
Vällnora	Males
Åby	Mixed
Åland	Males
Öster-Ekeby	Mixed

Table 3b. Comparison of habitat area and distance to nearest lake larger than 10 ha in home ranges of males and and home ranges of mixed sites (Mann Whitney U-test)

Parameter	Median male sites	Median mixed sites	P
Lakes and ponds	0.3286	16.1	>0.05
Creeks	1.118	1.118	>0.05
Distance to lake	2383	527.5	>0.05
Crop fields	104.7	130.7	>0.05
Coniferous and mixed forest	127.2	91.62	>0.05
Deciduous forest	0	8.100	>0.05
Densely populated area	0	0	>0.05
Clear-cuts	2.168	1.576	>0.05
Park-ways	127.0	0	>0.05

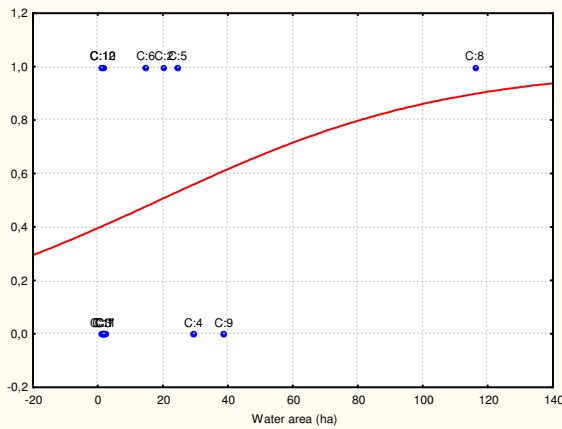


Fig. 2a: Water area including creeks
p = 0.31

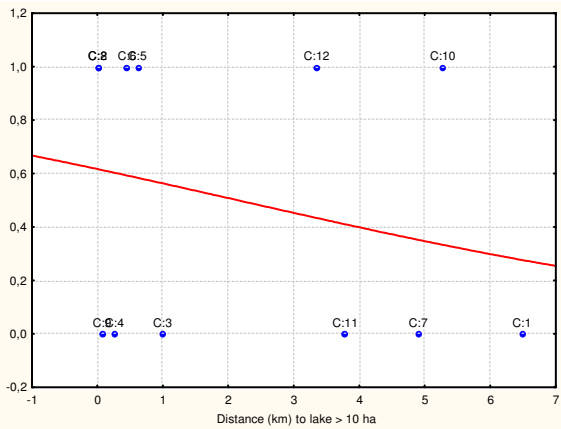


Fig. 2b: Distance to a lake larger than 10 ha
p = 0.39

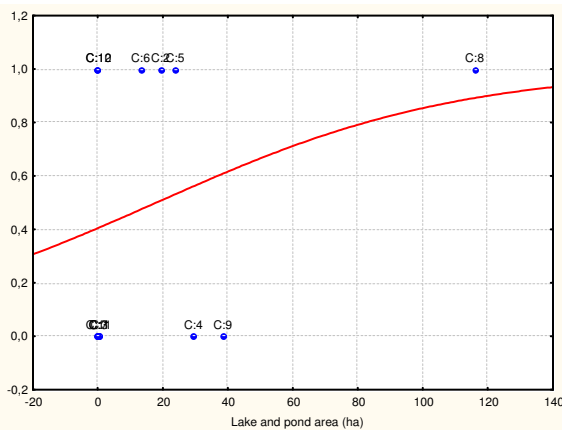


Fig. 2c: Lake and pond area
p = 0.32

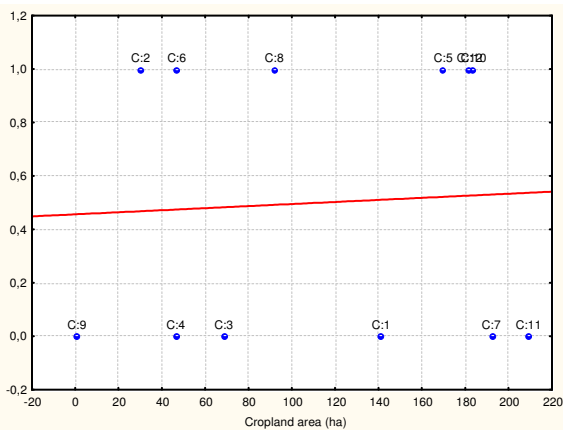


Fig. 2d: Crop fields area
p = 0.85

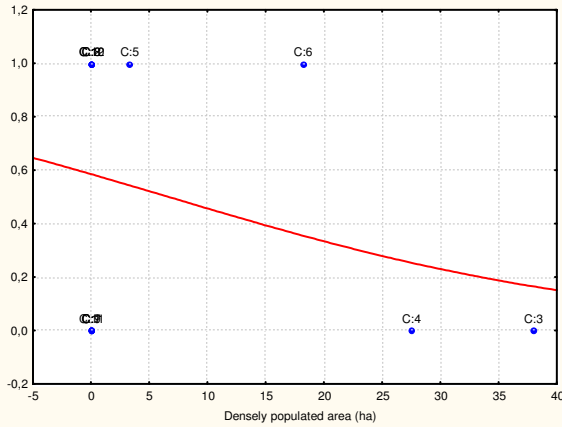


Fig. 2e: Densely populated area
p = 0.30

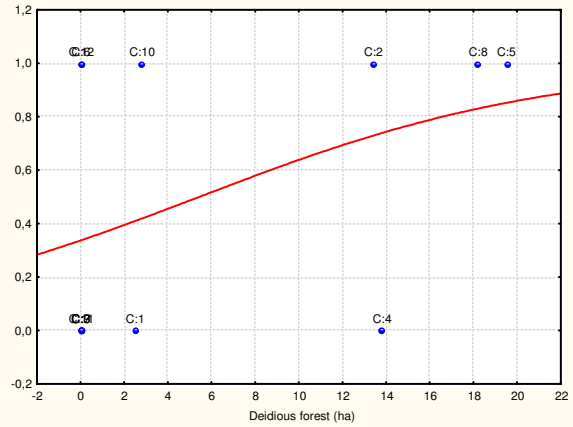


Fig. 2f: Decidious forest area
p = 0.14

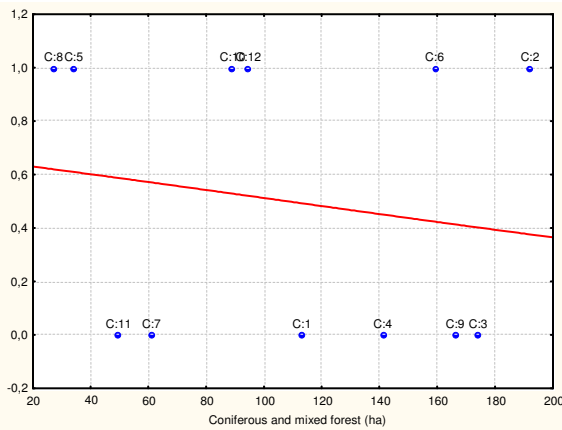


Fig. 2g: Coniferous and mixed forest area
p = 0.57

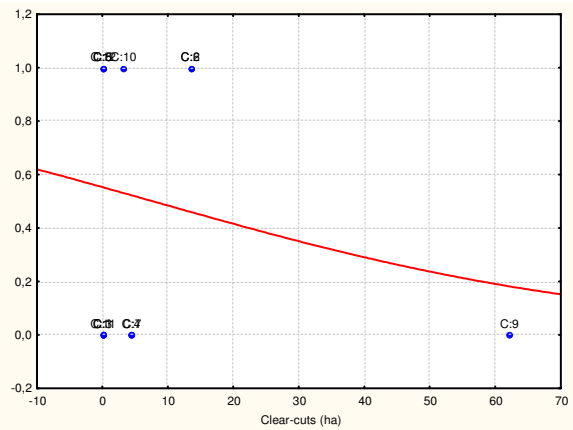


Fig. 2h: Clear-cuts area
p = 0.47

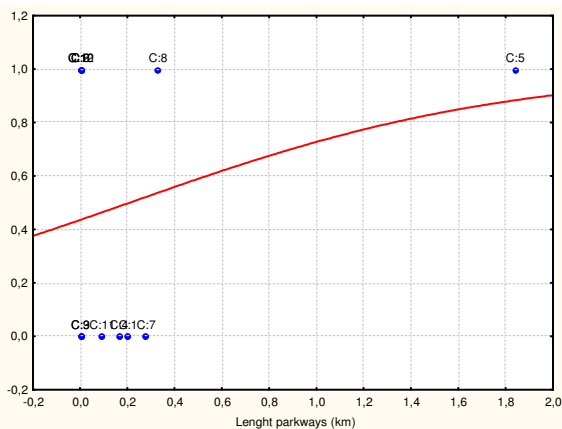


Fig. 2i: Length of parkways (km)
p = 0.38

Fig. 2a-i: Relations between presence of females at a foraging site and the area (ha) or length (km) of a within the home range, or the distance (km) to a lake of at least 10 ha. C1 – C12 represents the sites as to following: C1 Focksta, C2 Forsmark, C3 Lurbo, C4 Marielund, C5 Rånäs, C6 Skebo, C7 Tensta, C8 Vik, C9 Vällnora, C10 Åby, C11 Åland and C12 Öster-Ekeby. 0,0 at the y-axis means that there are no females at the site; 1,0 means presence of at least one female at the site.

Other species

A number of rare species have been found at the study sites, such as *Myotis dasycneme* (with similar ecology as *M. daubentonii*), *Pipistrellus nathusii*, *Vespertilius murinus* and *Myotis nattereri*. All these species were found only at mixed sites. Other species such as *Nyctalus noctula*, *Pipistrellus pygmaeus* and *Plecotus auritus* occur more frequently at mixed sites, but sometimes also at male sites. However, there were no significant difference between sites with only males (n=6) and sites with both males and females (n=6) in terms of number of species ($T = -1.642$ d.f. = 10, $p = 0.1316$) (Table 5b). *Myotis brandtii* and *M. mystacinus* are closely related and difficult to identify with ultrasonic detector. In surveys only based on ultra sound identification these two species were counted as *Myotis brandtii/mystacinus*. However, in some cases the survey was combined with trapping which most often made it possible to identify the species.

Table 5a. Species found at the sites with *Myotis daubentonii*. At three sites *Myotis brandtii* and *M. mystacinus* have not been distinguished.

Male sites	No of sites	Mixed sites	No of sites
<i>Eptesicus nilssonii</i>	6	<i>Eptesicus nilssonii</i>	6
<i>Nyctalus noctula</i>	3	<i>Nyctalus noctula</i>	5
<i>Pipistrellus pygmaeus</i>	4	<i>Pipistrellus pygmaeus</i>	5
<i>Plecotus auritus</i>	1	<i>Plecotus auritus</i>	4
<i>M. brandtii</i> or <i>M. mystacinus</i>	1	<i>M. brandtii</i> or <i>M. mystacinus</i>	3
<i>Myotis brandtii</i>	3	<i>Myotis mystacinus</i>	1
		<i>Myotis dasycneme</i>	1
		<i>Myotis nattereri</i>	2
		<i>Pipistrellus nathusii</i>	2
		<i>Vespertilio murinus</i>	2

Table 5b. Number of species at each site.

Site	Males or mixed	No of species
Focksta	Males	4
Forsmark	Mixed	5
Lurbo	Males	4
Marielund	Males	2
Rånäs	Mixed	9
Skebobruk	Mixed	3
Tensta	Males	3
Vik	Mixed	8
Vällnora	Males	4
Åby	Mixed	3
Åland	Males	3
Öster-Ekeby	Mixed	2
Total	Sites with only males	6
Total	Mixed sites	10

Discussion

This is the first study of how males and females are distributed in a landscape with only small climatic differences, and the study shows that there probably is spatial segregation of the sexes also in this area. The observations indicate that there are sites with only males and sites with a mixture of females and males, and that there were habitat differences between the sites. However, due to lack of data, it was not possible to confirm hypotheses. In order to find statistical differences between male sites and mixed sites it was obvious that a larger data set is required, both more individuals trapped at each site as well as more sites.

Differences between mixed areas and male areas in composition

In general the male sites were located at creeks surrounded by deciduous trees, often with large areas of crop fields in the home range. The mixed sites were in most cases located in or near a park, nearby a large lake.

Since there seem to be spatial segregation of males and females in Upland, landscape factors rather than climate and elevation is affecting where in the landscape males and females are found. Access to large water areas is likely to be an important factor for breeding females. It might be more energy effective to hunt close to the water surface than higher in the air (Jones & Rayner 1988) as well as there are acoustic advantages when foraging over smooth water (Siemers et al. 2001). There are also more Chironomidae in aquatic environments than in terrestrial environments (Barkley 1991, Gärdenfors 1991). During pregnancy the females energy demand increases (Encarnacao & Dietz 2006) and access to large water areas would be an advantage because of more insects and less energy use while foraging and also have the same advantages for the juveniles when they become fledgelings. A large water body will also not get overgrown or dessicate as easy as a smaller one. At some of the sites in this study where only males were found, the creeks were somewhat dessicated and overgrown by water-vegetation at the end of July. This reduces the access to open water and thus the availability of proper foraging ground for contingent fledglings.

Also parks are likely to be important, probably because they give good roosting opportunities thanks to old hollow trees. Parkland has earlier been discovered to be common around roosts (Parsons & Jones 2003).

Competition

Competition can be either intraspecific or interspecific, by exploitation or interference and it can be over roost sites and/or over foraging sites. Segregation of males and females into different areas due to competition by exploitation would occur e.g. if females are more motivated (because of pregnancy) than males or other species to find an optimal roost site, and thereby occupy sites earlier in the season than males or other species do. There are currently no data of differences in the time of occupation of roost sites for the sexes. Sexual segregation due to intraspecific competition by interference would occur if females are stronger than males (because of bigger size) or if males compete with each other over access to females.

Since Daubenton's bat is foraging close to the water surface there is probably no competition over food supply with other species except for *Myotis dasycneme*, which is rare and were only found occasionally at two of the sites in this study (both mixed sites). There might though be competition with other species over foraging sites in forests or over roost sites. Even if not significant, there were a few more species at the mixed sites than at the sites with only males.

There are data suggesting that roost sites are not a limited resource (Encarnacao et al. 2005, Senior et al. 2005). On the other hand, all hollow trees that seem to be available are not necessarily usable, they might be inhabited by other animals such as wasps or unsuitable for some other reason, such as predation by mustelids. Kapfer et al. (2008) documented that the roosts were aggregated in restricted areas and roost aggregation were not linked to the distribution of hollow trees. When bats changed roosts, they still stayed within a limited area.

There have been indications of territorial behaviour of Daubentons bat (Wallin 1961, Encarnacao et al. 2005), but not enough data to be able to explain the mechanism in detail. Intraspecific competition over females between males is also an eventuality, since males occurring near females are suggested to have higher fitness (Senior et al. 2005).

Conclusions

Segregation of males and females of Daubenton's bat into different areas seem to appear also in a landscape with only small differences in climate. The cause of the segregation is yet to be discovered but probably interference competition over sites in optimal foraging areas has a huge impact. The competition is either between males, between males and females or a combination. In future studies, focus should be on males. Philopatry of males between the years, whether males condition before inhabiting roost sites differ between the ones inhabiting sites with only males and the ones inhabiting mixed sites, age structure at sites, insect abundance and food quality at sites and differences in fitness between males at different sites are things to be studied to get closer to an answer to the reason behind the spatial sexual segregation in Daubenton's bat.

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