



# Sexually Segregated Habitat Selection in Daubenton's Bat *Myotis daubentonii*

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Swedish University of Agricultural Sciences, SLU  
Department of Wildlife, Fish, and Environmental Studies  
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## Abstract

Sexual segregation is a phenomenon present in many vertebrate taxa, including the bat order Chiroptera. Sexual segregation is a social and/or habitat separation based on sex and is driven by varying causes such as sexual dimorphism, resource and physiological limitations, predator avoidance and many other factors. It can be intrasexual and intersexual, as observed in the focal species of this study, *Myotis daubentonii* – Daubenton's bat.

Most studies of this temperate bat have been conducted in regions with an altitudinal gradient which have shown that the Daubenton's bat exhibits a temporal, intra- and inter-sexual segregation across an altitudinal gradient. With females and some males preferring the downstream and more productive habitats whilst other males create upstream colonies in the suboptimal foraging and roosting microclimates.

In this study, carried out in the central and southern parts of Sweden, I conducted a landscape analysis on mist net trapping data, accumulated over a period of 34 years (1986 -2020) to determine if sexual segregation occurred by habitat selection within a region with no significant elevation gradient. The results indicated that some landscape features were different between foraging sites where only males were found and those that had only females or both males and females. These included differences in the size of forests, distance to and size of water surfaces, built-up areas, and open lands, in addition to a sexually segregated habitat selection was observed across latitudinal and longitudinal gradients

*Keywords:* sexual segregation, Daubenton's bat, *Myotis daubentonii*, landscape analysis, habitat selection, foraging

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# 1. Introduction

## 1.1. Background

Sexual segregation is explained by social and/or habitat segregation (Ruckstuhl & Clutton-Brock, 2006). Habitat segregation occurs in different forms both among and within species and is driven by varying causes such as sexual dimorphism, resource and physiological limitations, predator avoidance and many other factors. Similarly, social segregation appears to be caused by various forces, which include differences in activity budgets, differing innate social preferences, intrasexual aggression in the presence of the opposite sex etc. (Levin, Roll, Dolev, Yom-Tov, & Kronfeld-Shcor, 2013; Ruckstuhl & Clutton-Brock, 2006). There are different hypotheses explaining the interplay between social and habitat segregation. The first suggests that habitat segregation drives social segregation; the second is that habitat and social segregation may be independent of each other; and the third that social segregation may drive habitat segregation (Ruckstuhl & Clutton-Brock, 2006).

Sexual segregation is present in vertebrates of different taxa (Ruckstuhl & Clutton-Brock, 2006). It occurs at different levels for different species, from embryos aggregating according to sex in the house mouse (*Mus musculus*) to social segregation in humans (Ruckstuhl & Clutton-Brock, 2006). It is also further scrutinised by looking at intersexual and intrasexual patterns of segregation within populations (Levin et al., 2013; Nardone et al., 2015). Most research on sexual segregation has been conducted on mammals and in particular, ungulates and carnivores (Levin et al., 2013; Ruckstuhl & Clutton-Brock, 2006).

Bats exhibit extensive sexual segregation even though sexual dimorphism is rare, and this is often ascribed to their intersexual energetic requirement variation (Levin et al., 2013). For temperate bats, altitudinal and latitudinal sexual segregation has been documented (Angell, Butlin, & Altringham, 2013; Levin et al., 2013; Ruckstuhl & Clutton-Brock, 2006). There is microclimatic variation along altitudinal gradients, with higher elevations tending to have lower temperatures and less productive foraging habitats (Angell et al., 2013; Becker, Tschapka, Kalko, & Encarnação, 2013; Burns & Broders, 2015). Formation of male colonies has also been linked to intraspecific information transfer about location of prey (Levin et al., 2013; Linton & Macdonald, 2019). As in other species, bats species that forage in areas of unpredictable food availability or those that regularly change roost sites have been shown to transfer information about the resources and

locations to fellow colony members (Kerth, 2008).

The sexual segregation in Daubenton's bat is temporal and occurs because of the bat migrating away from hibernation sites to foraging areas and forming summer roosts (Laine, Lilley, Norrdahl, & Primmer, 2013). During this migration, the males disperse and migrate over longer distances and are responsible for gene flow, whilst the females disperse closer to the hibernation sites selecting for sites close to optimal foraging sites (Laine et al., 2013; Linton & Macdonald, 2019; Nardone et al., 2015; Senior, Butlin, & Altringham, 2005). During summer, both males and females are stationary and random mating occurs; sporadic mating also occurs during the hibernation period (Senior, Butlin et al. 2005, Laine, Lilley et al. 2013). Females form nursery colonies, while males form more temporary and flexible colonies, or live solitary (Linton & Macdonald, 2019). It has been observed that lactating females travel back and forth between the foraging sites and to their offspring at the roosting sites several times a night, and this may account for part of the reason they require a shorter distance between the foraging and roosting sites than the males (Linton & Macdonald, 2019).

One possible explanation for sexual segregation in bats is that females are the dominant sex, and that they exclude males from the most optimal foraging sites, however, the competition decreases if the habitat is of exceptional quality (Nardone et al., 2015). This is a form of displacement hypothesis, suggesting that sexual segregation in a species is caused by the dominant sex chasing away the other sex from optimal habitats, forcing the subservient sex to look for other habitats, which tend to be suboptimal (Nardone et al., 2015; Ruckstuhl & Clutton-Brock, 2006). However, it is unclear if upstream males are displaced by dominant females, or by more aggressive downstream males (Nardone et al., 2015).

An alternative hypothesis is that some males avoid competition and disperse to suboptimal sites once the foraging efficiency decreases, being better suited for the microclimatic conditions of these unideal sites (Senior et al., 2005). Intrasexual segregation is also present in the Daubenton's bat, which results in mixed sex groups at lower altitudes and disproportionate abundance of males at the higher elevations (Nardone et al., 2015). Intrasexual aggression is thought to lead to intrasexual segregation, which leads to populations having varying levels of sexual separation (Nardone et al., 2015). In such populations there tend to be both mixed groups and groups comprising of only one sex.

Some studies indicate that potential overlap of foraging areas between low-altitude and high-altitude males depends on landscape features (Nardone et al., 2015). In the altitudinal segregation studies, downstream males have shown a preference for riparian vegetation, whilst the upstream males were generalists or preferred more open banks and had a more diverse habitat usage (Nardone et al., 2015).

Effective conservation and wildlife management relies on understanding and describing habitat landscape features of a species to better recognize habitat selection behaviour (Monarchino, Behan, & Johnson, 2020). Sexual and social behaviour information also provides invaluable insights into population dynamics, which are cardinal when developing effective detection, monitoring, and management protocols (Zarzoso-Lacoste et al., 2018). Furthermore, when studying species like bats which are also hosts of zoonotic

pathogens and the information on their sexual and social behaviour can be used to assess human health risk along with disease emergence and transmission models (Linton & Macdonald, 2019). In the eastern red bat (*Lasiurus borealis*), patterns of sexual segregation were dependent on the heterogeneity of the environmental conditions. In this species, in the absence of local landscape diversity, sexual segregation may not occur (Monarchino et al., 2020). Similarly, sexual segregation in Daubenton's bats foster genetic diversity by allowing for gene flow and reducing inbreeding, thus it is important to ensure that the mechanisms that facilitate this are preserved (Laine et al., 2013).

In 2009, a study on the Daubenton's bat was conducted in Uppland County in South-Central Sweden (Pasanen-Mortensen, 2009). That study looked at landcover type variables to distinguish between male sites and mixed/female sites and found no statistically significant variation. The present study is a follow up of that study and includes data from Pasanen-Mortensen (2009) and new data collected from other parts of Sweden.

## 1.2. Application and Purpose of Study

This study was intended to build on existing research on the *M. daubentonii* habitat in Sweden by assessing the spatial distribution and sexual habitat segregation of the bat. I used further data from a wider geographic distribution and timeframe for *M. daubentonii* than has been previously used (cf. Pasanen-Mortensen, 2009). The main objectives of my study were:

- i. To analyse the landscape and habitat use of the Daubenton's bat along small streams in Sweden.
- ii. To carry out a comparative analysis of the characteristics of streams which have only male, only female and both male and female Daubenton's bats in Skåne County and Uppland County.
- iii. To determine if sexual segregation, observed previously in Uppland in the absence of an elevation gradient is a general pattern in Sweden.

My hypothesis was that the observed sexual segregation is explained by significant difference in the landscape characteristics between male-only sites and the mixed sites.

## 2. Materials and Methods

### The Study Area

The study area consists of forty-eight locations sampled over a period of thirty-four years (1986 to 2020) in the summer months of June or July. It extends over the Central and Southern parts of Sweden, stretching from Gävleborg County in the north to Skåne County in the south (Figure 1).



Figure 1. Map of sampling sites included in this study (green filled in circles)

### 2.1. Study Species

The focal species of the study was Daubenton's bat *Myotis daubentonii*, a widely distributed Eurasian insectivorous bat species that predominantly trawl over water and may hunt in forests.

Females form roosts for reproduction close to lakes and larger streams, within 3 km from the water. Males might form roosts, but often more temporary and sometimes in different habitats than females, and far from large lakes (Linton & Macdonald, 2019). Sexual segregation in Daubenton's bat has been observed to be elevational in the use of roosting and foraging habitats (Linton & Macdonald, 2019). In the temperate regions, females have been shown to prefer low elevations of downstream habitats, with some males sharing parts of these habitats, whilst some males inhabit higher elevations (Nardone et al., 2015). Some of the attributes linked to the Daubenton's bat's sexual segregation are variation in energetic needs, reproductive success, survival benefit and male competition. (Encarnaç o, 2012; Linton & Macdonald, 2019; Nardone et al., 2015). However, few studies have been conducted in low altitude areas in which an elevational gradient is insignificant as is the case in my study area (Linton & Macdonald, 2019).

## 2.2. Field work

Data were collected from several bat surveys, performed from 1986 until 2020, in the south and centre of Sweden (Appendix 1). In general, potential bat trapping sites were located and investigated during daytime. The purpose was to exclude sites where trapping is impossible for practical reasons, or sites where bat occurrence were unlikely.

Selection criteria included: stream width 6-10m, no emerging or floating-leaved vegetation on the water, slow running water, shallow water that could be waded in, presence of riparian forest and preferably old buildings nearby. If most of these characteristics were present, it was determined that it was a potential foraging site for the Daubenton's bat, and the stream location was selected for a subsequent occupancy survey.

Sites that had been selected during the day were checked for the presence of bats during night using ultrasonic detectors set at a wavelength of 40-50 kHz. The ultrasound, in combination with observing their low flying behaviour, was used to distinguish Daubenton's bats from any other species that might be present.

Bats were trapped using mist nets that were mounted perpendicular to the streams at the arch of bridges (Figure 2). The nets were 8 m wide and 3 m high with a mesh size of 15 mm. The nets were set up around sunset (approx. 9:00 pm) and checked for bats up to ca. midnight or up to ca. 1 h after last observed bat activity, whichever came first. Trapped bats were disentangled immediately, put in cotton bags, and kept within a person's coat near the chest to ensure they were warm until sampling could be conducted.

Bats were handled as quickly as possible to reduce distress and exposure to the cold. Daubenton's bats were identified by their small body size, large and free feet, light brown skin, and the typical tragus shape (Dietz et al. 2007). The sex was detected by the presence or absence of penis. The age was determined by the shape of the finger joints (Kunz 1988).



*Figure 2. A mist net set up perpendicular to a stream at the archway of a foot bridge at a trapping site in Skåne*

Once all samples and data were recorded, the bats were banded with a ring to avoid double-sampling, and the number of the ring was recorded. Thereafter, they were placed on a nearby tree to recover and then fly off. All bats flew off the trees within 5 min.

### **Ethical considerations.**

No animals were injured during the study, and all individuals were released at the trapping site as soon as possible after examination and banding. Disposable gloves and facemask were used when trapping 2020, while during earlier bat sampling only gloves were used. Trapping and sampling of bats was approved by the Animal Ethics Committee in Uppsala (latest permit Dnr 5.8.18- 01713/2020), and all applicable institutional and national guidelines for the use of animals were followed.

## **2.3. Data Analysis**

Only one instance of sampling was included per sample site regardless of the number of times it had been sampled in previous or subsequent years. In addition, sites were categorised as male or female sites (Appendix 1). Male sites were determined by an expert who had collected the data and knowledge of the sites and behaviour and ecology of the bat. All other sites not specified as male were classified as mixed-sex sites and denoted as “female”, including those that may have had only males or females

trapped. These two categories (male and female) were used to carry out the Wilcoxon test and the logistic regression. For the linear regression models the proportion of males to females at each site was used.

#### *Landscape Analysis*

Around each trapping site we created a circular buffer with a 1km radius, creating a circumference of 6.28 km and an area of 314.2 ha around the site. Within this circular buffer, we created 5 buffer zones along the bank of trapping stream of 100 metres, 250 metres, 500 metres, 750 metres, and 1000 metres respectively (Figure 3). Landscape characteristics within in each of these buffer zones were then collected. These landscape variables (Table 1) included the areas of, arable land, coniferous and mixed forest, deciduous forest, low built-up area, orchards, open land categories and water surface. In addition, the slope and width of the stream were measured as well as, the distance of the trapping sites to the nearest water bodies of different sizes i.e., 0.001-0.01 Ha, 0.01-0.1 Ha, 0.1-1 Ha, 1-10 Ha, 10-100 Ha and greater or equal to 100 Ha, respectively.

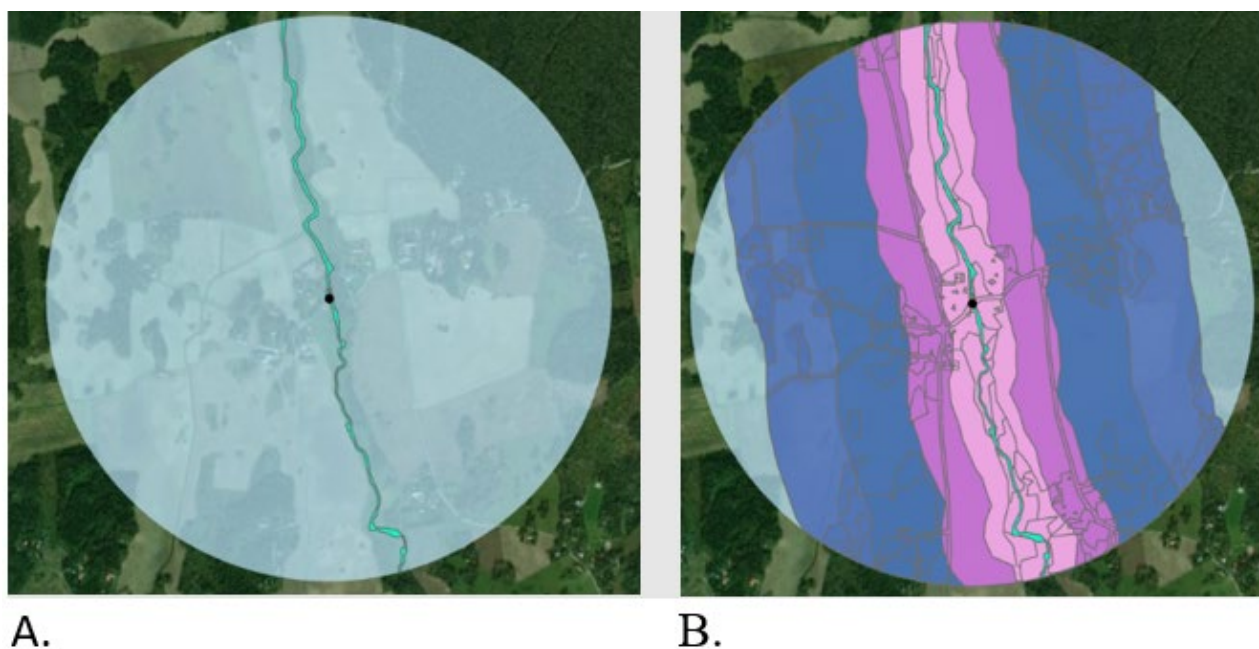


Figure 3. Figure showing how the trapping site was dimensioned for landscape analysis. Firstly, by a circular buffer with a radius of 1km around the trapping site (A) and then by longitudinal buffers (B) of 100 m, 250m, 500m, 750m and 1000m along the bank of the stream.

All landscape data was collected using Arc Pro 2.4.0 software (©2019 Esri Inc.) using the landcover data provided by on gis.slu.se. All statistical analyses were conducted using R programming (Team, 2020).

#### *Statistical analyses*

The statistical analyses conducted were the nonparametric tests of the male and mixed sites using the Wilcoxon test, as well as logistical regression modelling and linear regression modelling. I used all the variables determined to be significant by the landscape analysis (Table 1) as explanatory variables in all the three tests. However, the response variable was dependent on the test, for the logistic regression and Wilcoxon test, I used the groupings of 1 (male sites) and 0 ( female sites), whilst for

the linear regression model I used the proportion of males at all sites. For logistical regression, I applied a multiple generalised linear model (GLM) of the binomial(logit) family. For linear regression I used a multiple linear model (LM).

To select for the top ranked models in both types of regression a Stepwise model using both backward and forward direction was employed. This was done using the stepAIC package in R programming which incorporated all the variables into a model and then selected the best model using the Akaike information criterion (AIC) (Team, 2020).

*Table 1. Habitat variables that were included in the landscape analysis of the study area. The descriptions of the landcover follow those given by lantmäteriet (2019), other variables were created in Arc Pro 2.4.0 software (©2019 Esri Inc.)*

<b>Variable</b>	<b>Description</b>
<b>Arable land</b>	Land that is used for cultivation but not for fruit and berries that grow on trees
<b>Coniferous and mixed forest</b>	Land that has conifers or mixed conifers and deciduous forest. All types of trees and bushes may be included
<b>Deciduous forest</b>	Wooded land that consists of at least 90-95% continuous deciduous forest
<b>Distance to water =&lt; 100 Ha</b>	Distance of trapping site from water surface equal or larger than 100 Ha
<b>Distance to water 10-100 Ha</b>	Distance of trapping site from water surface 10-100 Ha large
<b>Distance to water 1-10 Ha</b>	Distance of trapping site from water surface 1-10 Ha large
<b>Distance to water 0.1-1 Ha</b>	Distance of trapping site from water surface 0.1-1 Ha large
<b>Distance to water 0.01-0.1 Ha</b>	Distance of trapping site from water surface 0.01-0.1 Ha large
<b>Distance to water 0.001-0.01 Ha</b>	Distance of trapping site from water surface 0.001-0.01 Ha large
<b>Low built-up area</b>	Dense low built up areas, with one-family and two-family terraced apartments and other types of family apartments no higher than two floors high. Includes all other associated land, such as roads, car parks and land with buildings.
<b>Orchards</b>	Land used to cultivate fruit and berries that grow on trees
<b>Other open land</b>	Land that is bare but not in a bare mountain region
<b>Other open land no forest contour</b>	Bare land that does not have a forest boundary
<b>Slope</b>	The slope along the stream from the trapping site. Used as proxy to determine the current of the water.
<b>Stream width</b>	The average width of the stream within the 1000m buffer
<b>Water surface</b>	Includes sea, lake, dam or water.
<b>X</b>	X coordinate of trapping site
<b>Y</b>	Y coordinate of trapping site



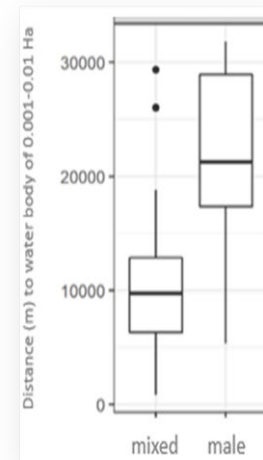
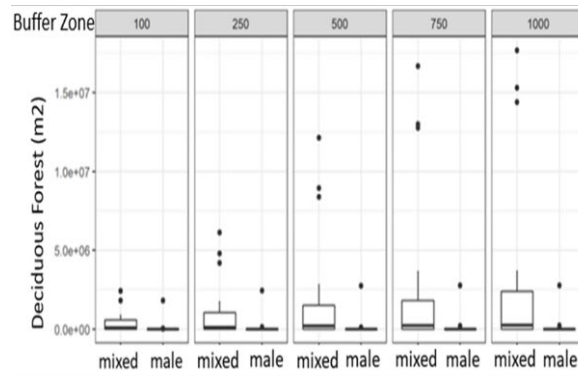
### 3. Results

The complete dataset comprised of forty-eight locations with four hundred and eleven Daubenton's bats sampled comprising two hundred and twenty-one females and hundred and eighty-eight males. Thirteen (twelve in Uppland and one in Skåne) of these sites were determined to be typical male sites and Thirty-five as mixed sites for the logistic regression analysis and nonparametric test.

The area covered by the deciduous forest was only significantly different between the male and mixed sites in the combined data set (All). The forest area was shown to be larger in the mixed sites in the 500m, 750 m and 1000m buffer zones (Figure 4). The difference between sites was not significant for the Uppland and Skåne regions when analysed separately.

The distance to the nearest water bodies between 0.001 Ha and 0.01 Ha was significantly different between male sites and mixed sites both for the complete data set as well as for the Upland subgroup (figure 5). Logistically this relationship showed that there was a greater likelihood of a site being male the further away it was from these small water bodies. This was the only significant variable of the logistic regression and only significant for the complete data set (figure 5, table 5).

Figure 4. Box plots showing the only significantly different variables between male and mixed sites according to the Wilcoxon test



Several of the variables showed a significant linear relationship w linear regression analysis (Table 2; Table 3). For the complete data set (All) analysis, easting (X-coordinate), slope and area of orchards and all had positive linear relationships.

In Uppland, the proportion of males also decreased with increasing distance from larger water surfaces (10 – 100 Ha) but

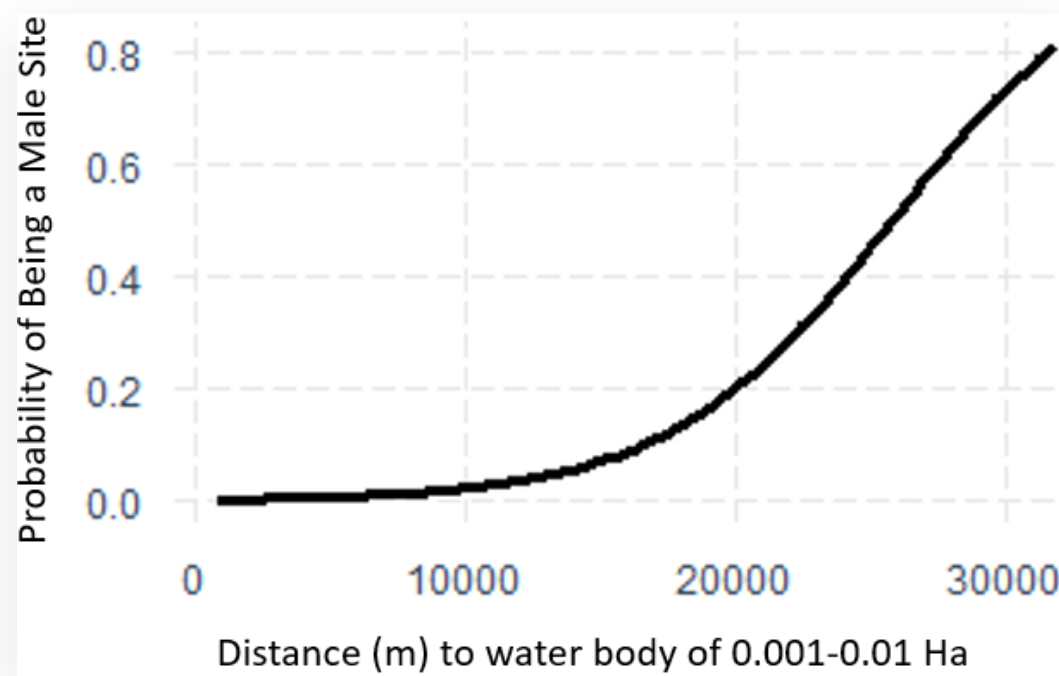


Figure 5. Logistic effect plot showing the probabaility of a site being male in relation to its distance to the nearest water body of 0.001-0.01 Ha

also showed the males were further away from the smaller water surfaces ( 0.001 -0.01 Ha) as well as the largest water bodies that were greater than 100 Ha (Table 2, Table 3).

Hence, the proportion of male sites increased when moving away from the largest water surface, foraged over faster flowing streams, with orchards in their vicinity and in eastern direction. However, the proportion of males decreased with increasing bare land when data was treated as one population, when subdivided, the opposite was true for Uppland.

Analysing data from Skåne and Uppland separately showed that different variables were important in the different regions.

Skåne showed significance with a positive relationship between the male proportion and area of orchards and bare land that does not have a forest boundary, as well as more males in the northern parts. Skåne also had more males in areas with less coniferous and mixed forests. This negative relationship with the coniferous and mixed forest was also evident for the proportion of males in Uppland. Males in Uppland foraged in areas with larger low built- up residential areas, low areas of water surfaces, in the south-easterly direction.

Table 2. Results showing the positive and negative linear relationships of the different variables and the proportion of males at the sites. \* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ , Bonferroni corrected

Variable	100		250		500		750			1000		
	All	Uppland	All	Uppland	All	Uppland	All	Skåne	Uppland	All	Skåne	Uppland
Coniferous and mixed forest	n.s	n.s	n.a	n.s	n.s	-	n.s	-	-	n.a	-	n.s
Distance to water body of 0.001-0.01 Ha	n.s	+	n.a	+	n.a	+	n.s	n.s	+	n.a	n.s	+
Distance to water body greater than 100 Ha	+	n.s	n.s	+	n.s	n.s	n.s	n.a	n.s	n.s	n.a	n.s
Distance to water 10-100 Ha	n.a	n.s	n.a	-	n.a	-	n.a	n.a	-	n.a	n.a	-
Distance to water body of 1-10 Ha	n.s	n.s	n.a	+	n.a	n.s	n.a	n.a	n.s	n.s	n.a	n.s
Low built-up area	n.s	-	n.s	-	n.s	-	n.s	n.a	-	n.a	n.a	-
Orchards	n.a	n.a	n.a	n.a	n.a	n.a	n.a	+	n.a	+	+	n.a
Other open land	n.a	n.a	n.a	n.s	n.a	+	n.a	n.a	+	-	n.a	+
Other open land no forest contour	n.a	n.a	n.a	n.s	n.s	n.a	n.s	+	n.a	n.a	+	n.a
Slope	n.s	n.s	n.s	n.s	+	n.a	n.s	n.s	n.a	n.s	n.s	n.s
Water surface	n.s	n.s	n.a	n.s	n.s	n.s	n.a	n.a	-	n.a	n.a	-
X	+	n.s	+	+	+	+	+	n.a	+	+	n.a	+
Y	n.a	n.s	n.a	-	n.a	-	n.a	+	-	n.a	+	-

Table 3: Results from multiple linear regression testing the effects of the landscape variables on the proportion of males at a site. \* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ ; n.s = not significant; n.a = not added to the model; Bonferroni corrected

Variable	100			250			500			750			1000		
	All	Skane	Uppland	All	Skane	Uppland	All	Skane	Uppland	All	Skane	Uppland	All	Skane	Uppland
Arable land	n.a	n.s	n.s	n.a	n.s	n.a	n.a	n.s	n.a	n.a	n.s	n.a	n.s	n.s	n.a
Coniferous and mixed forest	n.s	n.s	n.s	n.a	n.s	n.s	n.s	n.s	**	n.s	*	*	n.a	**	n.s
Deciduous forest	n.s	n.s	n.s	n.a	n.a	n.s	n.a	n.a	n.a	n.a	n.a	n.a	n.s	n.a	n.a
Distance to water body of 0.001-0.01 Ha	n.s	n.s	*	n.a	n.s	**	n.a	n.s	**	n.s	n.s	**	n.a	n.s	**
Distance to water body of greater than 100 Ha	*	n.a	n.s	n.s	n.a	*	n.s	n.a	n.s	n.s	n.a	n.s	n.s	n.a	n.s
Distance to water body of 10-100 Ha	n.a	n.a	n.s	n.a	n.a	*	n.a	n.a	**	n.a	n.a	**	n.a	n.a	*
Distance to water body of 1-10 Ha	n.s	n.a	n.s	n.a	n.a	*	n.a	n.a	n.s	n.a	n.a	n.s	n.s	n.a	n.s
Distance to water body of 0.1-1 Ha	n.s	n.a	n.s	n.s	n.a	n.a	n.s	n.a	n.s	n.a	n.a	n.s	n.a	n.a	n.s
Distance to water body of 0.01-01 Ha	n.s	n.s	n.s	n.s	n.a	n.s	n.s	n.a	n.s	n.a	n.s	n.s	n.a	n.a	n.s
Low built-up area	n.s	n.s	*	n.s	n.s	**	n.s	n.a	**	n.s	n.a	**	n.a	n.a	**
Orchards	n.a	n.s	n.a	n.a	n.s	n.a	n.a	n.s	n.a	n.a	*	n.a	*	*	n.a
Other open land	n.a	n.s	n.a	n.a	n.s	n.s	n.a	n.s	*	n.a	n.a	**	**	n.a	*
Other open land no forest contour	n.a	n.s	n.a	n.a	n.s	n.s	n.s	n.s	n.a	n.s	*	n.a	n.a	*	n.a
Slope	n.s	n.s	n.s	n.s	n.s	n.s	*	n.s	n.a	n.s	n.s	n.a	n.s	n.s	n.s
Stream width	n.a	n.s	n.a	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.a	n.s	n.s	n.a
Water surface	n.s	n.s	n.s	n.a	n.s	n.s	n.s	n.s	n.s	n.a	n.a	*	n.a	n.a	*
X-Coordinate	***	n.s	n.s	***	n.s	*	***	n.s	**	**	n.a	**	***	n.a	**
Y- Coordinate	n.a	n.s	n.s	n.a	n.s	*	n.a	n.s	**	n.a	*	**	n.a	*	**

## 4. Discussion

My study provides insight into the landscape characteristics of the foraging sites of the Daubenton's bat in Sweden. It shows that there is a sexually segregated habitat selection process at play even in regions with a low elevation gradient. Previous habitat studies have been carried out in other temperate countries, most of which occurred where an elevation gradient occurs (Nardone et al., 2015; Senior et al., 2005). In my study, several variables differed between male and mixed-sex foraging sites.

The result of the study shows that the distance to the nearest water bodies (i.e., lakes and watercourses of the size range of 0.001-0.01 Ha, 1-10 Ha, 10-100 Ha and greater than 100 Ha) was significant. A higher proportion of males compared to females used areas that were either closer to the smaller water bodies (0.001-0.01 Ha, and 1-10 Ha) or close to the very large water bodies of more than 100 Ha. However, a higher proportion of females foraged closer to the medium sized water bodies of 10-100 Ha). This may indicate an optimum water body size of 10- 100 Ha for the daubenton's bat, if the females indeed select the best sites. Perhaps, some water bodies are either too small or too large for the level of productivity required to meet the physiological needs of the nursing females. This may be related to other factors regarding the water bodies such as the water speed and occurrence of roosting sites around them. Within the buffers that the landscape analyses were conducted, the water surface area was larger in areas with a lower proportion of males foraging there. This would mean that the water bodies that the males sought were much further away than anticipated for the analysis. This is because distance to water body analysis was set up to find the nearest water body regardless of whether the water body fell within the created 314.2 Ha buffer. This would support the hypothesis that segregation is based on the males selecting or being displaced into habitats further away from large water surfaces.

The male and mixed sites differed regarding the deciduous forest area, within some of the buffer zones (500 m, 750 m and 1000m) with the male sites having smaller areas of deciduous forests around their sites than the mixed sites. This relationship to forests can also be seen in the Uppland and Skåne population with regards to the coniferous and mixed forests, the results imply that the males used sites with lower areas of this type of forest too. Still water surfaces and forests are indeed important characteristics for Daubenton's bat, the former for foraging and the latter for roosting (Dietz, Encarnaçao, & Kalko, 2006; Encarnacao, Kierdorf, Holweg, Jasnoch, & Wolters, 2005). This supports the hypothesis that males forage in suboptimal habitats.

The most significant and unexpected variables for the linear models was that of the longitudinal gradient (All and Uppland) and latitudinal gradient (Uppland). Indicating that the male sites are more common in the east. However, the latitudinal gradient showed that in Uppland the males segregated South whilst in the general data shows a segregation North. This segregation across the east-west- and north-south gradient is not unique to this study. Temperate bats latitudinal migration over winter has also been documented (Levin et al., 2013; McGuire & Boyle, 2013). A study on tri-colored bats (*Perimyotis subflavus*), has shown that they migrate south during the nursery months, with both sexes migrating but males migrating further than the females (Fraser, McGuire, Eger, Longstaffe, & Fenton, 2012). Perhaps a similar type of latitudinal and longitudinal migration occurs in Daubenton's bats. It may mean that the foraging sites in the western regions of Sweden have less productivity and/or predictability of prey. This may also be because of statistical "noise" created by the fact that sampling stretched out in a more Eastern direction given the shape of the country boundaries. For the latitudinal variation, an explanation might be that central parts are less productive and perhaps have less forest areas as they are closer to city areas, resulting in the females using sites further south and north. However, my data are insufficient to make a conclusion because of the non- random selection of trapping sites.

Other significant landscape features were areas of low built-up areas, arable land, orchards; and specific to the stream characteristics was the slope (proxy for the velocity of the water flow). The low built-up areas are low density residential areas, with mostly one-family or two-family houses. The buildings in this area generally at their highest two stories high. The relationship observed was that the larger the area, the lower the number of males observed in mixed populations. In Skåne, the significance in the differences between the male and mixed sites in the areas of orchards and open land showed that males foraged in areas with larger patches of open areas and fruit trees. These indicate that the males are foraging in areas that likely have a lower prey availability or at most unpredictability since the orchards may have mechanisms that eradicate insect species to protect from pest species e.g., the use of pesticides. However, it might also be possible that there may be other types of prey available to the males that they can utilize better than the females would.

All these variables point to the fact that more males than females use habitats that are not optimal for the Daubenton's bat, as the ideal habitats are well forested areas with still water surfaces nearby (Dietz et al., 2006; Encarnação, 2011).

## 5. Conclusion

The results of my analysis are consistent with a conclusion that landscape characteristics differ between male and female dominated foraging areas and sexual segregation within the Daubenton's bat, is also present in areas with no altitudinal gradient. My result indicates that distance to other water surfaces is important, but other factors seem to be involved such as area of deciduous and coniferous forests. Probably, there is also east-west gradient with higher proportion of typical male sites along small streams in the east, and a north-south gradient showing males foraging in more central regions. The results imply that sexual segregation is related to productivity and that males forage in areas with low food productivity and/or predictability.

However, concerted studies should be conducted to understand the reasons behind the landscape characteristics that were observed, to be able to recommend management/conservation applications. It would also be beneficial to investigate the observed segregation across the east-west and north-south gradient, perhaps by using a random sampling technique that would eradicate potential bias in site selection. It might also be of use to couple the habitat selection studies with genetic approaches to identify and distinguish between different populations (if present) to structure analysis accordingly.



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# Appendix 1

Table 1: Information on the sampling sites and bats (number and sex; F\*female, M male) trapped and included in the study.

Locality	County	X	Y	Years	Female	Male	Sex Class
<b>Kvarnbolund</b>	Uppland	643809	6636600	1986	0	4	M
<b>Mörby slott</b>	Uppland	682020	6629652	1986	0	2	F
<b>Ängelsberg</b>	Småland	556398	6648218	1990	12	0	F
<b>Focksta</b>	Uppland	632960	6630864	2003	0	10	M
<b>Lurbo bro</b>	Uppland	646119	6632487	2003	0	5	M
<b>Rånäs</b>	Uppland	684744	6632618	2003	0	1	F
<b>Norrsjön</b>	Uppland	663348	6634827	2004	0	1	F
<b>Norasjön</b>	Småland	647038	6538362	2005	0	2	F
<b>Nydammen</b>	Småland	583266	6809467	2005	1	4	F
<b>Åby, Vendelån</b>	Uppland	645147	6666188	2008	1	7	F
<b>Åland, Sävaån</b>	Uppland	627846	6639866	2008	0	5	M
<b>Forsmark</b>	Uppland	673609	6696927	2008	3	2	F
<b>Järsta, Vendelån</b>	Uppland	648813	6656715	2008	0	1	M
<b>Lyngsjö</b>	Skåne	442153	6199566	2008	1	3	F
<b>Skebobruk</b>	Uppland	701414	6653481	2008	28	2	F
<b>Svenstorp</b>	Skåne	433003	6148794	2008	12	3	F
<b>Tensta, Vendelån</b>	Uppland	648539	6658774	2008	0	7	M
<b>Vällnora</b>	Småland	686588	6651363	2008	0	3	F
<b>Viks slott</b>	Uppland	638402	6624598	2008	2	2	F
<b>Funbo</b>	Uppland	660079	6638932	2010	0	5	M
<b>Jädra</b>	Uppland	614804	6623623	2010	0	2	M
<b>Marielund</b>	Uppland	660806	6636797	2010	0	11	M
<b>Östra-Ekeby</b>	Uppland	644544	6668758	2010	10	7	F
<b>Silvhytteå</b>	Småland	564937	6705935	2010	40	0	F
<b>Vånsjöbro</b>	Uppland	617694	6623924	2010	0	13	M
<b>Reutersberg</b>	Småland	555783	6585880	2011	1	1	F
<b>Säva</b>	Uppland	634293	6627737	2011	0	1	M
<b>Vattholma, södra bron</b>	Uppland	652199	6656501	2011	7	12	F
<b>Bäckebo</b>	Uppland	566211	6305716	2012	0	3	M
<b>Kristinelund</b>	Småland	567584	6271754	2012	14	1	F
<b>Linnefors</b>	Småland	534587	6269395	2012	11	1	F
<b>Mortorp</b>	Småland	566564	6272052	2012	1	15	F
<b>Örsjö</b>	Småland	546241	6284167	2012	5	13	F

Locality	County	X	Y	Years	Female	Male	Sex Class
<b>Värnanäs</b>	Småland	571236	6262020	2012	3	1	F
<b>Åsum</b>	Skåne	418293	6167771	2013	2	2	F
<b>Bengtemölle</b>	Skåne	444720	6176102	2013	3	0	F
<b>Ellinge</b>	Skåne	392756	6186417	2013	3	3	F
<b>Stockamölla</b>	Skåne	398536	6201352	2013	9	4	F
<b>Trollenäs</b>	Skåne	390117	6192548	2013	2	5	F
<b>Tunbyholm</b>	Skåne	444733	6161629	2013	3	2	F
<b>Allevadsmölla</b>	Skåne	430813	6151542	2020	3	0	F
<b>Ängsbo, Haväng</b>	Skåne	446944	6175312	2020	6	1	F
<b>Bosarp, east of Brösarp</b>	Skåne	444990	6176175	2020	0	1	F
<b>Rålambsdal</b>	Skåne	439846	6216165	2020	6	6	F
<b>Röverkulans naturreservat</b>	Skåne	405796	6184196	2020	0	6	M
<b>Tobisviks camping, Simrishamn</b>	Skåne	458077	6158425	2020	13	5	F
<b>Tollarp, Malmvägen</b>	Skåne	435985	6198742	2020	16	0	F
<b>Vinslöv, south of the pond</b>	Skåne	432132	6218678	2020	3	3	F
Total					221	188	

\*F was used to denote both the sites that had only females and those with both male and female present. For the purposes of the binomial tests (i.e., Wilcoxon and logistic regression), sites which were not clearly male as determined by expert advice were considered mixed sites and denoted “F” here.

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