

Is *Myotis brandtii* a fussy little bat? – Habitat selection and impact of forestry on Brandt's bat (*Myotis brandtii*)

Är Myotis brandtii en kinkig liten fladdermus? – Habitatval och påverkan av skogsbruk på tajgafladdermus (Myotis brandtii)

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Abstract

Humans are expanding their land use with e.g. forestry, agriculture and urbanisation, which can have both positive and negative effects upon biodiversity. One taxon that has shown to be affected by forestry is bats, however, the impacts differ depending on forestry method and their foraging strategy. This study focused on the habitat composition around maternity colonies of the forest-living Brandt's bat (*Myotis brandtii*) in Sweden, with the objective to investigate how the species might be affected by forestry and if their presence of colonies can be predicted based on habitat composition. To do so, bat activity and insect abundance was measured in relation to a number of habitat variables (forest density, canopy cover and level of soil moisture), and in three types of forest habitats (coniferous forest, swamp forest and edge between forest and open areas). Insects were caught with suction traps and bat activity was surveyed with automatic ultrasound detectors. Habitat composition within 1 km radius from 14 colonies was compared to three control areas of 20 × 20 km.

Insect abundance and bat activity was not correlated. Insect abundance was highest at edge habitat, while bat activity was highest in swamp forests. High level of soil moisture was important for both insect abundance and bat activity, which suggests that drainage of forests is negative for forest-living bats. There was a trend towards more bats in medium dense forest, which suggests that the species is tolerant towards thinning of forests. Habitat coverage did not differ between colony areas and control areas, and the variance was large in colony areas. This indicates that *M. brandtii* occurs in the dominant type of landscape in the studied area. It was not possible to relate presence of colonies to occurrence or distribution to any habitat, making it hard to predict *M. brandtii* colony presence based on maps. Forestry methods in which a continuous crown cover is conserved is positive for forest-living bats, but the main conservation measure is to restore or create new forested wetlands.

Keywords: *Myotis brandtii*, habitat selection, forestry, insects, maternity colony

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1 Introduction

As the human population expands, so does the anthropogenic use of land, such as forestry, agriculture and urban development. Land use can have positive effects on biodiversity, when new habitats are created (Fahrig, 2017), but habitat loss and degradation can also have negative effects (e.g. Schmiegelow & Monkkonen, 2002; Hillers *et al.*, 2008; Farrow & Broders, 2011). To minimise negative effects and maximise positive effects, humans must challenge themselves to find smarter ways to use land and combine it with conservation. This paper will touch upon the combination of forestry and bat conservation.

Many bat species depend on forests for roosts, shelter and food, suggesting they are affected by forestry (Duchamp & Swihart, 2008; Law *et al.*, 2016). Extensive forestry, in e.g. Europe, has removed trees with cavities, forcing cavity-roosting bats to seek shelter in manmade structures, e.g. buildings (Kunz & Lumsden, 2003). Forest management includes clear-cutting, variable retention harvesting, pre-commercial thinning, thinning, drainage, planting etc. (e.g. Fries *et al.*, 1997; Humes *et al.*, 1999; Patriquin & Barclay, 2003; Peltomaa, 2007; Gustafsson *et al.*, 2012), and these methods have shown to affect bat species differently. Bats are adapted to specific vegetation structures, depending on e.g. wing morphology and echolocation call, and the foraging strategy is separated between species (Patriquin & Barclay, 2003; Owen *et al.*, 2004; Law *et al.*, 2018). Drainage of forestland, which was commonly used in Fennoscandia to increase productivity of forests in the late 1900's, had severe impacts on vegetation and plant composition (Peltomaa, 2007; Maanavilja *et al.*, 2014). Structural changes in forests due to forestry can change the abundance and distribution of insects (Batzer & Wissinger, 1996; Deans *et al.*, 2005), which is the main energy source of bats. For instance, edges created by forestry can be positive for insect abundance (Deans *et al.*, 2005; Gonzalez *et al.*, 2017), while drainage of forests are presumably negative for the otherwise high insect abundance in wetlands (Batzer & Wissinger, 1996; Spitzer & Danks, 2006).

All bats and their roosts are legally protected in Europe (Council Directive 92/43/EEC). In order to know how to protect bats and their roosts, it is important to

understand how bats choose habitats and roosts, and how the quality of the surrounding landscape impact on bat occurrence (Bellamy & Altringham, 2015). Bats have very energy-consuming foraging strategies, and energy limitation affects activity pattern, home-range and behaviour, especially during pregnancy and lactation, when most of the energy goes to the pup (Rydell, 1993; Sommers *et al.*, 2019). In general, the foraging ground seem to correlate with insect abundance (de Jong & Ahlén, 1991; Fukui *et al.*, 2006), and to maximise energy intake and minimise flight time, bat maternity colonies should be located in areas with high insect production (Tuttle, 1976).

This study focused on the forest-living *Myotis brandtii* (Figure 1). It is a small (about 5-7 g) insectivorous bat, mainly feeding upon small Diptera and Lepidoptera (Vaughan, 1997; Whitaker & Karatas, 2009; Vesterinen *et al.*, 2018). In May, the bat forms its colonies in trees and buildings (Sachanowicz & Ruczynski, 2001; Ahlén, 2011; Dietz & Kiefer, 2016), consisting of pregnant females. Pups are born in the end of June and the colonies dissolve in late July (Dietz & Kiefer, 2016). The species has been found to forage in coniferous forests and avoid open areas, such as clear-cuts or grassland (de Jong, 1995; Ekman & de Jong, 1996; Kammonen, 2015). *M. brandtii* was chosen as study species due to it being common in the study area and easy to find. Since it is a forest-living species, it is also potentially affected by changes in the forest caused by different types of forestry (Ekman & de Jong, 1996; Law *et al.*, 2016; Law *et al.*, 2018).

As an attempt to predict where *Myotis brandtii* might form colonies and see how forestry might affect the species, the surrounding landscape of maternity colonies of *M. brandtii* was investigated in east-central Sweden. I predicted a positive correlation between insect abundance and bat activity, and thus hypothesised that forestry methods that have negative effects upon insect production also are negative for bats. Further, I investigated what type of coniferous forests *M. brandtii* utilises, by evaluating bat activity and insect abundance in relation to forest structure and level of soil moisture. I hypothesised that areas with high level of soil moisture, such as swamp forests, are important for bat activity, based on high insect production at wet areas. Thus, I predicted that swamp forests are important elements in the landscape surrounding *M. brandtii* maternity colonies.

2 Methods

2.1 Study area

The field study was performed in June and July, 2018 and 2019, in east-central Sweden, predominantly in the province of Uppland (60°0'N, 18°0'E) (Figure 2), but also in adjacent provinces of Södermanland and Västmanland. The hemiboreal landscape of Uppland is dominated by forests (58 %), but arable land also covers large areas (24 %) (Maad *et al.*, 2009).

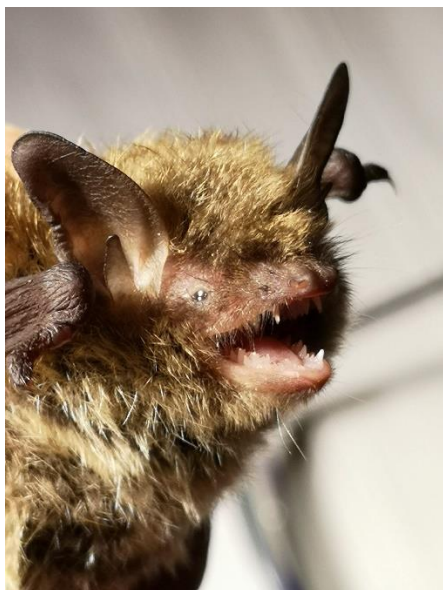


Figure 1. Female *Myotis brandtii*. Photo: Johanna Kammonen.



Figure 2. Distribution (orange) of *Myotis brandtii* in Sweden. The province of Uppland is marked in red. Map adjusted from Ahlén (2011) and smhi.se.

2.2 Bat colonies

The study focused on *Myotis brandtii* maternity colonies. In public appeals, citizens were asked to report known locations of bat colonies. Promising sites were visited to identify bats. A rough identification was made with ultrasound detectors (D240X, Pettersson Elektronik AB) when bats emerged from the colonies. Bats identified to the genus *Myotis* were trapped with mist nets for more detailed identification. In total, 16 colonies of *M. brandtii* were used in the digital landscape analysis, whereof nine were selected for the field studies (three 2018, six 2019). The colonies used in the field study 2018 were selected based on known bat activity. In 2019, colonies were selected based on accessibility to the city of Uppsala and presence of swamp forests.

2.3 Sampling sites

Two different methods were used for site selection of insect and bat sampling: bat activity and habitat composition. In 2018, the site selection was based on bat activity. In a former study, de Jong *et al.* (in prep), identified forest areas where bats were foraging, close to three selected colonies. Within these foraging areas one sampling site with high activity of bats per colony was selected for insect trapping and bat survey. The remaining sampling sites were placed systematically around the first site. During each night, sampling sites were located at three directions, 50 meters from the generator, meaning that two traps were 100 meters from each other, and the third trap was 70 meters (diagonally) from the other two. Over all nights, sampling sites were systematically located 50/70 meters apart (Figure 3). These sites were described according to their level of soil moisture, canopy cover and forest density. Soil moisture was categorised in three classes, based on vegetation: 1) dry sites, mainly covered with *Cladonia* or *Vaccinium vitis-idaea*; 2) medium wet sites, with more complex vegetation with herbs, grass and bushes (mainly *Vaccinium myrtillus*); 3) wet or moist sites, dominated by *Carex* or hydrophilic vegetation. Canopy cover was categorised as 1) open (more than 70 % of the sky visible); 2) half-open (about 30-70 % of the sky visible) or 3) closed (less than 30 % of the sky visible). Forest density was categorised in three classes based on number of trees >10 cm DBH/100m²: 1) low (0-4 trees); 2) medium (5-9 trees); 3) high (10-14 trees).

In 2019, the site selection was based on habitat composition. Three different habitats were selected: mature coniferous forest (> 60 years old *Picea abies* and/or *Pinus sylvestris*), coniferous swamp forest and edge between mature coniferous

forest and open grassland (hereafter referred to as forest, swamp and edge, respectively; Figure 4). These habitats were chosen to investigate potential differences between lush and wet forests in relation to insect abundance and bat activity. Edges were included due to their general use by bats for commuting and foraging (Morris *et al.*, 2010; Kalcounis-Rueppell *et al.*, 2013). Swamps and edges are also important insect habitats (Fowler *et al.*, 1993; Batzer & Wissinger, 1996; Spitzer & Danks, 2006).

2.4 Insect sampling

Insects were caught with suction traps (Kunz, 1988) powered by a portable gasoline generator. The traps were located in areas 100-1000 meters from *M. brandtii* colonies. The minimum range of 100 meters was chosen due to the sampling of bat activity – to avoid recording bats commuting to and from the colony, but record bats actively foraging. The maximum range of 1000 meters was chosen based on the relatively small home-range of the species (Kammonen, 2015). At 18 of 54 sampling sites in 2019, the maximum range of 1000 meters was exceeded, due to absence of suitable habitats within the range. Other criteria for the location of traps were proximity to a road (accessibility with car due to heavy weights of the equipment) and secluded from houses (to minimise disturbance and risk of theft).

During each sample-night, three traps were placed at most 100 m, straight north, south, east or west from each other. In the edge habitat, 2019, traps were located along the edge between forest and grassland. In 2018, three colony areas were investigated and categorised based on their vegetation structure (61 samples and 21 nights in total). In 2019, six colony areas were investigated based on three habitats (forest, swamp and edge; 54 samples and 18 nights in total).

The traps were started at sunset and ran for three hours. Captured insects were stored in glycol and later counted, dried in 80°C for 18h and weighted on a balance scale (Figure 4d).

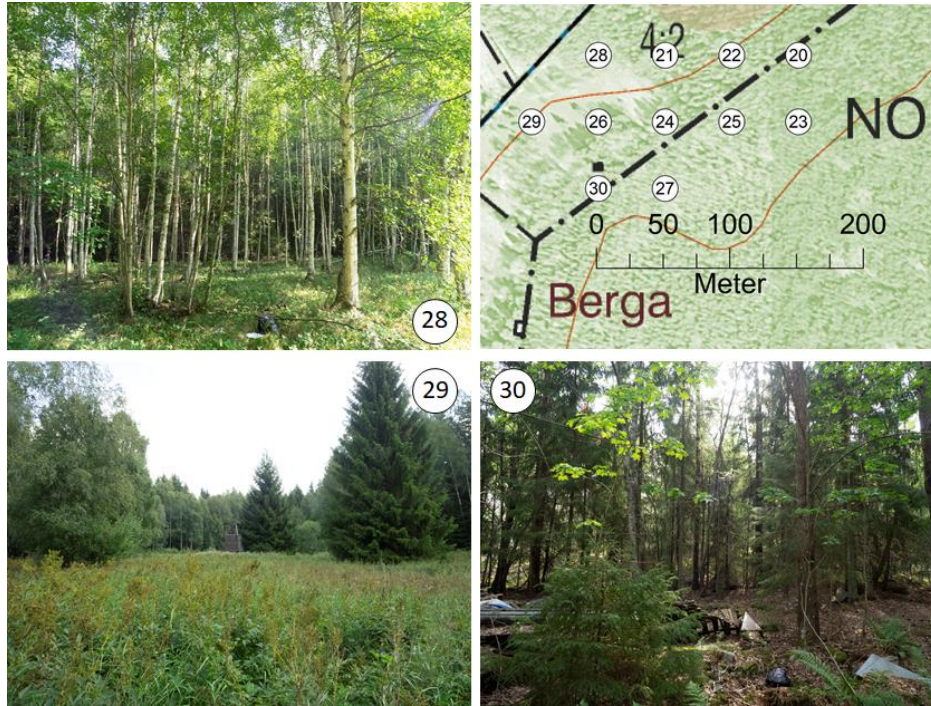


Figure 3. Sample design 2018, showing three sample sites (28, 29 and 30) from one night at the colony in Berga. The map demonstrates locations for each sample site. Photos: Marielle Cambroner.

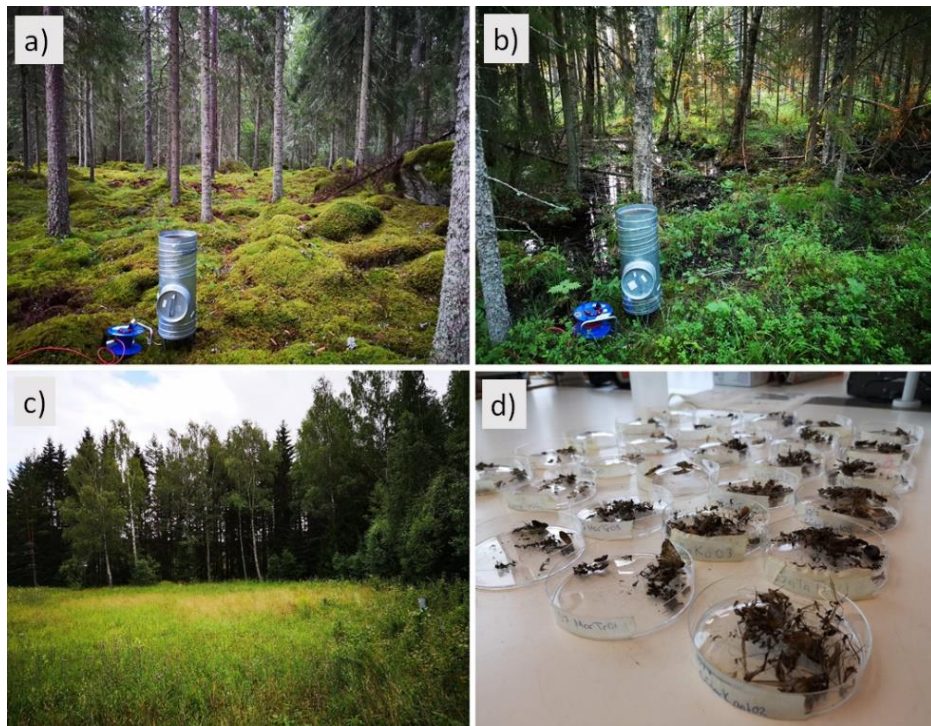


Figure 4. The three different habitats sampled in 2019: a) forest, b) swamp and c) edge. Picture d) shows dried and weighted insects. Photos: Johanna Kammonen.

2.5 Bat sampling

Bat activity was sampled at the sites of insect traps using automatic ultrasound detectors, so-called auto-boxes (D500X, Pettersson Elektronik AB). Auto-boxes were placed in trees (about 2 meters above ground), facing the interior of forest/swamp and along the edge. The data used from the auto-boxes spans for three hours after sunset. Bat recordings were identified using Omnibat (Ecocom AB) and Batsound (Pettersson Elektronik AB). Only data from *Myotis* recordings was used in the analysis. *Myotis* recordings were not identified to species, due to similarities of their echolocation calls (Ahlen & Baagoe, 1999). However, since all sampling sites were close to colonies of *Myotis brandtii*, it was assumed that the majority of all sounds was *M. brandtii*. Bat activity was measured as the number of *Myotis* recordings per auto-box and night. Foraging and commuting was not differentiated.

2.6 Landscape analysis

The landscape within 1 km radius around 16 *M. brandtii* colonies was digitised in ArcMap (version 10.7.1, ESRI Inc., Redlands, CA). The 1 km radius was chosen based on the relatively small home-range of the species (Kammonen, 2015). Seven major habitats were digitised with property maps and orthophotos as references (www.lantmateriet.se), namely: forest (both coniferous and deciduous), swamp forest, clear-cuttings (logged stands and possibly stands < 20 years), open grassland (both current and abandoned arable land), pasture (≤ 50 trees/ha), open wetland and open water (sea, lakes, ponds). In addition, larger streams, tree corridors and urban areas were digitized. Larger streams were categorized as open, open with vegetation or inside forest. Larger streams were clearly visible in orthophoto with a minimum width of about four meters. Tree corridors connected habitats, e.g. two forests on opposite sides of a grassland. Urban areas included larger roads, railways and larger built areas. Data for swamp forests and clear-cuttings was provided from the Swedish Forest Agency (www.skogsstyrelsen.se).

In addition to digitising the landscape within 1 km radius from the bat colonies, three control areas of 20×20 km were digitised. These areas were distributed south to north in the province of Uppland and contained two analysed *M. brandtii* colonies each (Figure 5). These control areas were more roughly digitised with only five habitats: forest, swamp forest, open areas, open water and urban areas. Forest included forest and tree corridors as well as larger streams inside forests. Again, the data for swamp forest was provided from the Swedish Forest Agency. Open areas included grassland, pasture, open wetland and clear-cuttings (no provided data used). Open water included sea, lakes, ponds and larger streams. Urban areas only included larger built areas, with no roads or railways.

Similarly to previous studies (e.g. Sachanowicz & Ruczynski, 2001; Bellamy & Altringham, 2015), distance to the closest large water body (≥ 1 ha) was measured, because of high insect abundance over still water (Zukal & Rehák, 2006) and high levels of bat activity in general (Walsh & Harris, 1996).

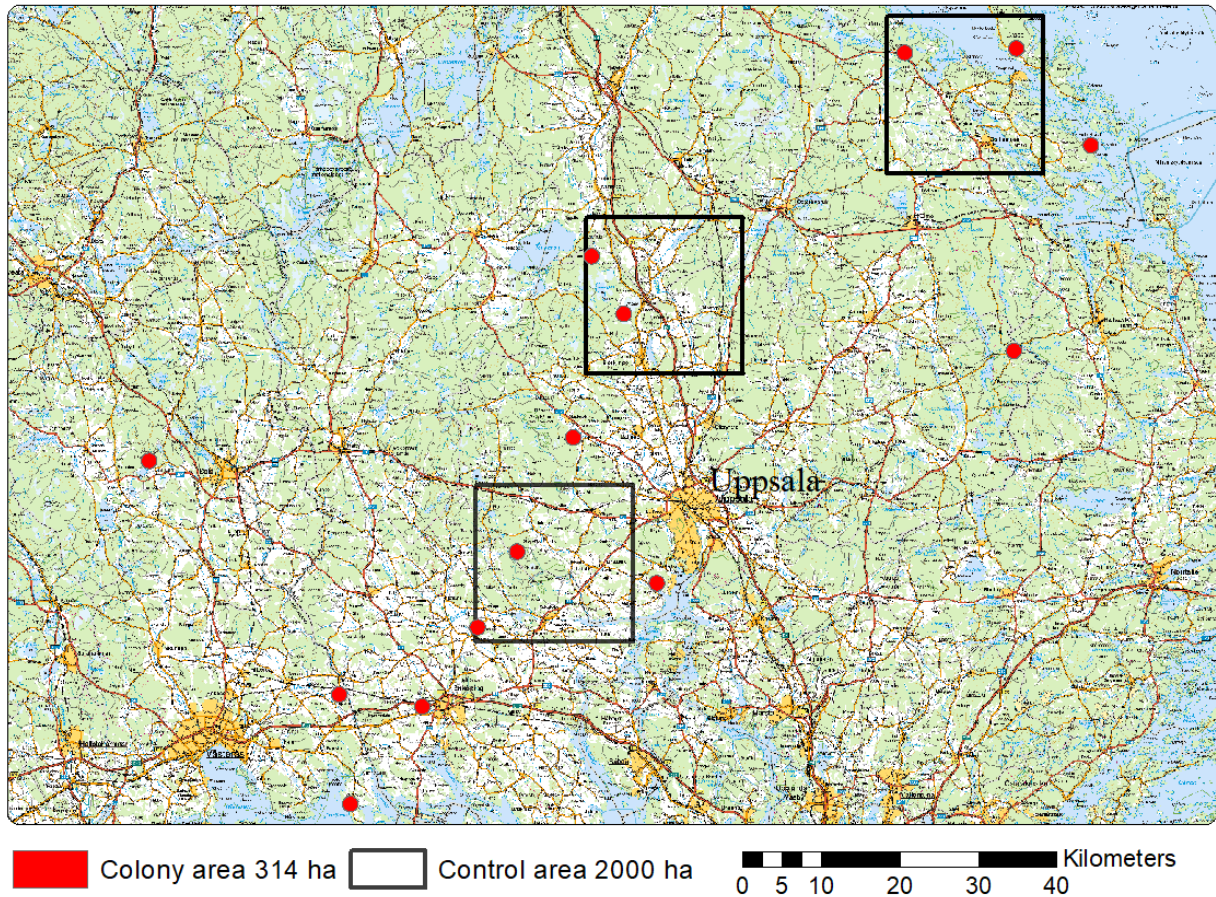


Figure 5. 14 of the 16 *Myotis brandtii* colonies (red dots) and the three control areas (black squares) in the province of Uppland, east-central Sweden.

2.7 Data analysis

Data was log base 10-transformed ($\text{Log}(1+x)$) and tested for normal distribution (Ryan-Joiner test). However, most data were not fitted to normal distribution. One exception was bat activity data which not differ from normal distribution. Therefore, Spearman's rank correlation test and Kruskal-Wallis was used in the analysis of insects, while ANOVA has been used to analyse bat data.

The landscape data was analysed with a one-sample z-test, with the alternative hypothesis: $\text{mean} \neq \text{hypothesised mean}$, to compare the observed habitat coverage around the colonies with the expected habitat coverage from the control landscape of Uppland. When comparing colonies to control landscapes, the digitised habitats from colony areas were pooled together to match the habitats of control landscape. In this comparison, only 14 colonies were used, based on distance to the province of Uppland.

Data analysis were made in Minitab 18 (Minitab, LLC). Alpha level 0,05 was used for all tests.

3 Results

3.1 Insect and bat sampling

Insect weight (g) and number were positively correlated ($p < 0,001$, Spearman rho = 0,620, $n = 115$). Because insect weight and number were correlated, only weight was further analysed as insect abundance. Most of the insects (94 %) belong to the order Diptera, which is one of the main prey insect orders of *M. brandtii* (Vesterinen *et al.*, 2018). Because of the dominance of Diptera, no further analysis was made based on insect orders.

There was a difference between median insect abundance in the three different habitats, 2019: forest, swamp and edge ($p = 0,001$, Kruskal-Wallis, $n = 54$), where insect abundance was highest in edge and swamp habitats (Figure 6a). There was also a difference in insect abundance in the different levels of soil moisture, 2018 ($p < 0,001$, Kruskal-Wallis, $n = 61$), with higher insect abundance in the most wet areas (Figure 6b). Insect abundance also differed in the three different classes of canopy cover, 2018, with more insects in half open canopy ($p = 0,044$, Kruskal-Wallis, $n = 61$) (Figure 6c). Insect abundance was, however, not correlated with density of forest, 2018 ($p = 0,374$, Kruskal-Wallis, $n = 61$) (Figure 6d, Appendix A).

Bat activity was significantly higher in swamp forest compared to forest and edge habitat ($p = 0,015$, ANOVA and Tukey test) (Figure 6a). There was no significant difference in bat activity in relation to soil moisture ($p = 0,812$, ANOVA), however, mean values indicate a trend towards more bats in the most wet areas (Figure 6b). Bat activity did not differ in relation to canopy cover ($p = 0,232$, ANOVA) (Figure 6c) or density of forest ($p = 0,525$, ANOVA), however, mean values indicate a trend towards more bats in medium dense forest (Figure 6d).

There was no correlation between overall (2018 + 2019) insect abundance and bat activity ($p = 0,781$, Spearman rho = 0,026, $n = 115$). The absence of correlation between insect abundance and bat activity was also prominent in the different

habitats (forest: $p = 0,102$, Spearman rho = $-0,398$, $n = 18$; swamp: $p = 0,100$, Spearman rho = $-0,400$, $n = 18$; edge: $p = 0,447$, Spearman rho = $0,191$, $n = 18$) (Figure 6a).

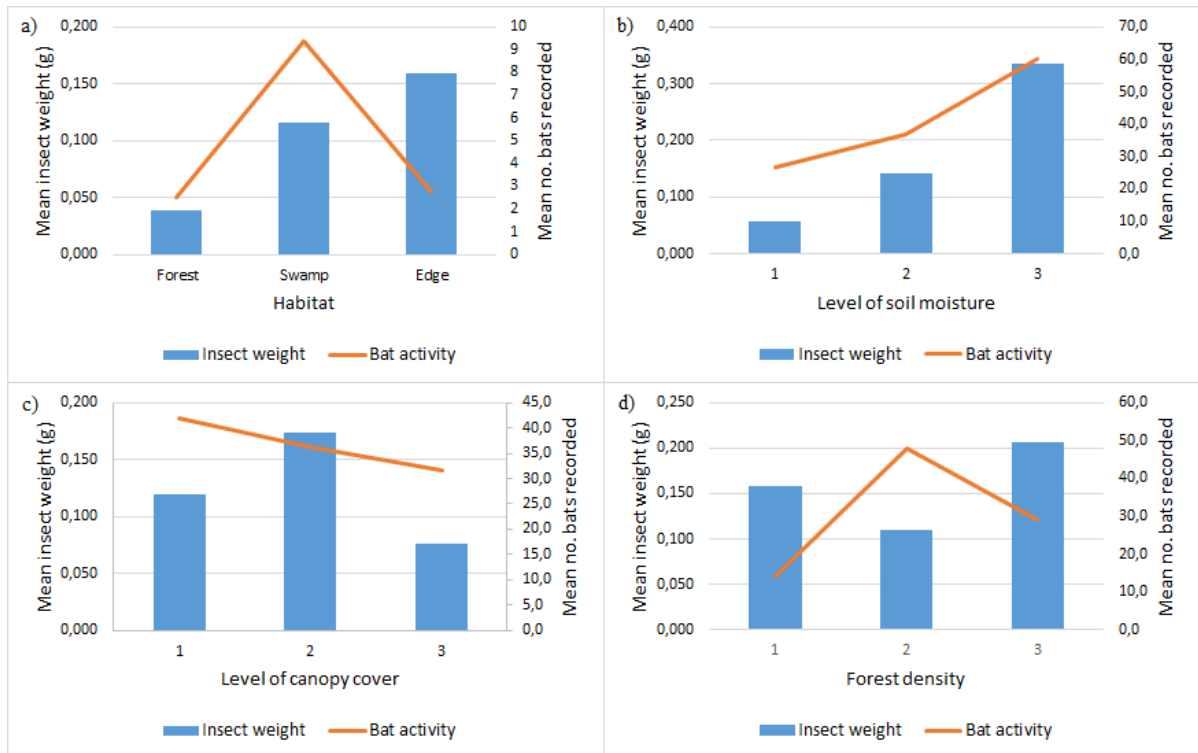


Figure 6. Insect weight and bat activity in relation to a) habitat, b) level of soil moisture (1 = dry, 2 = medium, 3 = wet), c) level of canopy cover (1 = open, 2 = half-open, 3 = closed) and d) forest density (1 = low, 2 = medium, 3 = high).

3.2 Landscape analysis

Forest and grassland make up the majority of habitats of the combined areas around *M. brandtii* colonies (16×314 ha), where forest was the dominant habitat (56 % and 21 % respectively, Table 1). Forest cover ranged between 21 and 75 %, while the range of grassland was 0-63 %. Swamp had a total coverage of 4 %, with the range of 0-31 % (Table 1, Figure 7, Figure 8, Appendix B).

There was no difference in habitat coverage between the landscape of colony areas (14×314 ha) and the control landscapes of Upland (3×2000 ha) (swamp $p = 0,736$; open $p = 0,571$; water $p = 0,244$; $n = 14$), except for forest ($p < 0,001$, $n =$

14) (Table 2). However, the mean coverage of forest was similar for colony areas and the control areas (54 % and 52 %, respectively).

There was a large variance in distance to nearest large water body (≥ 1 ha) from the colonies, with the closest being 144 m away and the furthest more than 4000 m away. In total, ten *Myotis brandtii* colonies were located within 1500 m of a large water body, whereof three of the water bodies were the Baltic Sea. Six colonies were located further than 1500 m away, whereof two were further than 4000 m away of a large water body (Table 3).

Table 1. Summary over habitat coverage within 1 km radius of the 16 colonies *M. brandtii* colonies.

Habitat	Mean	Range	StDev
Forest	56%	21-75%	17,4
Swamp forest	4%	0-31%	7,7
Clear-cutting	8%	0-30%	7,7
Grassland	21%	0-63%	20,2
Pasture	3%	0-9%	2,3
Open wetland	1%	0-6%	1,9
Open water	5%	0-48%	12,1
Larger stream (forest)	0%	0-0%	0,0
Larger stream (open)	0%	0-2%	0,5
Larger stream (open with vegetation)	0%	0-1%	0,3
Tree corridor	0%	0-1%	0,2
Urban	1%	0-6%	1,5
Edge (open, km)	19,8	10,6-29,7	5,4
Edge (water, km)	1,4	0-8,3	2,4

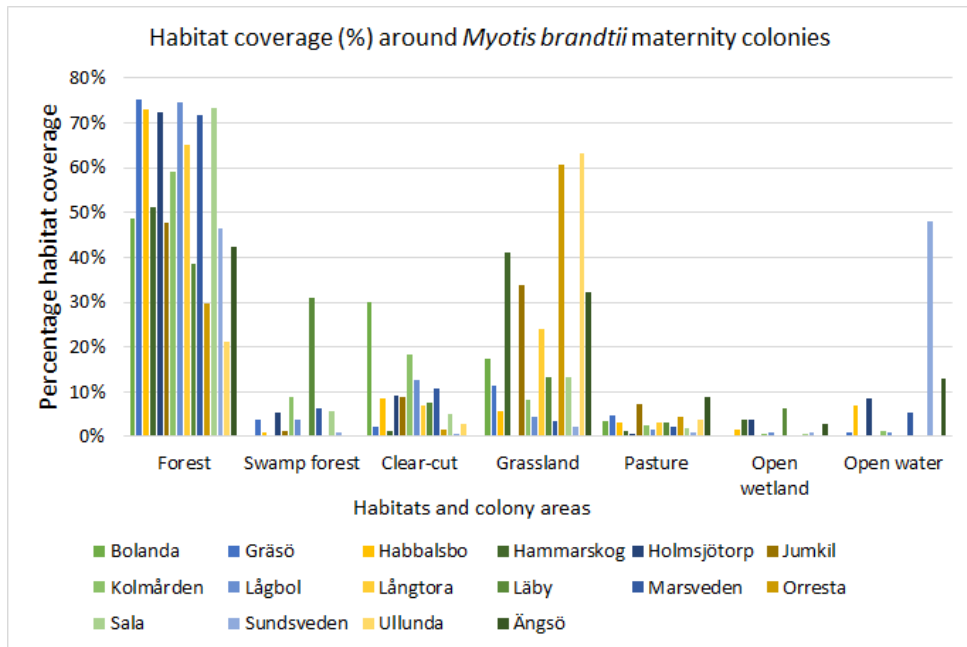


Figure 7. Variance in habitat coverage within 1 km radius across the 16 *Myotis brandtii* colonies. The seven main habitats are depicted: forest, swamp forest, clear-cut, grassland, pasture, open wetland and open water.

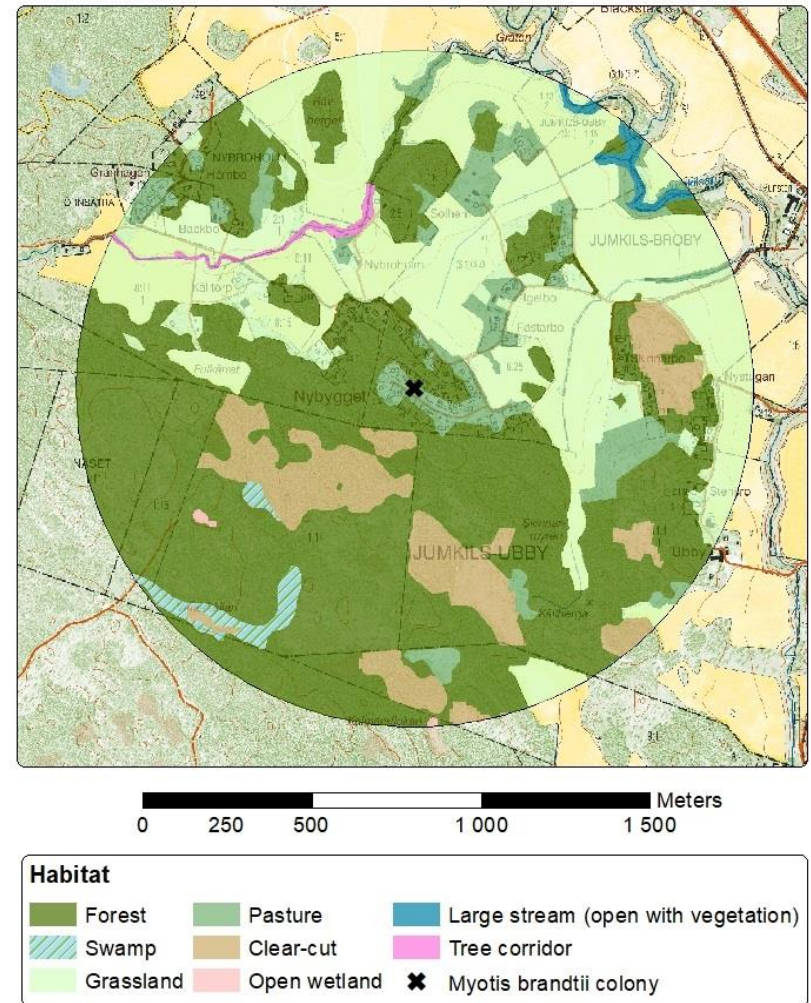


Figure 8. Example of digitised habitats within 1 km radius around a *Myotis brandtii* colony (Jumkil).

Table 2. Summary over pooled habitat coverage within 1 km radius of the *M. brandtii* colonies (14 × 314 ha) and the control areas in Uppland (3 × 2000 ha). Showing mean, range and standard deviation.

Habitat	Colony areas			Control areas		
	Mean %	Range	StDev	Mean %	Range	StDev
Forest	54%	21-76%	18,1	52%	50-54%	2,1
Swamp	4%	0-31%	8,1	4%	2-6%	2,1
Open	35%	5-70%	20	33%	19-44%	12,9
Water	6%	0-48%	12,8	9%	2-23%	11,9
Urban	1%	0-6%	1,6	2%	1-3%	1,2

Table 3. Distance (m) to closest large water body (≥ 1 ha) to each *M. brandtii* colony.

Colony	Distance (m)
Sundsveden	144
Kolmården	200
Holmsjötorp	215
Marsveden	215
Habbalsbo	488
Ängsö	590
Gräsö	757
Lågbol	900
Hammarskog	940
Sala	1200
Långtora	1840
Jumkil	2084
Läby	2530
Bolanda	2777
Orresta	>4000
Ullunda	>4000

4 Discussion

This study demonstrates the importance of wet forests for insect production and bat activity. However, the relation between bat activity and insect abundance in general, seem to be more complicated, since bat activity also relates to vegetation structure. Further, the study demonstrates that *Myotis brandtii* colonies are present in the dominant type of landscape in Uppland, suggesting that the requirements in habitat composition matches the overall landscape.

Measuring insect abundance can be difficult and require a large number of samples, both spatially and temporally (Ekman & de Jong, 1996). This may explain the lack of correlation between bat activity and insect availability in this study. However, a potential correlation between insect abundance and bat activity is not only related to the amount of insects per se, but also vegetation structure and habitat selection by bats (Grindal & Brigham, 1999; Gonsalves *et al.*, 2013). My results coincide with those of Grindal & Brigham (1999) that found no significant correlation between activity of the studied bats and insect abundance in southern Canada. In England, Todd & Waters (2017) found no correlation between insect activity and bat activity (*Myotis daubentonii* and *Pipistrellus pipistrellus*) along a river. However, other studies have found that bat activity is correlated to insect availability (e.g. de Jong & Ahlén, 1991; Fukui *et al.*, 2006; Gonsalves *et al.*, 2013). Fukui *et al.* (2006) experimentally tested the correlation between foraging bats (*Myotis macrodactylus* and *M. ikonnikovi*) and insect abundance along a stream in Japan, and found significantly more bats in control areas than in areas with experimentally excluded insects. de Jong & Ahlén (1991) found that bats in Sweden (mainly *Eptesicus nilssonii* and *P. pipistrellus*) followed the availability of insects through the season, where different habitats were important at different periods. Gonsalves *et al.* (2013) found that the activity of *Vespadelus vulturnus* followed the abundance and distribution of its prey mosquito in Australia. Gonsalves *et al.* (2013) also found that *V. vulturnus* preferred to forage in the open saltmarsh even when mosquitoes were equally available in the adjacent cluttered coastal swamp forest. However, when mosquitoes were scarce in the saltmarsh, cluttered coastal swamp forest was

used according to its availability. Grindal & Brigham (1999) found that the studied bats in southern Canada avoided foraging in cluttered forest, even though insect abundance was highest in forest and that the bats roosted there. In my study, insect abundance was highest in edge habitat, however, bat activity was low at edges. This is an additional explanation as to why there was no correlation between insects and bats, since the studied species of bat avoid foraging in open areas (de Jong, 1995; Kammonen, 2015), and thus also avoid edge habitats.

Insect abundance was highest at the most wet locations in 2018, and high in swamp forests 2019 (highest in edge), demonstrating the importance of wet areas for insect production. It has previously been shown that wet areas generate high insect abundance (e.g. Batzer & Wissinger, 1996; Spitzer & Danks, 2006). However, Vinnersten *et al.* (2014) found that the number of emerging insects decreased with an increased period of floods, in wetlands and swamps in Sweden, suggesting that the amount of water itself is negative for many insect taxa. Further studies may be needed to evaluate insect abundance in relation to forested wetlands. Higher insect abundance at edges compared to forest interior has been demonstrated (e.g. Gonzalez *et al.*, 2017), however, Grindal & Brigham (1999) found higher insect abundance in forests compared to edges.

My prediction that wet areas would be important for bat activity is supported by significantly more bats in swamp forest 2019, and a trend towards higher bat activity in the most wet areas 2018. Few studies have focused on the relation between bats and swamp forests in boreal, or even temperate areas, but see Ciechanowski *et al.* (2011) and Nummi *et al.* (2011) for positive effects upon bats from beaver dams. However, several studies from tropical and subtropical areas demonstrate that swamp forests and other forested wetlands are important for different bat species, depending on foraging strategy (e.g. Struebig & Galdikas, 2006; Gonsalves *et al.*, 2013). Clement & Castleberry (2013) developed a model based on the forest-dwelling bat *Corynorhinus rafinesquii* in subtropical Georgia, USA, predicting the number of colonies and their densities in relation to forest wetland width and duration of flooding. The model predicted more colonies and higher densities in wider forest wetlands as well as those with longer periods of flooding, and the authors suggest the model can be used for other bat species.

Bat activity was not significantly correlated with forest structure (i.e. density or canopy cover). There was, however, a trend towards more bats in areas with more open canopy cover. This suggests that small glades are probably not negative for the species, in contrast to large clearings. There was also a trend towards more bats in medium dense forests, which suggests that *M. brandtii* tolerates management of forest interiors, such as thinning, but probably not clear-cutting. In Finland, Wermundsen & Siivonen (2008) found that *M. brandtii*/*M. mystacinus* foraged predominantly in medium cluttered, coniferous woodland. This supports that *M.*

brandtii is tolerant to thinning of forests, and the authors even propose this action as a conservation measure (Wermundsen & Siivonen, 2008). While thinning of forests appear tolerable, or even positive, for *M. brandtii* (Wermundsen & Siivonen, 2008), clear-cutting or draining of forests are probably negative for the species. Whether *M. brandtii* forage in open areas (such as clear-cuts) or not, was not investigated in this study, but has been done previously. Radio-tracking results show that *M. brandtii* avoids foraging in open areas (de Jong, 1995; Kammonen, 2015), suggesting that clear-cutting as a harvesting method is negative for this species of bat. *M. brandtii* might avoid large open areas due to predation risk from opportunistic avian predators (Speakman, 1991) and interspecific competition (Kurek *et al.*, 2017; Roeleke *et al.*, 2018). To my knowledge, no studies have investigated the effects of drainage in boreal forests upon bats. Draining of forests in northern Europe has caused a major decrease in the amount of swamp forests (Maanavilja *et al.*, 2014). Based on the results from this and other studies, swamp forests are important for both insect production and bat activity (Struebig & Galdikas, 2006; Gonsalves *et al.*, 2013). In Sweden, drainage to improve forestry or agriculture was common until 1980. It is nowadays rare, but is still used in connection to clear-cutting, thus large-scale restoration should be considered (Bernes, 1994, 2001).

The habitat composition within the colony areas (14×314 ha) did not differ from the control landscape of Uppland (3×2000 ha), i.e. there was no difference in the amount of e.g. swamp or forest. There were also large variations in habitat coverage around the colony areas (16×314 ha) in the more detailed analysis (e.g. forest 21-75 %, swamp 0-31 %, grassland 0-63 % and edge length between forest and open areas 10,6-29,7 km). The length of edges varied largely, and this together with low bat activity in edges suggests that edge-length is unimportant for colony-site selection of *M. brandtii*. The importance of swamps and high level of soil moisture for both insects and bats have been demonstrated in this study, however, due to the large variation in swamp coverage, *M. brandtii* does not seem to require large areas of swamp in proximity to their colonies. These results suggest that the dominant type of landscape in Uppland is suitable for *M. brandtii* colonies, making it hard to predict colony locations based on maps at landscape level. It is possible, however, that there are differences in microhabitats, that doesn't show on maps. Insect abundance is probably important together with high level of soil moisture and forest interior habitats. Not only swamp forests have high level of soil moisture, but e.g. temporary pools and small bogs are also rich in water and positive for insect production (Batzer & Wissinger, 1996; Spitzer & Danks, 2006). Further studies are needed to evaluate at a finer level what causes *Myotis brandtii* to choose locations for their colonies, e.g. more detailed investigation of soil moisture in relation to bat abundance.

In general, different types of lakes, ponds and streams are positive for bats and insect abundance (Walsh & Harris, 1996; Zukal & Rehák, 2006). However, there

are studies showing a negative relation between *M. brandtii* and larger lakes (Sachanowicz & Ruczynski, 2001; Bellamy & Altringham, 2015). One possible explanation may be sensitivity to interspecific competition, with e.g. *Myotis daubentonii* and *Pipistrellus pygmaeus* that more frequently forage over water (Kurek *et al.*, 2017). The large variance in distance to nearest large (≥ 1 ha) water body in this study, suggests that proximity to this type of water is not related to *M. brandtii* colonies. The majority of colonies in this study (9 of 16) were closer than 1000 m from large water bodies, whereof five were closer than 500 m. On the other hand, five were located more than 2000 m away, whereof two more than 4000 m away.

Different bat species may be affected differently by forestry, depending on e.g. foraging strategy, wing morphology, echolocation calls and roost type (Patriquin & Barclay, 2003; Owen *et al.*, 2004; Law *et al.*, 2018; Huang *et al.*, 2019). For instance, bats that forage in open habitats use echolocation calls designed to detect items at long distances and also have long and narrow wings, enabling fast flight (Norberg, 1989; Schnitzler *et al.*, 2003; Russ, 2012). Bats that forage in edges and more cluttered environments, on the other hand, use a variety of echolocation calls that gives detailed information about the nearest surroundings. They usually have shorter and broader wings, enabling slow but manoeuvrable flight in dense vegetation (Norberg, 1989; Schnitzler *et al.*, 2003; Russ, 2012). Bats adapted to open habitats can be positively affected by forestry, when more open forests, edges and clear-cuts are created (cf. Ethier & Fahrig, 2011). On the other hand, forestry may have negative impacts on species specialised to highly cluttered environments, especially if they also roost in trees (Huang *et al.*, 2019). *M. brandtii* forages in medium cluttered forests (Zukal & Reháč, 2006; Wermundsen & Siivonen, 2008) and roosts in trees as well as in buildings (Sachanowicz & Ruczynski, 2001), which might explain why this species appears to be tolerant towards thinning of forests.

To conclude, *Myotis brandtii* occurs in landscapes dominated by production forestry, and is probably favoured by thinning and continuous canopy-cover forestry, which could be employed as conservation measures. Thinning can be beneficial for bats, since forests can be used more efficiently for foraging (Humes *et al.*, 1999; Wermundsen & Siivonen, 2008). Adapted forestry with a continuous canopy-cover (i.e. clear-cuts are avoided) containing trees of various sizes and ages (i.e. structurally heterogenous), can be beneficial for forest-living bats (Pommerening & Murphy, 2004). Probably, the most important aspect in the conservation of forest-living bats is rewetting of forested wetlands. A next step for this study can be to further evaluate forested wetlands, based on e.g. their size and duration of flooding, and connect them to presence of forest-living bats.

5 Conclusions

Myotis brandtii is present in the dominant type of landscape in east-central Sweden, and it is difficult to predict *M. brandtii* colonies in these areas based on maps and the data used. The results of this study show a clear connection between soil moisture and insect abundance as well as bat activity, suggesting that swamp forests and other wet forested areas are important for *M. brandtii* colonies. However, the species do not seem to require large amounts of swamp forests, meaning that the presence of a *M. brandtii* colony cannot be predicted by swamp forests alone. Further studies are needed to investigate the relation between forested wetlands and forest-living bats.

No correlation between insect abundance and bat activity was found. Insect abundance was highest at edges, while bat activity was low at these habitats, suggesting that vegetation structure is more important than insect abundance in habitat selection of this species of bat. However, forest density does not appear to be crucial in habitat selection, even though there was a tendency towards more bat activity at medium dense forests. In all studied areas, normal production forestry was employed, further suggesting that the species is tolerant towards thinning of forests. One area of conflict can, however, be large areas of clear-cutting, if not enough forest is retained in connection to colonies. Additionally, the most negative impact from forestry upon *Myotis brandtii* is drainage of forests. Therefore, the most important conservation measure for *M. brandtii*, and probably for forest-living bat species in general, is to preserve, restore or create new swamp forests and other forested wetlands.

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Appendix A

Table A1. Raw data for each sample site. Showing habitat, level of soil moisture (1 = dry, 2 = medium, 3 = wet), level of canopy cover (1 = open, 2 = half-open, 3 = closed), forest density (number of trees/100m²), number of insects, insect weight (g) and number of recorded *Myotis*.

Sample site	Soil moisture	Canopy cover	Forest density	Habitat	Insect number	Insect weight (g)	Bat activity
2018							
Berga 01	1	1	1	-	910	0,064	3
Berga 02	2	2	7	-	201	0,205	4
Berga 03	2	1	8	-	104	0,039	0
Berga 04	2	2	8	-	158	0,133	6
Berga 05	1	2	8	-	222	0,113	1
Berga 06	2	1	3	-	1106	0,243	23
Berga 07	1	3	2	-	137	0,033	51
Berga 08	1	2	5	-	415	0,058	19
Berga 09	1	3	9	-	549	0,172	8
Berga 10	2	2	6	-	708	0,254	4
Berga 11	1	3	9	-	323	0,042	44
Berga 12	1	3	13	-	257	0,077	72
Berga 13	1	3	14	-	319	0,031	9
Berga 14	1	3	13	-	619	0,1	87
Berga 15	3	2	5	-	633	0,275	2
Berga 16	3	2	3	-	2036	0,947	7
Berga 17	3	2	13	-	1577	0,762	35
Berga 18	2	2	9	-	289	0,057	104
Berga 19	1	2	7	-	274	0,004	84
Berga 20	1	3	4	-	243	0,045	16
Berga 21	1	3	9	-	25	0,001	64
Berga 22	1	2	6	-	118	0,041	24
Berga 23	1	3	9	-	61	0,006	28
Berga 24	1	2	7	-	434	0,045	24
Berga 25	2	2	1	-	332	0,035	12
Berga 26	2	2	5	-	301	0,067	11
Berga 27	3	3	6	-	133	0,059	6
Berga 28	2	1	0	-	750	0,176	12
Berga 29	1	3	5	-	192	0,043	6
Habbalsbo 01	2	2	14	-	246	0,157	1

Table A1 (continued)

Sample site	Soil moisture	Canopy cover	Forest density	Habitat	Insect number	Insect weight (g)	Bat activity
Habbalsbo 02	2	2	10	-	675	0,261	19
Habbalsbo 03	7	2	2	-	268	0,221	1
Habbalsbo 04	2	2	1	-	383	0,12	7
Habbalsbo 05	3	3	1	-	197	0,134	14
Habbalsbo 06	3	2	2	-	179	0,14	2
Habbalsbo 07	6	1	2	-	800	0,079	8
Habbalsbo 08	3	2	2	-	182	0,159	36
Habbalsbo 09	1	2	1	-	419	0,134	26
Habbalsbo 10	7	3	2	-	1401	0,209	5
Habbalsbo 11	7	2	2	-	768	0,109	28
Habbalsbo 12	6	2	2	-	453	0,219	8
Habbalsbo 13	0	3	1	-	389	0,077	5
Habbalsbo 14	6	2	2	-	301	0,051	8
Habbalsbo 15	3	2	2	-	384	0,08	9
Jumkil 01	6	1	1	-	229	0,028	12
Jumkil 02	0	1	1	-	553	0,034	1
Jumkil 03	5	2	2	-	1241	0,05	14
Jumkil 04	9	2	1	-	1800	0,167	31
Jumkil 05	1	1	1	-	1171	0,118	4
Jumkil 06	7	2	3	-	1026	0,056	7
Jumkil 07	10	2	2	-	950	0,126	8
Jumkil 08	8	2	2	-	658	0,032	4
Jumkil 09	13	1	2	-	576	0,056	15
Jumkil 10	12	2	3	-	1056	0,288	16
Jumkil 11	7	2	2	-	1490	0,301	249
Jumkil 11:2	8	3	1	-	1169	0,221	408
Jumkil 12	9	2	3	-	961	0,072	49
Jumkil 13	9	2	3	-	1358	0,136	30
Jumkil 14	6	2	2	-	146	0,079	408
Jumkil 15	7	1	3	-	612	0,053	11
Jumkil 16	6	2	2	-	1126	0,241	1
2019							
Bolanda 01	-	-	-	Edge	913	0,183	1
Bolanda 02	-	-	-	Edge	880	0,113	1
Bolanda 03	-	-	-	Edge	1855	0,381	1
Bolanda 04	-	-	-	Forest	409	0,061	1
Bolanda 05	-	-	-	Forest	788	0,055	0
Bolanda 06	-	-	-	Forest	861	0,127	2

Table A1 (continued)

Sample site	Soil moisture	Canopy cover	Forest density	Habitat	Insect number	Insect weight (g)	Bat activity
Bolanda 07	-	-	-	Swamp	194	0,045	35
Bolanda 08	-	-	-	Swamp	429	0,022	59
Bolanda 09	-	-	-	Swamp	332	0,046	1
Hammarskog 01	-	-	-	Edge	378	0,041	0
Hammarskog 02	-	-	-	Edge	571	0,093	1
Hammarskog 03	-	-	-	Edge	391	0,117	2
Hammarskog 04	-	-	-	Forest	24	0	3
Hammarskog 05	-	-	-	Forest	27	0	3
Hammarskog 06	-	-	-	Forest	12	0	7
Hammarskog 07	-	-	-	Swamp	96	0,04	18
Hammarskog 08	-	-	-	Swamp	134	0,079	11
Hammarskog 09	-	-	-	Swamp	187	0,085	8
Holmsjötorp 01	-	-	-	Edge	1684	0,456	22
Holmsjötorp 02	-	-	-	Edge	1053	0,094	1
Holmsjötorp 03	-	-	-	Edge	1610	0,142	4
Holmsjötorp 04	-	-	-	Forest	601	0,046	5
Holmsjötorp 05	-	-	-	Forest	996	0,075	1
Holmsjötorp 06	-	-	-	Forest	1111	0,033	3
Holmsjötorp 07	-	-	-	Swamp	568	0,089	2
Holmsjötorp 08	-	-	-	Swamp	735	0,157	5
Holmsjötorp 09	-	-	-	Swamp	775	0,251	0
Marsveden 01	-	-	-	Edge	195	0,131	1
Marsveden 02	-	-	-	Edge	88	0,076	6
Marsveden 03	-	-	-	Edge	137	0,119	4
Marsveden 04	-	-	-	Forest	71	0,041	1
Marsveden 05	-	-	-	Forest	92	0,023	4
Marsveden 06	-	-	-	Forest	106	0,059	0
Marsveden 07	-	-	-	Swamp	336	0,14	2
Marsveden 08	-	-	-	Swamp	313	0,086	1
Marsveden 09	-	-	-	Swamp	508	0,141	7
Sala 01	-	-	-	Edge	5	0,002	0
Sala 02	-	-	-	Edge	17	0,003	1
Sala 03	-	-	-	Edge	5	0	1
Sala 04	-	-	-	Forest	38	0,035	0
Sala 05	-	-	-	Forest	48	0,02	13
Sala 06	-	-	-	Forest	62	0,022	0
Sala 07	-	-	-	Swamp	401	0,426	5
Sala 08	-	-	-	Swamp	377	0,204	1
Sala 09	-	-	-	Swamp	239	0,162	2

Table A1 (concluded)

Sample site	Soil moisture	Canopy cover	Forest density	Habitat	Insect number	Insect weight (g)	Bat activity
Sundsveden 01	-	-	-	Edge	515	0,15	0
Sundsveden 02	-	-	-	Edge	386	0,278	3
Sundsveden 03	-	-	-	Edge	495	0,488	0
Sundsveden 04	-	-	-	Forest	58	0,015	1
Sundsveden 05	-	-	-	Forest	48	0,024	0
Sundsveden 06	-	-	-	Forest	36	0,057	1
Sundsveden 07	-	-	-	Swamp	42	0,019	1
Sundsveden 08	-	-	-	Swamp	66	0,047	6
Sundsveden 09	-	-	-	Swamp	71	0,036	5

Appendix B

Table B1. *Habitat coverage (ha) and length (km) of edge between forest and open grassland/water for each of the 16 M. brandtii colonies in 2019.*

Colony	Forest	Swamp forest	Clear-cut	Grassland	Pasture	Open wetland	Open water	Stream (forest)	Stream (open)	Stream (open with vegetation)	Tree corridor	Urban	Edge km (forest-open)	Edge km (forest-water)
Bolanda	152,38	1,31	94,53	54,69	11,29	0	0	0	0	0	0	0	27,5	0,0
Gräsö	236,49	12,13	7,34	35,47	14,75	1,39	2,89	0	0	0	0,74	2,9	22,9	0,3
Habbalsbo	228,92	3,13	26,78	17,49	9,54	4,64	21,45	0,59	0	0	0	1,62	22,1	2,4
Hammarskog	160,48	0	4,37	129,45	4,08	12,17	0,46	0	0	0	0,6	2,52	21,2	0,0
Holmsjötorp	227,38	17,26	28,41	0,69	1,54	12,17	26,71	0	0	0	0	0	12,5	5,4
Jumkil	149,83	3,51	27,88	106,3	22,52	0,26	0	0	0	2,14	1,6	0	23,8	0,0
Kolmården	185,99	28,1	57,18	26,03	8,14	1,61	4,37	0	0	0	0,74	1,98	29,7	0,8
Lågbol	234,48	12,19	39,51	13,96	4,85	2,87	3,16	0	0,1	0	0	3,97	23,8	0,2
Långtora	204,2	0	21,73	75,24	9,53	0,62	0	0	0	0	0	2,82	20,9	0,0
Läby	120,93	97,62	23,67	41,23	9,67	20,23	0,14	0	0	0	0,62	0,16	14,1	0,0
Marsveden	224,84	19,72	33,64	10,88	7,17	1,43	16,44	0	0	0	0	0	14,2	2,5
Orresta	93,62	0	5,04	190,71	14,2	0	1,13	0	0	0	0	9,43	16,4	0,0
Sala	230,49	17,66	16,32	41,87	5,73	2,03	0	0	0	0	0	0	16,3	0,0
Sundsveden	146,14	2,94	1,95	7,11	2,68	2,7	150,58	0	0	0	0	0	10,6	8,3
Ullunda	65,99	0	9,06	198,29	11,76	0	0	0,8	4,86	4	0	19,35	18,2	0,0
Ängsö	133,32	0	0	100,89	27,29	8,91	40,31	0	0,52	0	0	2,87	22,6	3,2
Range	66-236,5	0-97,6	0-94,5	0,7-198,3	1,5-27,3	0-20,2	0-150,6	0-0,8	0-4,9	0-4,0	0-1,6	0-19,4	10,6-29,7	0-8,3
Mean	174,72	13,47	24,84	65,64	10,30	4,44	16,73	0,09	0,34	0,38	0,27	2,98	19,8	1,4