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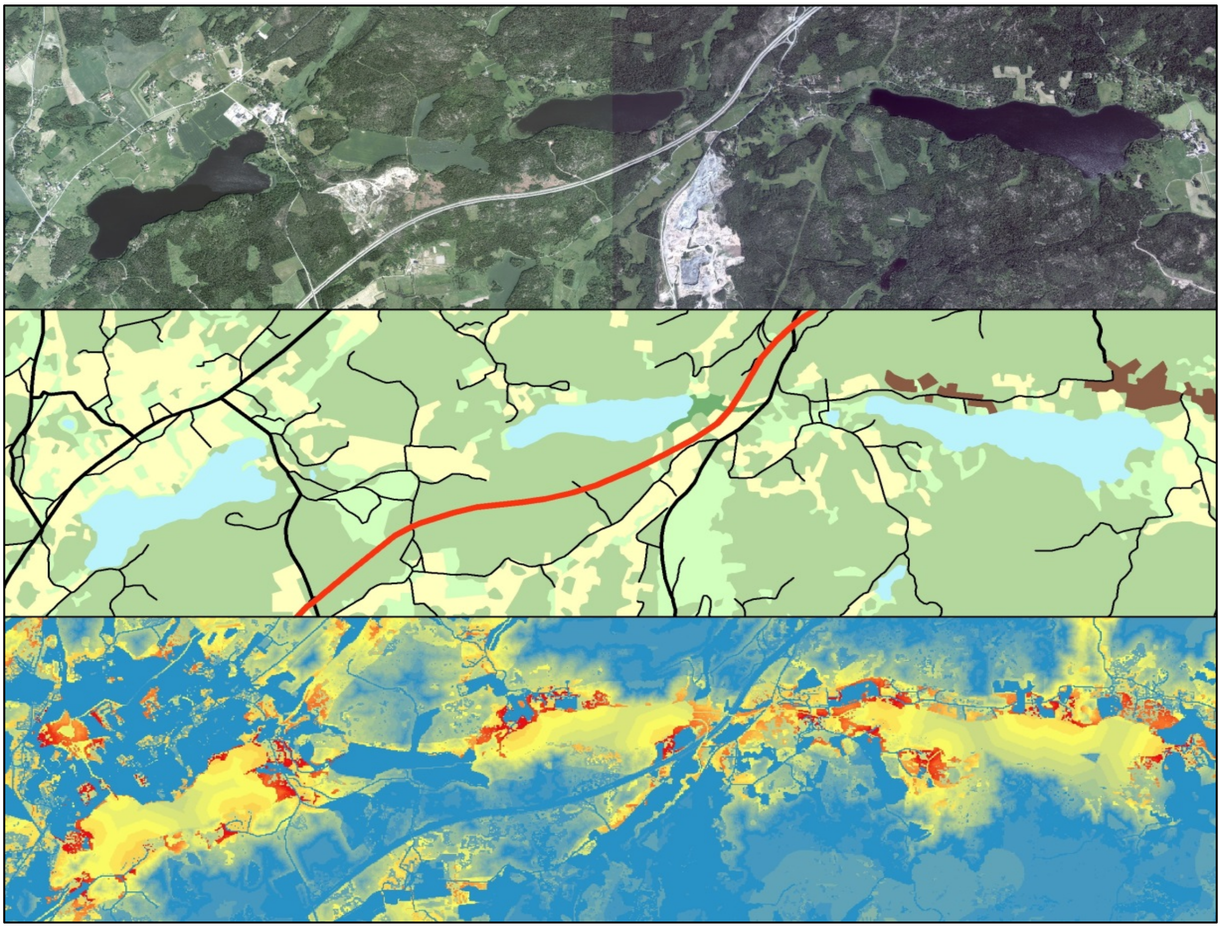
Predicting bat occurrence

Evaluation of a connectivity-based habitat index for Swedish bats

Gesa von Hirschheydt



Master´s thesis 30 hec
Uppsala 2018

CBM Swedish Biodiversity Centre

Independent project/Degree project / SLU, Department of Ecology 2018:14

Predicting bat occurrence - Evaluation of a connectivity-based habitat index for Swedish bats

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Credits:	30 hec
Level:	A2E
Course title:	Independent project in Biology – Master's thesis
Course code:	EX0565
Place of publication:	Uppsala
Year of publication:	2018
Cover picture:	Gesa von Hirschheydt
Title of series:	Independent project/Degree project / SLU, Department of Ecology
Part no:	2018:14
Online publication:	https://stud.epsilon.slu.se
Keywords:	bats (Chiroptera), bat habitat index, ecological impact assessment, flight friction, cost distance analysis, landscape permeability

The project was conducted at:

CBM Swedish Biodiversity Centre

Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology

Abstract

Ecological impact assessments are required for all large infrastructure or exploitation projects because of their effects on environment and species. Methods that would make such assessments more standardised, efficient and reliable are highly desirable in today's society, where many species are decreasing due to human-induced habitat modifications. This thesis evaluates the performance of a habitat index for Swedish bat species (bat habitat index, BHI), which has the potential to be used as a tool for impact assessments. Previous studies have shown that bats are negatively affected by large roads because they represent a barrier for movement and because the noise associated with the traffic impedes efficient foraging. The BHI takes the barrier effect of the highway into account by assigning it the lowest value for permeability. Acoustic effects in proximity to the highway are ignored by the BHI. For this study, 50 sites were inventoried for four nights using automatic ultrasound recorders to get an empiric measure of bat occurrence that could be compared to the BHI's predictions and the distance to the highway E18 which crosses the study area. The correlation between the predicted values from the BHI and the observed bat activity (number of recordings) or species richness was tested using generalised linear mixed models. Among the models with the same response variable, the best-performing model was selected based on a bias-corrected AIC (Akaike Information Criterion). The results show that the BHI is a good predictor for the number of species that regularly occur at a given site (i.e. species that were observed in a minimum of three out of four nights), but not for the total number of species. The BHI performed also much better at predicting the activity of forest-living species than overall bat activity. Instead of the expected positive correlation between the distance to the highway and bat activity, the observed negative correlation suggests that the BHI overestimates the barrier effect of the highway. This could easily be corrected by adjusting the permeability of highways in the construction of the BHI. For further improvement of the BHI, I also suggest that the goals are set more explicitely by deciding which species the BHI should focus on (e.g. all species or only forest-living species) and which measure of bat occurrence it should predict (e.g. regular occurrence of species, total species richness or activity).

Keywords: bats (Chiroptera), bat habitat index, ecological impact assessment, flight friction, cost distance analysis, landscape permeability

Populärvetenskaplig sammanfattning

Miljökonsekvensbeskrivningar (MKB) krävs vid all planering av infrastruktur- och exploateringsprojekt. En MKB består delvis av konsekvensbeskrivningar för arter, eftersom stora projekt kan påverka djur och andra organismer negativt genom att förstöra lämpliga boplatser och födoområden (habitatförlust) eller genom att förhindra spridning (barriäreffekt). Syftet med detta arbete var att utvärdera ett index som förutsäger förekomsten av fladdermöss beroende på lokala och regionala miljöförhållanden. Indexet (bat habitat index, BHI) är baserat på tre grundkartor som representerar täthet av insekter, fladdermössens flygpreferenser och var det finns möjliga koloniplatser för dräktiga honor. De grundkartorna baseras på det senaste kunskapsläget och är skapade av experter utgående från tillgängliga terräng- och habitatkartor samt resultat från olika inventeringar. Genom att definiera motorvägar som olämplig flygmiljö ingår barriäreffekter av motorvägar i indexet vilket gör det speciellt användbart i MKB för konstruktion av stora motor- eller järnvägar.

Inom denna studie inventerades 50 lokaler fördelade över ett område på ca 850 km^2 i Stockholms län under juli månad 2017. På varje lokal sattes automatiserade inspelningsboxar som registrerar ultraljud (och alltså fladdermössens läten) upp och boxarna spelade in allt ultraljud under fyra nätter. Varje lokal fick ett värde för fladdermössens aktivitet (antal inspelningar), artantalet över samtliga fyra nätter och antalet arter som registrerades regelbundet (minst tre av fyra nätter). För att analysera hur väl BHIs förutsägelser och avstånd till motorvägen korrelerar med de observerade värdena för aktivitet och artantal, användes ett statistiskt kriterium som kallas för Akaike Information Criterion (AIC) och som tillåter jämförelser mellan olika modeller. Resultatet från denna analys visar att BHI är bra på att förutsäga antalet arter som regelbundet använder en lokal, men att indexet inte är bra på att förutsäga totalt antal arter på en lokal eller aktivitet av alla fladdermöss. Det är mycket bättre på att förutsäga aktivitet av de fladdermusarter som är skogslevande (d.v.s. brunlångöra, dvärg-, troll- och sydpipistrell, mustasch-, taiga- och fransfladdermus) än den totala aktiviteten av alla fladdermöss. Resultatet från korrelationen mellan aktivitet och distans till motorvägen antyder att BHI överskattar barriäreffekten av motorvägen. Detta skulle lätt kunna korrigeras genom att höja motorvägens lämplighet för fladdermöss i grundkartorna.

Utöver utvärderingen av indexets förmåga att förutsäga förekomsten av fladdermöss, diskuteras för- och nackdelar med detta index (BHI) och dess möjliga tillämpningsområden. Dessutom utpekas viktiga antaganden som måste beaktas vid tolkningen och det ges förslag för framtida utveckling av indexet. Det viktigaste förslaget är att målet med BHI bör formuleras tydligt innan nästa utvärdering.

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Introduction

Environmental Impact Assessments (EIA) are a common tool for identifying potential conflicts between economic development plans and environmental conservation. In Sweden, it is legally required to conduct an EIA prior to the realisation of large exploitation and construction projects (*SFS 1998:905*; see also Faith-Ell, 2015). The compilation of an EIA usually takes a long time and requires competences in many different areas of environmental exploitation and conservation. One important part of the EIA is the Ecological Impact Assessment (EcIA) that predicts potential effects on species and populations. The purpose of this study is to evaluate the performance and utility of a tool called Bat Habitat Index (BHI), which would facilitate the EcIA of projects that can have an impact on bat fauna. If performing satisfyingly, the BHI could for example be used when planning the construction of roads and railways or in the EcIA of exploitation practices in forestry, mining or quarrying. Bats are together with ungulates, amphibians and reptiles one of the main groups of interest to the Swedish Transport Administration and can be used in EcIA for infrastructure (Trafikverket, 2015).

There are 19 bat species in Sweden (Ahlén, 2011) of which nine (47 %) are considered threatened according to the national Red List (Artdatabanken, 2015). The most recent evaluation of the conservation status of Swedish bat species shows that only six out of 19 (32 %) species have favourable conservation status, one (5 %) had unsatisfying conservation status, and twelve species (63 %) were evaluated as having bad conservation status (Eide, 2014). These results are thought to stem primarily from limited knowledge about the species' exact population sizes and trends and do therefore not represent confirmed population declines (Eide, 2014). Nevertheless, part of Sweden's environmental objectives is to sustain biodiversity and to manage wildlife in such a way that species reach and remain at favourable conservation status (*SFS 1998:808*; see also Sweden's environmental objectives by the Swedish Environmental Protection Agency). All Swedish bat species are listed in appendix IV of the Habitats Directive by the European Union (*Council Directive 92/43/EEC*) and they are therefore legally protected from hunting, handling or any type of disturbance (*SFS 2007:845*). This also implies an obligation to maintain environmental conditions that ensure the long-term persistence of this organism group.

Several studies have produced evidence that roads affect bats in different ways, the majority of which reduce overall population fitness. Carcass searches, for example, have revealed considerable numbers of traffic casualties in different regions and for different species (Lesiński *et al.*, 2011; Gaisler *et al.*, 2009; Russell *et al.*, 2009). Because insectivorous bats primarily use their hearing as sensory organ when foraging (e.g. Lazure & Fenton, 2011), traffic noise has been associated with decreased foraging efficiency (Luo *et al.*, 2015; Siemers & Schaub, 2011; Schaub *et al.*, 2008) as well as overall avoidance of highways (Bennett & Zurcher, 2013; Zurcher *et al.*, 2010). While avoidance behaviour protects bats from colliding with vehicles, it also prevents them from reaching potential foraging or breeding habitats on the other side of the road. This means that the road acts as a barrier for movement, for example in the Bechstein's bat *Myotis bechsteinii* (Kerth & Melber, 2009). Berthinussen and Altringham found a higher number of species further away from the road than right next to it (2012) which suggests that some species perceive the negative effects of roads more strongly or at greater distances. Overall, studies have demonstrated a reduction in bat activity in proximity to major roads (Kitzes & Merenlender, 2014; Berthinussen & Altringham, 2012) with effects extending up to a distance of 1.6 km. Being able to predict how the construction of a road might affect the occurrence of bats is therefore essential for species conservation.

In order to create a tool that would facilitate the prediction of the impact of large habitat modifications on bats, Oskar Kindvall from the consulting agency Calluna AB has developed a spatial index for bat occurrence in Sweden, in collaboration with Johnny de Jong from the Swedish Biodiversity Centre. Their index, so far unpublished and hereafter referred to as Bat Habitat Index (BHI), integrates the knowledge accumulated in the scientific literature as well as additional expert knowledge to make a well-informed prediction of bat occurrence, based on habitat suitability for foraging and landscape connectivity. The purpose of this thesis is to evaluate the performance of the BHI. I gathered data about activity and species richness of bats at 50 sites with known BHI values to 1) see whether field data was significantly correlated with index values, 2) investigate whether any pattern emerged from the sites where index and field data conflicted that might explain this deviation, and 3) discuss the limitations, assumptions and the potential of the BHI to make suggestions for the future development and utilisation of this tool.

Background

Bat activity in proximity to highways

While there is still a lot to be discovered about how exactly bats are affected by roads, several studies observed that bat activity is reduced in proximity to major roads (Kitzes & Merenlender, 2014; Berthinussen & Altringham, 2012). In California, Kitzes and Merenlender (2014) observed a doubling in total bat activity at 300 meters distance from a highway compared to adjacent to it. Individual species analyses revealed that this pattern was consistent for the four most common species (Kitzes & Merenlender, 2014). Berthinussen and Altringham (2012), too, present data from the UK where total bat activity increased with distance from large roads. In their case, activity continued to increase up to 1.6 km away from the road, with activity at 1.6 km being three times higher than directly at the road. This represents a substantially larger scale of impact than what was found in the North American study. The BHI considers the presence of a barrier effect imposed by highways. It does, however, not contain a direct measure of the distance to the highway which means that potential acoustic effects are ignored. In order to account for such effects, the effect of distance was assessed directly in this study.

Sampling efficiency

Systematic inventories yield valuable information about the distribution and habitat requirements of many species (e.g. *Svensk Fågeltaxering*), but they are very costly. Rare or highly specialised species are often missed by systematic sampling (Seber & Salehi, 2013; Hirzel & Guisan, 2002) and this inventory method is therefore not likely to provide much insight into their ecology and distribution. Bats are not distributed randomly in the landscape (e.g. Ducci *et al.*, 2015). One way to make sampling more efficient is to focus field efforts on locations where the probability of occurrence is higher than in other locations. More observations can be made than if sampling is done systematically or even randomly across the landscape (Hirzel & Guisan, 2002). Spatial models or indices predicting those locations, such as the BHI, are a useful tool to make field efforts more efficient.

Habitat selection models

Different methods have been developed to model and predict habitat selection in species of plants, insects and vertebrates. The simpler ones are indices of habitat suitability where the index values depend on the given habitat variables and their importance for the focal species. The researchers decide which variables to include in the model. They can either 1) select variables based on previous literature and additionally conduct their own field study (e.g. Yi *et al.*, 2014; Diuk-Wasser *et al.*, 2010), 2) gather and analyse field data made available by other sources (e.g. Johnson *et al.*, 2016; Bellamy & Altringham, 2015; Rondinini *et al.*, 2011), or 3) create a new model where the variables were chosen based on experts' judgement (e.g. Radinger *et al.*, 2017; Leblond *et al.*, 2014; Yi *et al.*, 2014; Doswald *et al.*, 2007). An ideal model is able to point out areas or habitat variables that are of importance and that, when modified, might substantially impact the species. By highlighting these sensitive areas or habitat variables, such models allow for the prediction of potential conflicts and are therefore a valuable tool in conservation biology in general. The BHI is an index where the importance of habitat types and landscape features is estimated by experts. Rating habitat types and features according to their expected importance for bats and combining them into a final index, the BHI indicates the occurrence of bats based on local habitat quality and regional landscape connectivity without requiring a large dataset from previous inventories.

Habitat selection by bats

The research field of habitat selection by bats has produced a large amount of knowledge about their ecology and behaviour, with increasingly detailed and accurate methods as new technologies are developed (e.g. Kniowski & Gehrt, 2014; Verboom & Huitema, 1997; de Jong & Ahlén, 1991). Most importantly, bats have been shown to concentrate at sites with high abundance of flying insects, which serve as the main food source (Hagen & Sabo, 2012; Fukui *et al.*, 2006; de Jong & Ahlén, 1991). When observing bats in the wild, however, habitat selection due to foraging opportunities cannot be separated from habitat selection due to movement strategies. For example, bats might prefer moving along linear structures because it facilitates orientation or keeping close to higher structures to be less easily perceived by predators. Nevertheless, bats seem to prefer certain structures. Amongst the most utilised habitats are edge zones of open water bodies (Nelson & Gillam, 2017; Wordley *et al.*, 2015; Kniowski & Gehrt, 2014; Seibold *et al.*, 2013). Here, bats do not only find large amounts of insects for feeding, but also drinking water which they require regularly (Seibold *et al.*, 2013). Deciduous and mixed forests, preferably semi-open or in patchy constellations, offer ideal hunting grounds for many bat species and are often used as orientation guides when commuting (Ducci *et al.*, 2015; Kniowski & Gehrt, 2014). Finally, in an otherwise homogeneous landscape, vertical structures such as hedges or tree-lines are favoured for both foraging and movement (Wordley *et al.*, 2015; Ducci *et al.*, 2015; Kelm *et al.*, 2014; Ashrafi *et al.*, 2013; Verboom & Huitema, 1997). Crossings of monotonous cropland, on the other hand, is avoided (Kniowski & Gehrt, 2014). The BHI takes both the insect availability and movement preferences by bats into account.

Methods

Bat Habitat Index (BHI)

The main goal behind the construction of the BHI was 1) to create an index that would correlate with bat occurrence and 2) to separate the reason for bat occurrence into underlying processes. The latter makes it possible to not only predict *whether* bats utilise the habitat, but also *why* they do so. Further conclusions can then be drawn from this insight. The split was done by creating three primary maps, each representing one of the underlying factors, and combining these maps in several steps to create the final BHI. The primary maps are described in detail in the following paragraphs. All the information from these paragraphs is taken from a detailed description on how the BHI was constructed (Oskar Kindvall, Calluna AB, unpublished report from December 2017).

The first primary map was created to represent insect abundance (IA) over all three seasons, because food availability is an important determinant of bat occurrence (Hagen & Sabo, 2012; Fukui *et al.*, 2006; de Jong & Ahlén, 1991).

The second primary map was made to represent the landscape permeability for bats. Bats spend some time commuting between different places such as feeding places and these commuting routes can be crucial for populations at the regional level. For an accurate prediction of bat occurrence, it is essential to know which routes they choose to take. The second primary map was done in the form of flight friction (FF), a measure that is inversely proportional to permeability and which can directly be used in spatial network analyses such as cost distance analyses. FF values range from 0 to 100, where 100 represents highest possible friction or lowest permeability. In addition to predicting local habitat selection, the integration of FF into the BHI allows for more large-scale network analyses and thus makes the BHI not only a local predictor of habitat suitability, but also a predictor of connectivity at the landscape level.

The third and last primary map was created to predict point locations for potential colony sites, which here are defined as nursing colonies for female bats with their offspring. Availability of roosting sites is essential to determine local bat occurrence, independent of foraging opportunities.

Creating these three primary maps from raw input data required several steps. First, the habitat types and structures that are assumed to be of interest to bats had to be chosen. Secondly, each habitat type or structure had to be given a specific value reflecting its importance for the respective variable (insect abundance or flight friction; potential colony sites were only presence/absence points). Finally, depending on the combination of several habitat types or structures, this value had to be adjusted to lead to the best possible prediction. The step of setting values to different habitat combinations is probably the most crucial step in the construction of the BHI and thereby possibly the most important determinant of its overall performance. Depending on the sensitivity of the prediction to different values, small changes might lead to large differences in the final BHI and therefore in its performance. The values given to the different habitat combinations are shown in Table 1. All input data was gathered from publicly available sources to make the future utilisation of the index possible to everyone. The sources were CadasterENV from Metria, different monitoring programs from the Swedish University of Agricultural Sciences (SLU, either directly downloaded from their database or obtained via County Administrative Boards of Stockholm and Uppsala) and from the GSD terrain map from Lantmäteriet. Appendix 1 contains the names of the layers and maps that were used in the creation of the primary maps as well as the sources that made them available.

The different steps for creating the BHI follow the seasonal behaviour of bats. It starts with the spatial distribution of food resources for bats during spring. At this time of the year, bats emerge from hibernation and are in urgent need of large amounts of insects. At the same time, insect abundance is still relatively low (Meyer *et al.*, 2016). Bats are therefore likely to concentrate at sites with large amounts of insects. For a local bat population to survive, however, there must be a certain number of such good patches within a reachable distance. Therefore, a first cost distance analysis was performed, based on the primary map of flight friction and starting at each landscape fragment having value 5 for insect abundance (i.e. richest foraging places). From the resulting polygons, only areas of at least one hectare were selected. These patches were considered functional key feeding habitats during spring.

Later in summer, when the next generation of insects emerges from water bodies and spreads into other areas, bats can find good feeding places elsewhere and start establishing breeding colonies. This dispersal was simulated with a second cost distance analysis starting at the identified functional key habitats. Within the resulting polygons, all patches with an estimated insect abundance of 4 or more were selected. It was expected that bat colonies would only establish relatively close to these rich feeding patches. A third cost distance analysis was applied, starting at these feeding patches. All potential colony sites within the resulting polygons were selected. After all the previous steps, these sites fulfil the criteria of being within reach from spring key habitat patches as well as from good feeding areas for the summer. Starting from these selected colony sites, a fourth cost distance analysis was applied and its result will subsequently be referred to as colony movement (CM). In a last step, the CM was linked to the insect abundance of the respective raster cells in order to create the final index, the BHI. Figure 1 shows a spatial example of how BHI values might look depending on the primary maps of insect abundance, flight friction, potential colony sites and the colony movement. In order to see how different habitat structures were rated in terms of IA and FF (e.g. water body or highway), Figure 1 also includes an orthophoto and a terrain map. Due to its high friction value and a low value for insect abundance, the highway clearly stands out in all index maps.

Table 1. Rating of habitat types and structures according to their assumed correlation with insect abundance and flight friction. *This table is taken with permission from Kindvall's unpublished report about the construction of the BHI. Quality refers to the quality of a habitat for bat foraging, i.e. the abundance of flying insects throughout three seasons of the year. Flight friction is inversely proportional to the permeability of a habitat for bats.*

Habitat type	**Basic quality**	**Added if within pasture**	**Quality if close to water**	**Quality if close to lake**	**Basic friction**	**Friction if close to shoreline**	**Friction if close to forest edge**
Pine forest (not on wetland)	2	1	3	3	10	10	1
Spruce forest (not on wetland)	2	1	3	3	10	10	1
Mixed coniferous forest (not on wetland)	2	1	3	3	10	10	1
Mixed forest (not on wetland)	2	1	3	3	10	10	1
Deciduous forest (not on wetland)	3	1	4	5	5	5	1
Deciduous hardwood forest (not on wetland)	3	1	4	5	5	5	1
Deciduous forest with deciduous hardwood forest (not on wetland)	3	1	4	5	5	5	1
Temporarily non forest (not on wetland)	1	1	2	2	5	5	1
Pine forest (on wetland)	2	1	3	3	10	10	1
Spruce forest (on wetland)	2	1	3	3	10	10	1
Mixed coniferous forest (on wetland)	2	1	3	3	10	10	1
Mixed forest (on wetland)	2	1	3	3	10	10	1
Deciduous forest (on wetland)	3	1	4	5	5	5	1
Deciduous hardwood forest (on wetland)	3	1	4	5	5	5	1
Deciduous forest with deciduous hardwood forest (on wetland)	3	1	4	5	5	5	1
Temporarily non forest (on wetland)	1	1	2	2	5	5	1
Open wet land	3	1	3	3	3	3	1
Arable land	0	1	0	0	60	60	10
Non-vegetated other open land	1	1	1	1	30	30	1
Vegetated other open land	1	1	2	2	5	5	1
Built-up areas	0	0	0	0	30	30	1
Non Built-up areas	0	0	0	0	30	30	1
Inland water surfaces	3	0	3	3	60	1	1
Marine water surfaces	1	0	1	1	60	3	1
Highways	0	0	0	0	100	100	100

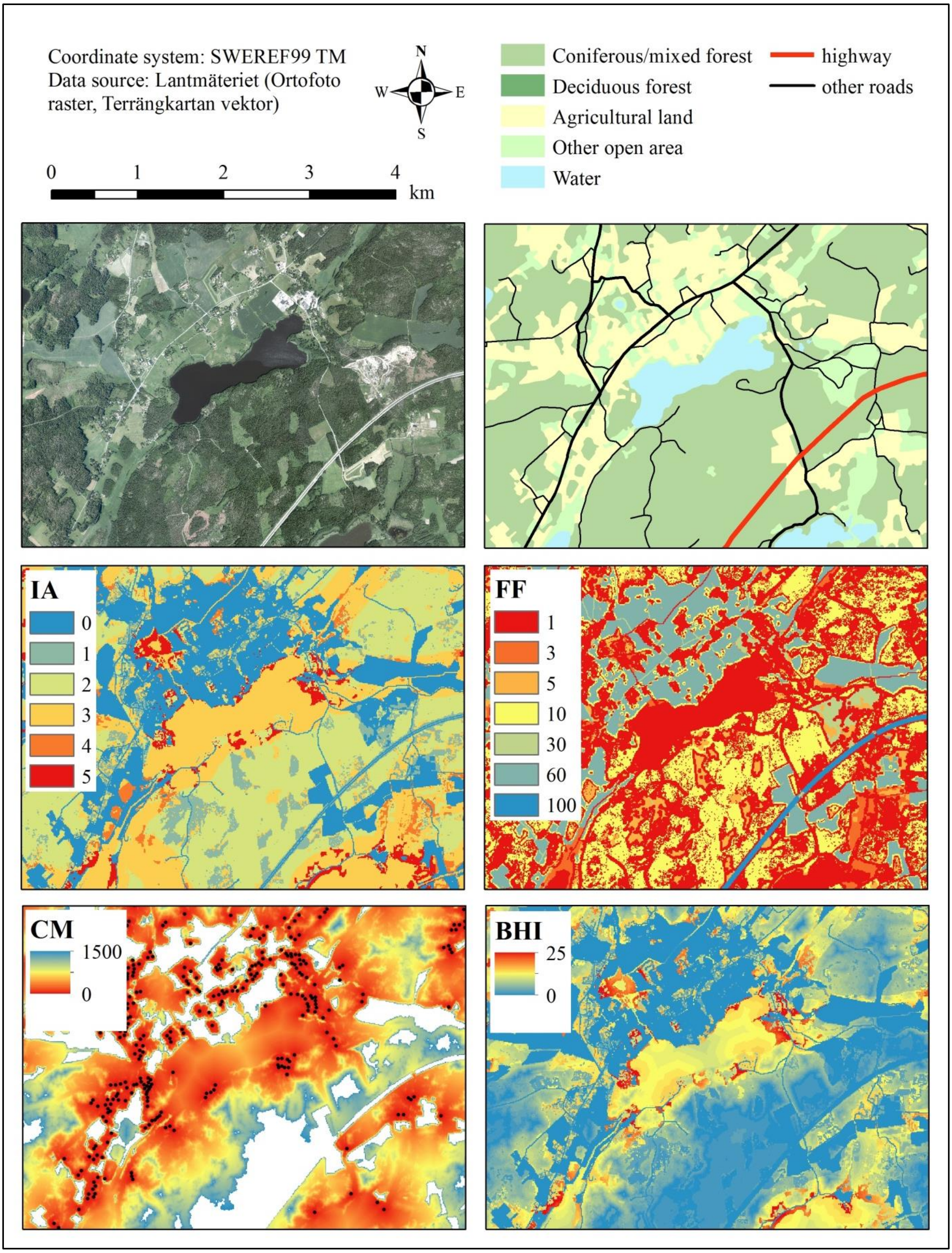

Figure 1. Illustration of different stages of the BHI. *The maps display different variables from the same location. The first row shows an orthophoto (left) and a simplified terrain map (right), followed by the primary maps for insect abundance (IA) and flight friction (FF) in the middle row. Colony movement (CM) on the bottom left represents the penultimate stage in the construction of the BHI; the black dots in this map indicate potential colony sites. The final bat habitat index (BHI) is shown on the bottom right. In all maps, red colour represents favourable conditions for bats, whereas blue colour represents unfavourable conditions.*

Site description and fieldwork

The study area was located around and southwest of Norrtälje in Stockholm County, Sweden (Figure 2), extending to Rimbo in the west and to Brottby in the south. This area was chosen for two reasons. First, all input data were available for the entire area. Second, this area encompasses a large portion of the highway E18, which made it possible to evaluate the importance of a major road for bat occurrence.

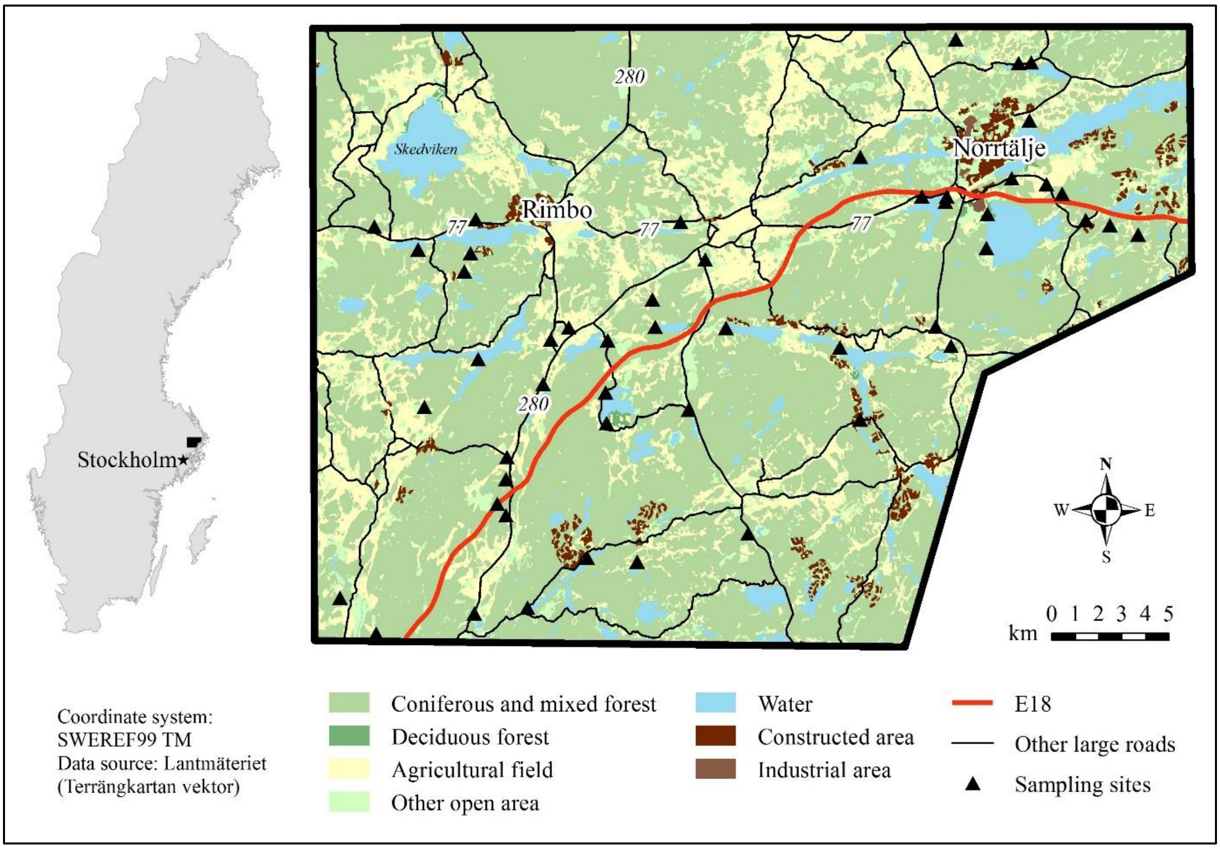

Figure 2. Location of the study area. *The study area, here surrounded by the thick black line, has an area of approximately 850 km² and belongs to the county of Stockholm. The highway E18 crosses the area from southwest to northeast. The 50 sampling sites were distributed according to a stratified random sampling method.*

Sampling sites were chosen according to a stratified random method that covered BHI values across the entire gradient of possible values (0-25) and that positioned the same amount of sites near and far from the highway. In a first step, 1000 points were randomly distributed in the study area with a min. distance of 60 m to each other, using ArcMap 10.4.1 (ESRI, 2016). For each of these points, the mean BHI value of all cells lying within a 30 m radius around this point (BHI_{30}) was extracted (using the function *spatial statistics as table* in ArcMap) and all points were sorted into one of three categories depending on their BHI_{30} values: high (values 17-25), intermediate (8-14) and low (3-6). In addition to the importance of the local BHI, I expected that the interaction between the local habitat (30 m radius) and the surrounding habitat would be important for the number of bats, because a small patch of good habitat would only be used if it lied within a larger good patch. Therefore, the mean BHI of all cells lying within a ring of 170 m breadth around the 30 m radius was extracted to be used as a second variable in the analysis. Based on the mean BHI of the surrounding habitat (BHI_{170}), all 1000 points were further sorted into groups: high (17-25), intermediate (8-14) and low (3-6). To see whether proximity to the road had an effect on the performance of the BHI or the occurrence of bats, the points were further split into two groups, depending on whether they were close to (< 2000 m) or far away from (> 2000 m) the highway E18. In these three steps, the 1000 points were split into 3 x 3 x 2 (= 18) groups. From each of these groups, the two to three random points were picked as sampling locations. Points in the middle of water or open areas were excluded. Due to practicalities in the field, some locations had to be slightly adjusted. Practicalities included finding a suitable tree, avoiding crossing fences or other private ground, or making an agreement with a house- or landowner on where to install a recorder. A list with the coordinates of the 50 final locations as well as their associated index variables can be found in Appendix 3. The distribution of the sampling sites is shown in Figure 2. Every site was inventoried four nights, with the fourth repetition being at least nine days after the first repetition and with an interval of min. two days between two repetitions of the same location (five exceptions where inventories were performed on two consecutive days). All data were gathered during 23 nights between the 3rd and the 27th of July 2017. During this time, average night temperatures were always above 8 °C, total precipitation was less than 3 mm and wind speed never exceeded 3 meters per second (calculated per night from hourly observations between 9pm and 6am; data from the weather station Norrtälje; SMHI). The climatic conditions were judged as suitable for bats and no observations were excluded due to weather.

Twenty D500X Ultrasound Recorders (Pettersson Elektronik, Uppsala) were used to record bat calls. They were placed onto branches of trees at three to six meters height with the microphone facing the direction least covered with leaves, needles or branches. The recorders were set to operate passively at low-power mode from 9.30pm to 4.30am during the first period of the study and after the 16th of July from 9pm to 5am, in order to adjust to a later sunrise and earlier sunset. The device started recording only when a sound above 20 kHz was detected. Recordings were stored as WAV files on a memory card placed inside the box. A minimum intervall of 5 seconds between two consecutive recordings was set in order to avoid emptying the batteries too quickly. Due to an error in the field, unfortunately not all boxes had the same settings for recording length. The majority of the boxes recorded for a 5-second time span, but a few boxes (and more in the beginning of the study) recorded for only 3 seconds each time. The number of recordings resulting from a box with 3-second recordings could not easily be converted to the number of recordings that would have been trigged if recording length was 5 seconds. To nevertheless control for its major effects on the number of recordings, the length of recording was added as a covariate in the statistical models (see Statistical evaluation of the BHI).

Sound analysis

All sound files were analysed using the software Omnibat version 1.16 (Ecocom, 2017). This software visually compares the sonogram of each recording with those of an internal library with confirmed recordings. It calculates the percentage of overlap between the recording and the different categories of the library and then assigns the recording to the category with the highest percentage. This means that a recording containing two species will be identified as the onethat the software estimates to be more dominant. If the overlap does not exceed a certain threshold, the identification by the software is tagged as uncertain. The categories that the software can identify are the different bat species potentially occurring in Sweden, the corresponding bat genera, the bat suborder Microchiroptera or other categories such as crickets, other animal sound or junk. All sound data from this study was in a first step sorted by the software. This facilitated the second step where every file was looked at manually to either confirm or correct the category suggested by the program, and to add species tags where more than one species was recorded. Where species identification required more detailed analysis of call intensity, length or frequency, the software Batsound (Pettersson Electronics) was used. Later during the process of data handling, the identity of the original recording was omitted and only the number of recordings per species kept, which means that a single recording including three different species would in the end count as three bat recordings. Bat calls were identified to the lowest taxonomic level possible. In several cases, the best possible identification was made to genus or order level. The higher taxonomic levels were *Myotis* sp., *Eptesicus* sp., *Nyctalus* sp. and Microchiroptera. Recordings with these identifications were included in the total number of recordings for that given box, but they were counted as a species (in the number of species per box) only if no bat of the same taxonomic group was recorded within the same box. If for example *Myotis* sp. was identified in recordings of a box, but also *Myotis daubentonii* was identified in recordings of the same box, it could not be assumed for certain that the recordings of *Myotis* sp. were triggered by another species. Therefore, the total number of species for that box included only one species of *Myotis*, and not two, even though there is a small chance that one species might have been missed. If, on the contrary, no other species of the genus *Myotis* could be identified to species level within the same box, the total number of species for that box still included one species of *Myotis*, even though the species' identity was unclear.

Statistical evaluation of the BHI

The performance of the BHI was statistically tested using two datasets, both derived from bat recordings during this study. The first dataset contained information about the number of species per site, with a sample size of 50. Three measures of species richness were evaluated: 1) total number of species (number of species recorded at least once during the four nights of recording), 2) number of regular species (number of species recorded during at least three out of four nights, and 3) number of very regular species (number of species recorded in each of the four nights). These variables had to be evaluated at site level, because they were only available when all samples from the same site were included. At site level, the performance of the BHI was assessed using generalised linear models where the response variable (i.e. the different measures of species richness) followed a Poisson distribution.

The second dataset was used to assess bat activity at the level of a box, which means a sample size of 200, but with only 50 independent samples (four samples each from 50 sites). Activity was analysed as 1) the total number of recordings and the guild-specific number of recordings, i.e. the sum of the number of recordings for all species belonging to the respective guild of 2) forest species, 3) aerial hawking species and 4) water-surface species. For these guild-specific analyses, the species were divided largely based on their ecological foraging habitat, i.e. forest (including forest edges and narrow spaces), open spaces and open water. Forest species included all species of the genera *Pipistrellus* and *Plecotus* as well as the species *Myotis brandtii/mystacinus* and *M. nattereri*. The guild of aerial hawking species (i.e. open space hunters) was composed of the genera *Nyctalus*, *Eptesicus* and *Vespertilio* and the group of water-surface bats comprised *Myotis daubentonii* and *M. dasycneme*. Ambiguous identifications such as *Myotis* sp. and Microchiroptera were ignored. In addition to these measures of activity, the number of species recorded during the given night was also assessed. Analyses at box level were performed using generalised linear mixed models (GLMM; *glmer* function from the *lme4* package; Bates *et al.*, 2015) with number of recordings/species as Poisson-distributed response variable. Sampling site and box were treated as random effects factors, because observations from the same site are not independent of one another and because boxes can differ in sensitivity which might result in different detection probabilities (Dietz & Kiefer, 2016). Because bat activity was significantly correlated with the date, the day since the beginning of the study was added as covariate in all models of this dataset. Length of recordings was included as a covariate in the models for total activity, activity of forest species and activity of aerial hawking species, because it significantly affected the response. Like this, it was possible to account for some of the variance caused by the different recording lengths. The models for total activity and activity of aerial hawking species also included a significant interaction between date and recording length, because there had been more boxes with shorter recording lengths in the beginning than in the end of the study.

For both datasets, the predictor variables of interest were extracted from maps in different stages of development in the construction of the BHI. Values were taken from the primary maps for insect abundance (IA) and flight friction (FF), the penultimate step of the construction of the BHI, called colony movement (CM), and from the final index (BHI). For each sampling site, mean values of the BHI, IA, FF and CM were calculated for areas of 30, 200 and 500 m radius around the position of the box (notation BHI_{30}, IA_{200} etc.) to explore the influence of scale. The BHI value was also averaged over a circular ring of 170 m breadth surrounding the 30 m radius. Additionally, the shortest distance between each site and the highway E18 was calculated. All statistical analyses were performed in R (R Core Team, 2017). In order to assess the effect of the highway, it was tested in addition to and in interaction with values of BHI. All explanatory variables can be found in Appendix 3 together with the geographic coordinates of the sampling sites.

For each statistical model, the Akaike Information Criterion (AIC; Akaike, 1998) was extracted and the bias-corrected AICc for small sample size was calculated (according to recommendation by Burnham & Anderson, 2002). Within each set of models (i.e. all models sharing the same response variable), the difference (Δ) in AICc between each model and the model with the lowest AICc was calculated. The ΔAICc has the advantage of being a standardised measure of model performance and therefore allows comparison between sets of models with different response variables. The best models (lowest AIC or ΔAICc = 0) were selected and statistical significance and effect sizes were extracted to be discussed in this thesis. Correlation between response variables was assessed with a Pearson correlation test.

Results

Species occurrences

In a total of 48 205 recordings that were triggered during this inventory, 16 030 bats could be identified. The other recordings contained sounds made by other animals (primarily bush-crickets), rain or human-induced sounds like traffic noise. In total, twelve different bat species were recorded. A complete table with the number of recordings per species for each box is given in Appendix 2. The species observed at most sites were the Northern bat *Eptesicus nilssonii*, the Common noctule *Nyctalus noctula* and the Soprano pipistrelle *Pipistrellus pygmaeus* (48, 46 and 44, respectively, of a total of 50 sites; Figure 3). The Northern bat and the Common noctule were also the most active species, together representing 71 % of all recordings (n = 16 030; Figure 4). Because both species belong to the guild of aerial hawking bats, this species group was also by far the most active (74 % of all recordings; Figure 5). On the other extreme of the spectrum, the Nathusius's pipistrelle *Pipistrellus nathusii* was only recorded 18 times and the Pond bat *Myotis dasycneme* only three times.

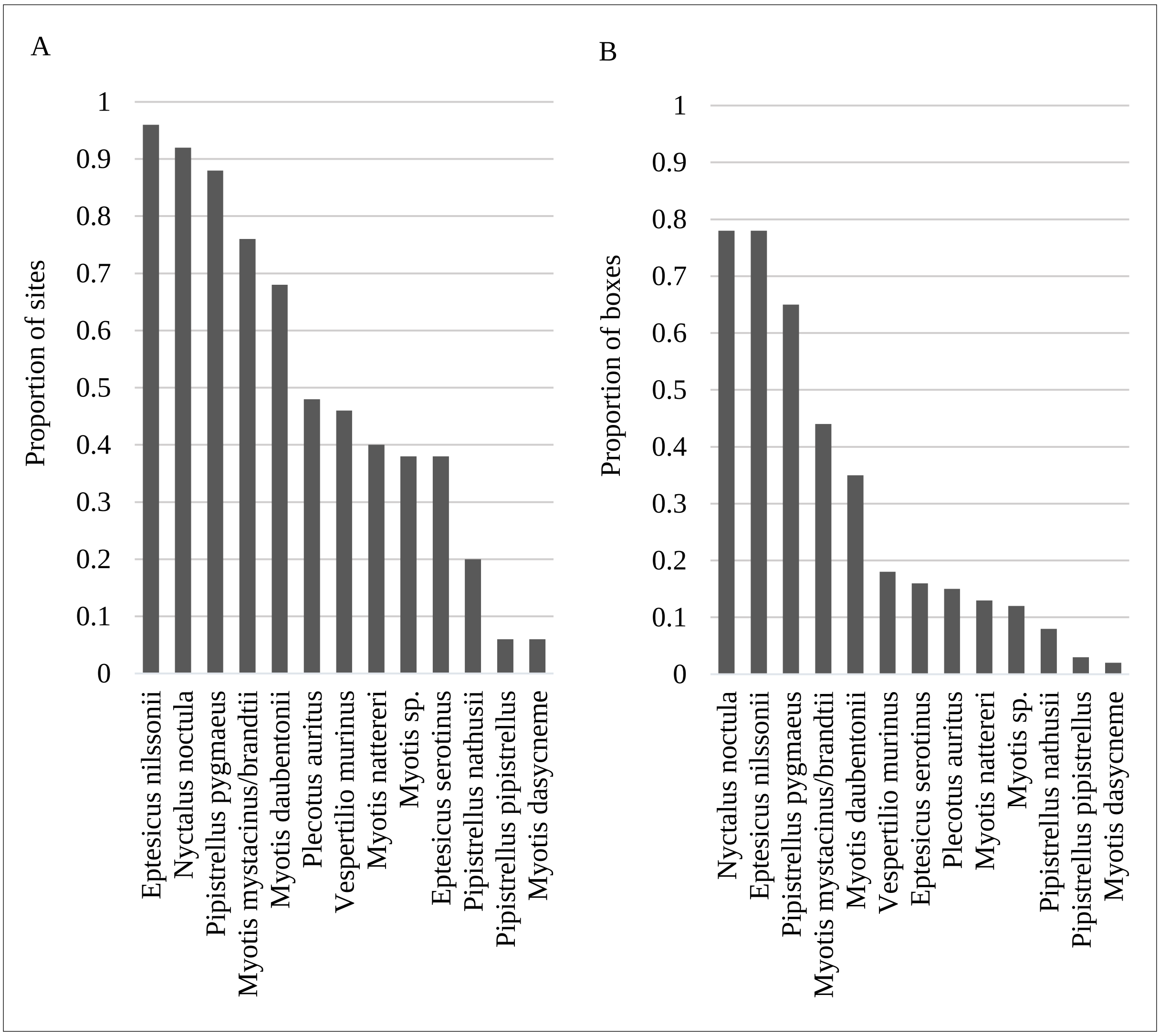

Figure 3. Proportion of sites (A) and boxes (B) where species were recorded. *The proportion of sites (n = 50) and boxes (n = 200) represents the number at/in which a species was observed at least once. The two aerial hawking species Northern bat* (Eptesicus nilssonii) *and Common noctule* (Nyctalus noctula) *and the forest-living species Soprano pipistrelle* (Pipistrellus pygmaeus) *were the most common species, both in the geographical extent and in the overall occurrence in boxes.*

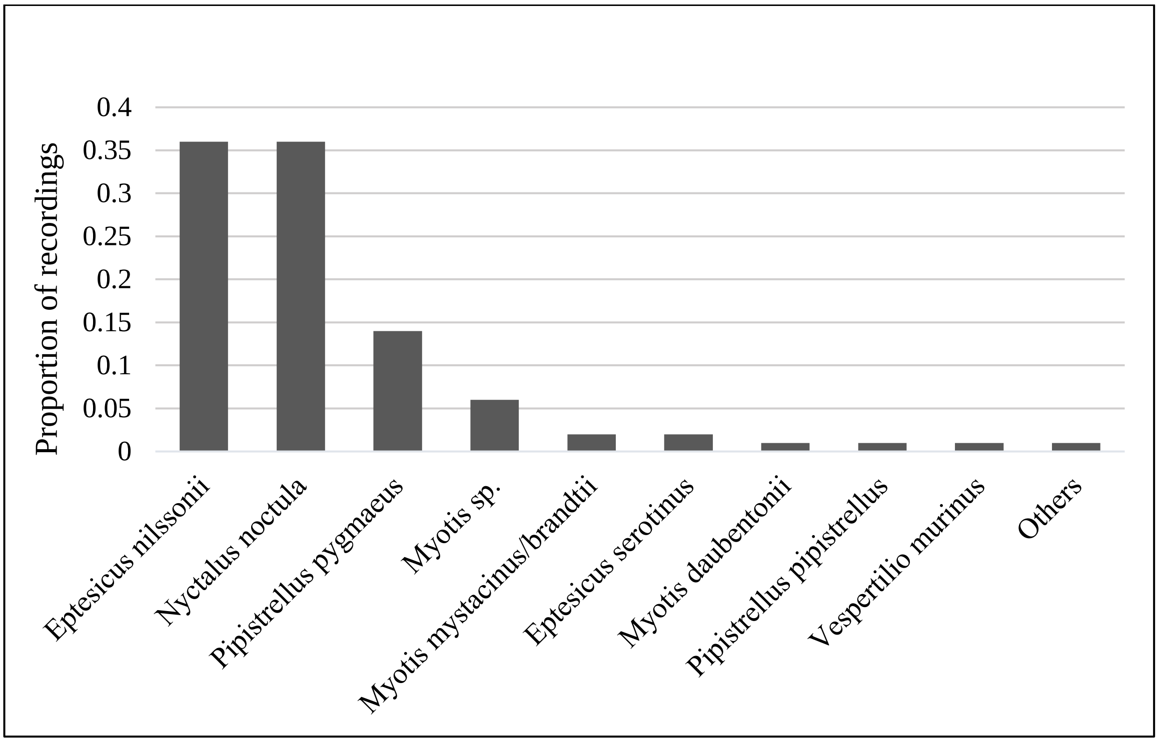

Figure 4. Recording frequencies of different species. *The bars represent the proportion of recordings for each species (or taxonomic unit) compared to the total number of recordings (n = 16 030). All species with less than 0.01 % of all recordings are summed together.*

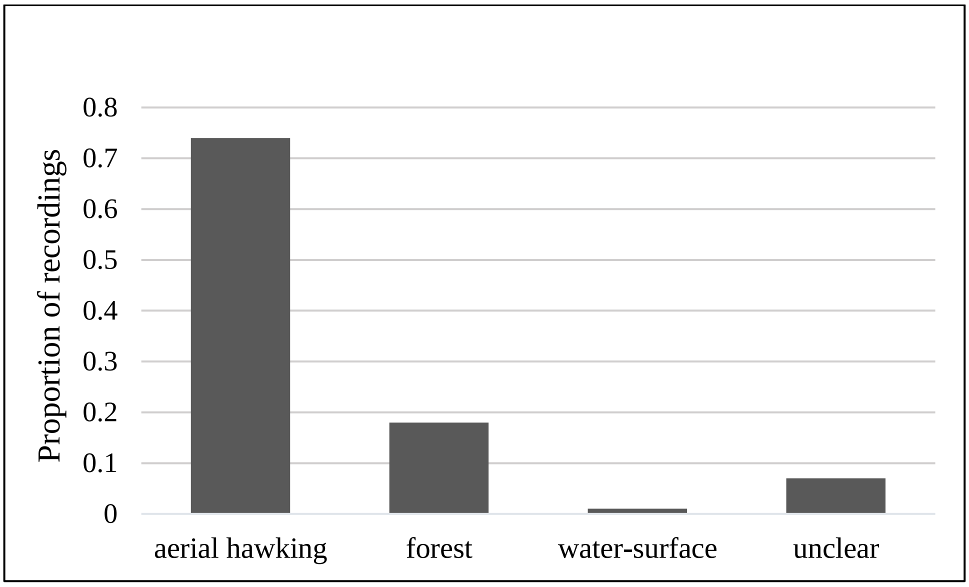

Figure 5. Recording frequencies of different ecological guilds. *Bars represent the proportion of recordings for each guild compared to the total number of recordings (n = 16 030). Recordings of* Myotis *sp. or Microchiroptera were ambiguous and could therefore not be assigned to any of the guilds.*

Statistical evaluation of the BHI

For all measures of species richness, the model consistently performing best was the one with CM_{30} as the single independent variable (Table 2). The correlation was not significant for the total number of species (p-value = 0.198), but highly significant for the number of regular species and the number of species per night (p-values of 0.00467 and 0.001148, respectively) and very highly significant for the number of very regular species (p-value = 0.000378; Table 3).

For the total activity, the best-performing model included the explanatory variables BHI_{200} (p-value = 0.0551), distance to the highway (p-value = 0.0248) and their interaction (p-value = 0.0694). The same variables were included in the best model for the activity of forest species; BHI_{200} (p-value = 0.00169), distance to the highway (p-value = 0.36693) and their interaction (p-value = 0.01934). The best-performing model for the activity of aerial hawking species included only CM_{30} (p-value = 0.0129). FF_{30} was the only significant predictor of activity of water-surface bats, but all models with this response variable were strongly zero-inflated (129 data points of 200 had the value 0) and this result is therefore not discussed here, because it might not be reliable.

Total activity per night was significantly correlated with the number of species recorded (Pearson's r = 0.44, p-value < 0.001) and the total number of species per site was significantly related to the number of very regular species (r = 0.54, p-value < 0.001) and regular species (r = 0.6, p-value < 0.001).

Table 2. Comparison of ΔAICc values of statistical models. *The first column shows which variables were included in each model and whether they were tested separately, in addition (+) or in interaction (*). The variables were bat habitat index (BHI), flight friction (FF), insect abundance (IA), colony movement (CM) and distance to the highway E18 (dist). The subscript stands for the area over which the respective values were averaged, 30, 200 and 500 (m) refer to the radius of a circle surrounding each site. All models in the first three columns were based on a sample size of 50 (i.e. one observation per site). Models in the last five columns were based on a sample size of 200 (i.e. one observation per box). The best models are marked with dark grey colours; light grey colours indicate ΔAICc values smaller than 2. Models where ΔAICc values were larger than 2 for all response variables are not shown.*

	n = 50			n = 200				
Explanatory variables	**Total number of species**	**Number of regular species**	**Number of very regular species**	**Number of species**	**Total activity**	**Activity forest species**	**Activity aerial hawking species**	**Activity water-surface species**
BHI_{30}	0.73	5.16	9.90	4.61	5.23	6.38	5.26	6.11
BHI_{200}	1.00	4.99	9.00	5.64	3.16	1.49	4.68	4.23
BHI_{500}	1.68	6.00	10.87	8.23	5.70	5.63	5.75	6.14
FF_{30}	0.69	6.54	12.32	6.03	6.78	8.31	5.65	0.00
FF_{200}	1.62	8.74	16.52	9.97	6.50	10.53	5.07	7.41
FF_{500}	1.09	8.89	16.19	9.90	6.03	10.71	4.49	8.02
IA_{30}	1.59	8.43	15.49	8.82	6.77	9.99	5.62	7.54
IA_{200}	1.46	7.48	13.20	8.32	5.77	4.55	5.83	5.74
IA_{500}	1.71	7.81	13.11	9.32	6.68	7.58	5.64	7.00
CM_{30}	0.00	0.00	0.00	0.00	0.21	4.90	0.00	4.28
CM_{200}	0.81	3.40	8.70	4.78	0.78	5.11	0.91	5.28
CM_{500}	1.67	4.93	12.02	7.82	3.50	7.54	3.67	6.17
BHI_{30} + dist	1.35	7.37	11.53	4.94	3.63	8.09	4.90	7.85
BHI_{200} + dist	1.62	7.19	10.62	6.06	1.02	2.98	4.14	5.89
BHI_{200} + dist + BHI_{200}*dist	3.27	9.46	12.42	7.99	0.00	0.00	5.06	5.01

Table 3. Effect sizes and significance levels of the best-performing models. *Only those models with ΔAICc values of 0 were investigated for effect sizes and significance of effects. Total number of species, number of regular species and the number of very regular species were tested using the dataset with 50 samples (one per site), the other response variables were tested using the dataset with 200 samples (one per box). Grey colours highlight the variables, their effect sizes (i.e. estimate) and the p-values for their effects. Random effects factors and covariates are not shown.*

Response variable	**Residual deviance**	**Df**	**Explanatory variables**	**Estimate**	**SE**	**Z-value**	**P-value**	
Total number of species	27.4	48	CM_{30}	-0.0003	0.0002	-1.287	0.198	ns
Number of regular species	43.9	48	CM_{30}	-0.0012	0.0004	-2.829	0.00467	**
Number of very regular species	48.6	48	CM_{30}	-0.0022	0.0006	-3.555	0.000378	***
Number of species	769.2	195	CM_{30}	-0.1737	0.0534	-3.252	0.001148	**
Total activity	5063.3	191	BHI_{200}	0.3443	0.1795	1.918	0.0551	.
			dist	-0.3958	0.0176	-2.244	0.0248	*
			BHI_{200}*dist	-0.3760	0.2071	-1.816	0.0694	.
Activity forest species	2048.7	192	BHI_{200}	0.5649	0.1799	3.139	0.00169	**
			dist	-0.1588	0.1761	-0.902	0.36693	
			BHI_{200}*dist	-0.4846	0.2072	-2.339	0.01934	*
Activity aerial hawking species	3982.7	193	CM_{30}	-0.5826	0.2343	-2.487	0.0129	*
Activitiy water-surface species	466.5	195	FF_{30}	-0.6877	0.2545	-2.702	0.0069	**

Discussion

This study evaluated the performance of the BHI, a habitat index for Swedish bats, by correlating bat occurrence data with predicted index values. The results suggest that the index performs well when predicting the number of regularly occurring species as well as the activity of forest-living species. In the following sections, I discuss the find of an unexpected species, I make suggestions for improvement of the predictions for overall species richness and overall bat activity and I discuss the strength, the potential and the limitations of the BHI.

Species occurrences

Twelve bat species were recorded during this inventory (counting the species complex of *Myotis mystacinus/brandtii* as a single species). Out of 13 bat species known to occur in the county of Stockholm, only the presence of Barbastelle *Barbastella barbastellus* could not be confirmed. As Whiskered bat *Myotis mystacinus* and Brandt's bat *M. brandtii* are acoustically indistinguishable, their presence could only be confirmed at the level of their species complex. It is worth mentioning that the Common pipistrelle *Pipistrellus pipistrellus* was recorded 170 times at three different sites, of which one site was frequented every night. These observations represent so far the most northern finds of this species in Sweden (compared to its distribution range given by Ahlén, 2011). Because of its very restricted distribution range and small population size, it is categorised as Critically Endangered on the Swedish Red List (Artdatabanken, 2015). The sudden appearance of the Common pipistrelle this far north could be an indication that the species is increasing in population size and expanding its distribution range. When including the observations of *Pipistrellus pipistrellus,* the total number of species recorded in the county of Stockholm is now 14.

Statistical evaluation of the BHI

Prediction of species richness

For all measures of species richness, models with the BHI as explanatory variable performed worse than models with the colony movement variable (CM). This result suggests that the last step in the creation of the BHI should be omitted. The last step is the overlay of the colony movement with insect abundance, where colony movement is the result of a cost distance analysis that started from the selected colony sites. Once the possible colony sites have been selected (based on insect abundance and landscape permeability), the local permeability alone is apparently enough to predict occurrence of bats. This could be based on the fact that areas that contain potential colony sites have already been selected for high insect abundance in previous steps. When focusing only on these insect-rich areas, there may be enough insects anyway so that bats can follow their habitat preferences instead of having to balance feeding efficiency with flying preferences.

The BHI performed much better at predicting the number of very regular species than the total number of species. This suggests that either the habitat structures included in the BHI are of primary importance in determining the regular use of a site or that the scale at which these structures play a role is well represented in the index. The opposite seems to be true for species occurring only once or twice. Partially, this difference might be due to species passing the site on their way to another place (i.e. only few recordings compared to many recordings that would be triggered by foraging behaviour). It is also possible, however, that the choices of these individual bats depend on factors not included in the BHI at all, such as population dynamics. If the BHI is supposed to realiably predict the total number of species, it might be necessary to include further parameters and processes into the index.

Prediction of activity

The BHI variable in the model for overall bat activity only had a marginally significant effect on the response. When instead predicting the activity of only forest-hunting species, the BHI had a highly significant effect. These results suggest that the relative weighting of habitat types underlying the BHI does indeed represent habitat preferences of forest bats better than those of aerial hawking or water-surface bats. As these species are amongst the more vulnerable bats, both in terms of conservation status and affectedness by habitat modifications (Artdatabanken, 2015; Trafikverket, 2015), this bias of the BHI might be desirable for its future use.

For the interpretation of the BHI's predictions, it is essential to know at which scale its underlying factors operate. The only way to evaluate this is to compare the BHI's performances at different scales. The results suggest that the scale at which the BHI works best depends on what it is supposed to predict. All measures of species richness were best predicted at a scale of 30 m radius. The same was true when predicting the activity of aerial hawking species. For both the total activity and the activity of forest species, however, the BHI performed best at a scale of 200 m radius. This pattern is surprising. Assuming that foraging individuals triggered the majority of the recordings, I would have expected overall activity to be dependent on habitat characteristics at smaller rather than at larger scale. In contrast, I would have expected the number of species to be better explained by large-scale habitat factors, because I expected that the number of species would increase due to commuting (not foraging) individuals and that commuting behaviour, in turn, would depend on the availability of foraging sites in the surrounding environment. Unfortunately, I cannot find any explanation for this counterintuitive result.

When deciding the location of the sampling sites, the distance from each potential site to the highway E18 was calculated and an equal amount of sites was selected close to (< 2000 m distance) and far away (> 2000 m) from the highway. Originally, this threshold was chosen because Berthinussen and Altringham (2012) found an increase in bat occurrence up to distances of 1600 m from a highway and I wanted to make sure to sample sites across this entire distance and beyond. Berthinussen and Altringham (2012) did not directly investigate the factors leading for their result, but it is likely to be a combination of barrier effects and effects caused by traffic noise and light. In the BHI, the barrier effect of the highway is already accounted for in the final index values, because the highway is assigned the highest friction of all habitat types. It does moreover consider the suitability of the habitat offered by the road itself. Effects not included in the BHI values are those caused by traffic noise and lights of cars or street lamps. The distance to the highway was tested as additional predictor variable in the statistical models to see whether the road had any effect on bat occurrence that the BHI had not accounted for. A positive effect of the distance to the highway on bat activity in the statistical model would have suggested that there is a stronger effect of the highway than is included in the BHI. This result would have provided an indication for the strength of this effect, which in turn could have been used to adjust the values that go into the BHI. The estimated effect of distance on overall bat activity, however, was negative (-0.396). The total number of recordings was higher closer to the highway when the variance explained by the BHI was removed. Although unexpected, there are two possible explanations for this negative effect of distance to highway on bat activity. The first one is that the highway indeed represents such a strong barrier that bats concentrate on both sides on their way to new hunting or breeding grounds, because they cannot cross the road directly and therefore fly along it in search of a possibility to cross. For two reasons, this explanation does not seem to be the best in this case. First, such a concentration would happen within the first few hundred meters from the road. This scale is only represented by three sites in this study (three sites at less than 300 m from the highway) and it is unlikely that the present analysis had the statistical power to detect such an effect. Second, the BHI focuses on bat movement during summer, particularly predicting the movement of reproducing females. As they are bound to a central place (colony site), females tend to hunt in proximity to the colony, often revisiting the same hunting grounds (Dawo *et al.*, 2013). This implies good knowledge of the surrounding habitat and suggests that the roosting site was selected in acquaintance with foraging areas that lie within reach. Colony-based females are unlikely to try to cross the highway every night in search for other foraging areas, because this behaviour would only imply a cost in valuable time that they could otherwise spend on feeding. The only bats who would therefore move along the highway in search for a crossing are bats on the move to an entirely new place. As this study was performed in the the middle of summer, i.e. the peak of bat activity and reproduction, I estimate it unlikely that there were sufficiently many dispersing bats to explain the negative effect of the highway on bat activity. In my opinion, the second and more plausible explanation for the observed results lies in the values defined for the flight friction of the highway at the base of the BHI. When creating the BHI, it was assumed that the highway represents an almost unpenetrable barrier for bats (see Table 1). The highway might, however, be *more* penetrable than initially expected (and any other negative effects together would not equal the difference between the real and the expected barrier effect). In this case, the BHI would underestimate bat activity in proximity to the highway. This indicates that the overall effect of the highway on bat activity is overestimated by the BHI, without being able to separate between barrier and other effects. The conclusion to draw from this is that increasing the permeability of the highway in the flight friction map might be a way to improve the BHI's performance.

Interpreting the BHI

Two underlying processes

The big advantage with the BHI is that it splits the prediction of bat occurrence into two separate processes thought to be underlying this occurrence; food availability and flight friction. By taking flight friction into account, the index includes a measure of connectivity. In an increasingly fragmented landscape, connectivity is important for the persistence of populations and species (Rocha *et al.*, 2017; Dool *et al.*, 2016). Especially in the planning of large infrastructure projects, e.g. construction of new highways or railway roads, connectivity is an important factor when assessing potential environmental impacts because the planned structure crosses the area and therefore might significantly reduce the connectivity for some species (Trafikverket, 2015).

As opposed to the BHI, other habitat selection models are created by simply correlating the occurrence of a species with local habitat characteristics, so called species distribution models (e.g. De La Cruz & Ward, 2016; Razgour *et al.*, 2011). Whereas these models have the advantage of being based entirely on empirical data, they do not take connectivity *between* different sampling sites into account. It is therefore not possible to distinguish between a site used for foraging and a site used as a movement corridor. The same is true for inventories that assessed bat activity. Both with a simple habitat model or with inventory data, a site used for commuting only might appear less important than a foraging site because bats do not spend an equal amount of time there. Depending on the landscape and the distribution of structures, this conclusion might be wrong. Some of the foraging sites might only be accessible due to a small movement corridor that allows bats to reach all the other sites. Figure 6 shows a hypothetical example of such a landscape and illustrates how the BHI is able to detect the importance of connectivity where other habitat models or simple field inventories would not. By comparing the final BHI map with the underlying map for flight friction, one would be able to distinguish between a site used for foraging (high BHI) and a site used for movement (very low flight friction and with high flight friction on both sides). Alternatively, the BHI could be calculated twice for the area of interest, once with a landscape at its current state, once including the planned modification (e.g. highway cutting through the landscape). Allowing the visualisation of landscape connectivity and the importance of movement corridors is the strength of the BHI and makes it very suitable for impact assessments in an ever more fragmented landscape.

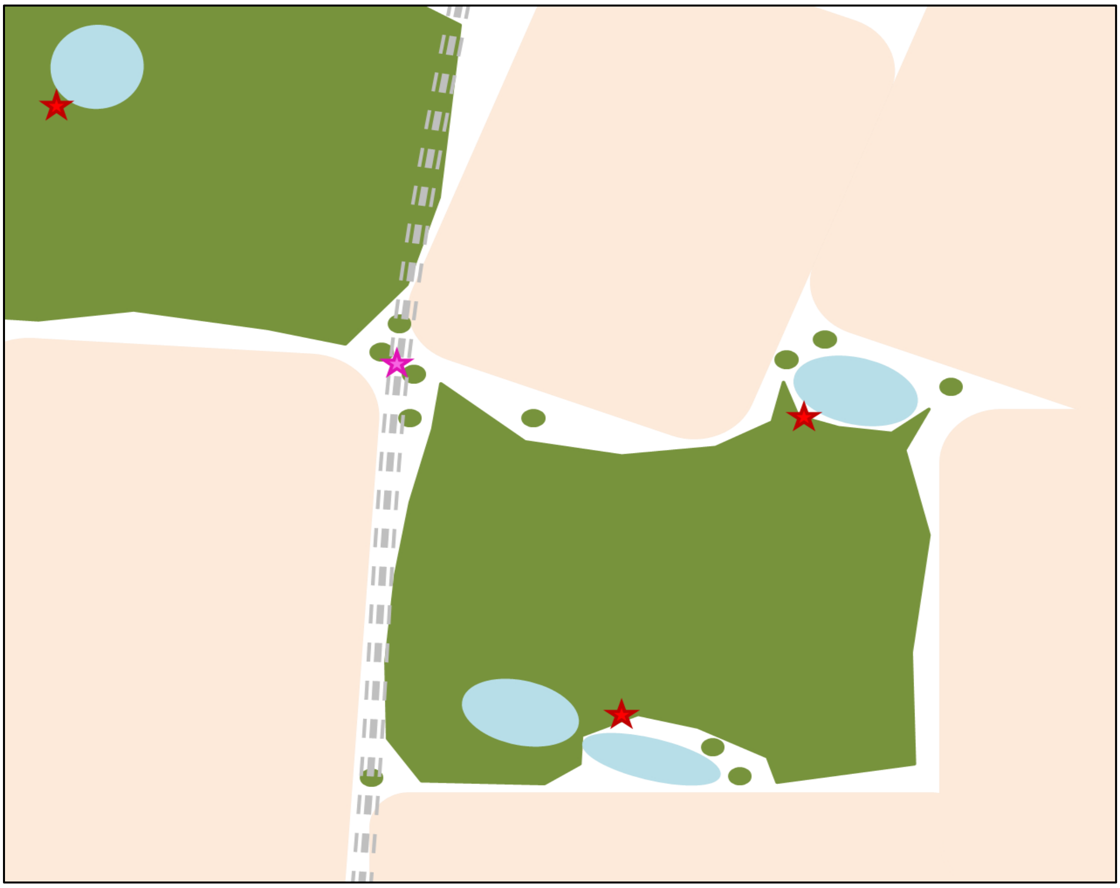

Figure 6. Hypothetical landscape illustration. *This hypothetical landscape illustrates the importance of connectivity between suitable sites and the potential of different assessment methods to detect the importance of movement corridors. Beige represents agricultural fields (unsuitable habitat for bats), green stands for suitable forest habitat, blue shows surface waters, the dashed grey line shows the suggested position of a new highway and the stars show the position of sampling sites. Bat activity is probably much higher at the red sites than at the road site (pink). Also habitat suitability, based on presence or absence of habitat structures alone, would be much higher around the lakes than in that small stretch of trees connecting the two patches. However, the only reason why bats can be present at the two red sites to the right is because this small stretch of trees at the pink site allows them to reach them. A look on the map of flight friction of this area would make it obvious that this small stretch of trees is crucial for connectivity of the landscape for bats.*

Potential vs. occurrence

When interpreting the BHI, it is important to keep in mind that it is not per se an index of bat *occurrence*, but rather an index of *potential occurrence*. It assumes that only insect abundance, flight friction and the presence of potential colony sites determine bat occurrence. This assumption can hardly be met for any species. In addition to variations between years and random events (stochasticity), which occur independent of habitat characteristics, there are also behavioural factors which are not included in the BHI. Some bats, for example, use a certain core area of their home ranges exclusively (e.g. Dawo *et al.*, 2013). If there are several potential colony sites within flight reach from each other, such a species would require the other places to be empty. Even more bat species need and use an entire network of roosting sites over a reproductive season, because roosting sites are switched every couple of days (Kühnert *et al.*, 2016; Willis & Brigham, 2004). This would mean that potential colony sites would be empty when the inventory takes place, even though they are utilised at another time. Because the BHI does not consider those factors, there will always be a certain error in its predictions.

Summer index for females

The BHI is tailored to predict habitat use of individuals bound to central places (here, i.e. colony sites) during summer. In bat terms, this is equivalent to saying that it focuses on the habitat use of pregnant and lactating females. Potential roosting sites for solitary or small groups of males as well as any habitat use by those is ignored. Also, the BHI is designed to predict bat occurrences during summer. It identifies key foraging habitats during spring but does not predict areas for foraging and mating in autumn nor the location of hibernating sites. A location with low BHI values can therefore not directly be interpreted as never being utilised by bats. The BHI focuses on summer foraging as reproductive success depends largely on conditions encountered during this period.

Geographic comparability

The BHI should be interpreted as a relative index within a region. The number of species differs strongly along a north-south gradient through Sweden with all 19 species being present in the south and only one in the north (Ahlén, 2011). Index values in the south should therefore not be directly compared to index values far north, because the maximum possible number of species is not equal. With increasing latitude (and thereby decreasing species richness), the index might steadily lose power in predicting species richness as the maximum possible species richness approaches one, but might stay useful in predicting abundance or habitat use. As a rule of thumb, index values should only be compared at a local to regional scale, i.e. in areas not larger than 25-30 km (like this study) to ensure similar conditions for species composition.

Evaluating the BHI

Detection probability

It was mentioned previously that the BHI predicts the *potential* occurrence rather than the *actual* occurrence of bats and that occurrence data, as gathered in this study, are therefore suboptimal for evaluating its performance. To be yet more precise, the data gathered do not exactly represent the actual occurrence of bats within a strictly defined area; instead, the data represent the bats that were recorded by the bat boxes located at a defined spot. When designing the study, it was assumed that the average distance at which bats would be recorded was 30 meters. This distance, however, depends strongly on the type of habitat surrounding the box. In dense vegetation the distance is shorter while in open areas like fields the distance is considerably larger (Dietz & Kiefer, 2016). The distance also depends on the species. Aerial-hawking species like the Common noctule *Nyctalus noctula* emit calls that are at the same time very high in volume and very low in frequency (17-22 kHz) which makes them detectable by bat boxes at up to 80 m distance (Dietz & Kiefer, 2016). Other species like the Brown long-eared bat *Plecotus auritus*, on the other hand, call so quietly that they can only be recorded at a few meters distance (ca. 5 m; Dietz & Kiefer, 2016). The BHI takes neither variation in habitat structure nor calling properties of different species into account. Both affect the detection probability of bats in the field and might therefore explain some of the residual variance. Including vegetation density in the statistical models would probably have improved the model fit to the data. I suggest that future studies take measurements of vegetation density at all sampling sites and control for it in the analysis.

Not sampling any locations with prediction 0

When choosing potential sampling sites, the randomised points were sorted into three categories, with low, intermediate and high average BHI. The lowest category started with the minimum value 3, because most locations with lower BHI values fell into agricultural fields or open water. As all recorders were supposed to be hung up in trees, it did not seem possible to sample such locations. In retrospect, it would have been very informative to *specifically* sample locations where the BHI is very close or identical to zero. If reality deviates from the prediction in these locations, it might be highly desirable to adjust the index accordingly. Knowing which sites are certainly not worth being sampled would be a big advantage and should certainly be done in future evaluations.

Weather

Weather conditions during the study period were judged as suitable for bats and were not further included in the statistical analysis. Nevertheless, variation in these conditions might have led to slight differences in bat activity and could explain some of the residual variance. As the sample size was already relatively small compared to the number of parameters statistically evaluated, I refrained from including weather in the models, as I did not consider it a priority. With a larger sample size, however, I would recommend to at least include temperature, precipitation and wind speed as environmental covariates.

Optimising the BHI

Setting the goals

At its current state, the BHI correlates with both bat activity and the number of regular bat species. For its further development, the first and most important step would be to clearly define the goals. There are at least two key goals to be defined. The first one is the species-specificity. The present BHI is designed as an index for overall bat occurrence. It is neither specific to a single species nor represents an actual average over all species in Sweden. The habitat preferences of forest-living bat species were intentionally weighted more strongly in the BHI than the preferences of other groups, because conflicts occur most frequently with those species (Trafikverket, 2016). Predictions of such an index are, however, difficult to interpret and lead to larger errors, which is why smaller focal groups might be preferable. Species-specific indices would be of great value, but are difficult to obtain due to a lack of detailed information for rare species. One suggestion to narrow down the focal group is to create guild-specific indices. The ecological differences between the focal species would be minimised (which would make predictions more precise and easier to interpret) at the same time as more problematic groups such as forest species could be targeted explicitly.

The second goal that needs to be defined is which measure of bat occurrence the BHI is supposed to predict. If the focus should be on activity, there are different measures of activity to choose from: activity of single species, single guilds or total bat activity. If the number of species is considered a more useful tool, the decision has to be made between regular species and all species. Although these are significantly correlated, this correlation might not be tight enough to use either as a surrogate for the other. So far, the BHI is much better at predicting the number of regularly occurring species (p-value < 0.001 vs. 0.198). In decision making, single observations of rare species are often a more powerful argument against exploitation than the regular occurrence of common species. Therefore, there might be more use in optimizing the index towards predicting the total number of species rather than the number of regular species. Occurrence of rare species, however, might be strongly influenced by population dynamics (e.g. low overall population size) and stochasticity. Both make an accurate prediction difficult and would require the inclusion of additional parameters into the BHI. In any case, deciding on what the index should predict before it is further developed would guarantee a goal-oriented and efficient working effort.

Optimising the primary maps

The BHI's performance depends on the accuracy of the primary maps of insect abundance, flight friction and available colony sites. The values for insect abundance and flight friction are, for the moment, set manually according to the best available information and expert estimation. If the rating of habitat types or structures does not correspond to reality, this has direct implications for the performance of the index. Ideally, the underlying factors would be evaluated separately. To find the ideal values for insect abundance, for example, a study could be designed where insect abundance is sampled in all different habitats included in the primary map. Flight friction, on the other hand, is more difficult to test, because in the real world, movement behaviour of bats is not based on flight preferences alone. Bats sometimes also feed during commute flights, which suggests that they are at the same time selecting for low friction and high food availability. These two processes can therefore not be entirely separated which makes the empiric evaluation of the flight friction map difficult.

There are other ways of finding the ideal combination of values; a powerful computer could generate the BHI output of all possible value combinations and could fit a dataset of empirical bat observation data to the BHI. The combination that would lead to the best fit of the BHI to the empirical data would be the best possible combination. The advantage of this method is that all combinations would be tested. It does, however, require a very powerful computer, given the number of possible combinations, and a very large sample size.

Alternatively, an optimizing algorithm could be used to find the combination of values that leads to the best fit with the emprical data. Such an algorithm would start with one combination of values and then apply a change of one unit to one of the values at the time. If predictive power improved (model fit of empirical data to BHI), the next value is modified. Instead, if the first change led to a loss in predictive power, the change is reversed, and another parameter is modified. This procedure continues, until the best value combination is reached. As this method settles with one parameter as soon as its value is locally optimised, not all combinations are tested, and the method does therefore not require an equally powerful computer. The fact that not all value combinations are tested, however, is at the same time a disadvantage, because it means that the algorithm can get stuck in a local optimum, never reaching the best combination. This could be avoided by allowing the algorithm to make larger modifications every couple of steps, e.g. changes by two or three units (Lin *et al.*, 2012). Such algorithms are commonly used in the evolutionary research field (e.g. Yu & Gen, 2010), with the aim to find the relative contributions of different factors such as natural selection, mutation or recombination to the direction of evolutionary change. These two optimizing methods are purely mathematical and will not necessarily lead to the combination of values that correlates best to the actual abundance of insects or flight friction for bats. Nevertheless, it might improve the BHI's performance and, if tested on a large enough data set, could make the BHI a more reliable tool for predicting bat occurrence.

The performance of the BHI is strongly dependent on its accuracy at predicting potential colony sites (third primary map). A too generous definition of potential colony site might lead to an overestimation of bat occurrence, whereas a too restrictive definition might erroneously define entire areas as unsuitable. During the first two field days of this study, visits to predicted potential colony sites were undertaken and it was found that the BHI tends to be too generous when it comes to identifying which types of houses are suitable for bat colonies. Several houses that did not look accessible to bats had been predicted suitable. In contrast to the BHI's generosity in predicting buildings as colony sites, it has also been pointed out that its prediction of *natural* colony sites (i.e. old and hollow trees) is rather restrictive. Petter Bohman, consultant at the agency Naturcentrum, says that he has found bat colonies in trees that do not concur with the characteristics defined as suitable in the BHI, in very young trees for example. If this is the case, the BHI might underestimate the occurrence of bats. Predictions of the suitability of potential colony sites could be improved by investigating selection by bats experimentally or by reviewing literature about roosting site characteristics.

Areas of use for the optimised BHI

Once the BHI is sufficiently optimised and evaluated, it could be used as an indicator in preliminary assessments of conflict potential of infrastructure or exploitation projects. It has the advantage of taking landscape connectivity into account, something particularly important for impact assessments of infrastructure projects. Besides the BHI's advantages compared to other habitat models, there are also general arguments for using a spatial index when sampling compared to sampling without it. The main advantage is that an index is transparent when it comes to arguments underlying its prediction as opposed to an interpretation of the landscape based on personal experience. Varying amounts of experience are known to lead to biases and large subject-dependent differences in inventory results (Fitzpatrick *et al.*, 2009; Faanes & Bystrak, 1981; Wallin, 1949). The input data is publicly available and the steps for the construction of the BHI are known. Spreading this index among consulting agencies and other potential users and agreeing on a common interpretation of the index would lead to a standardisation of inventory methods and therefore increased comparability of results. The success of an inventory would thus be independent of the experience of the respective field personnel, which would guarantee consistency in the quality of inventories. The second big advantage of using an index is that it makes sampling more efficient, e.g. by maximising the number of bat observations per unit effort. As alternative to maximising the number of bat observations, the efficiency could equally be increased by minimizing the number of sites that have to be sampled in order to find the most important bat commuting routes.

Conclusion

The BHI is significantly correlated with bat occurrence. The index performed particularly well when predicting the number of regular species as well as the activity of forest bats. It did not perform well when predicting overall bat activity or the total number of species. In many cases, the penultimate stage in the construction of the index (i.e. colony movement) performed better than the final index and therefore I would suggest omitting the final step in the development of the BHI. Drawing more detailed conclusions from my evaluation of the BHI is hampered by its unusual nature. Many factors have been included in its construction in many consecutive steps and the effects of the individual factors or interactions are impossible to disentangle once they are combined into a single number. The final index values have lost the connection to their original justification. In order to achieve an optimal choice of values, independent of their biological meaning, a mathematical optimisation of the parameters behind the index should be considered. Insect abundance might be tested explicitly in the field to obtain more optimal relative weightings of habitat characteristics. The most important step for an effective optimisation of the index is however to clearly define what it should be used for, ideally prior to further modifications and evaluations. Nevertheless, the BHI has potential to become a useful tool in making bat sampling more efficient and standardised at a larger scale.

Acknowledgements

Many different people were involved in this thesis at different stages of its development. I would like to thank all those people for their collaboration, help and support in a largely chronological order. One person, however, participated in nearly all stages of this project, and therefore I would like to give special thanks to Claus Rüffler already here. He helped me with many of the challenges I encountered during my thesis and gave me advice and inspiration when I got stuck or when I was looking for further ideas of improvement. He repeatedly spent several hours discussing the design of the sampling, my plans for the analysis and the BHI's advantages and disadvantages and even gave me ideas for the outline for the written report. This thesis would not be nearly as good without his input.

I would like to thank Simon Kärvemo for helping me with ArcGIS when I was planning the fieldwork.

I also want to thank Meagan Tunón who helped me during the first couple of days in the field and who took any unexpected happenings (like a bunch of wild boars for example) with a remarkably cool head.

Throughout the entire month of fieldwork, I was also accompanied by the most flexible, sharp-thinking and congenial assistant I could have imagined. Enormous thanks to Lara Millon for her physical support, mental encouragement and sharp brain! She certainly improved the quality of the field data and made the challenging fieldwork much more enjoyable for me.

It would not have been possible to make this study at all without the collaboration of the house owners, farm managers and neighbours whom I met during the fieldwork and who agreed on having a recording device in a tree beside their house or on their ground. They did not mind having people sneak around on their property at midnight, holding detectors in their hands. I would like to thank them for their trust and collaboration.

Much of the sound analysis was done by consultants from the agency Ecocom. Thanks to Alexander Eriksson, Lara Millon, Björn Palmqvist and Martin Brüsin for spending so many hours searching for and identifying blue smears of all shapes and sizes.

The statistical analysis of my data was strongly improved by the integrated help of Charles Campbell, Göran Arnqvist and Malin Aronsson who gave me ideas, advice and R-code and who corrected me when my suggestions were going in the wrong direction. Special thanks particularly to Malin who gave me detailed and very valuable feedback on my statistical models and R-code via e-mail while participating in a conference.

In March, a workshop took place in Skara where consultants from all over Sweden came to discuss the BHI. I would like to thank all participants of this workshop for their interest, their feedback and their participation in the exercises and discussions from which I received valuable input for the interpretation of the BHI and the results from my study.

The project of my thesis would not have existed if Oskar Kindvall had not created the BHI. I would like to thank him for this impressive work, his well-written and detailed description of the construction of the BHI and the interesting discussions with him.

This written report was proofread by Eduardo Ottimofiore and Simon Hunt. I would like to thank them for their valuable feedback, their time and their encouragement.

I also want to thank my opponent, Hanna Modin, for her critical eye and always constructive feedback on my report, presentation and the project itself.

Thanks to Andreas Seiler who was the examiner of this thesis project and who encouraged me to do all bureaucratic work in time.

Finally, I would like to thank Johnny de Jong for supervising me in this project. He had sketched the outline of the project but left me space to develop my own ideas and to shape the project according to my interests. Thanks to Johnny also for sharing his expertise about bats and for his good sense of humour.

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Appendices

Appendix 1

Appendix 1. Sources of the input layers used to construct the BHI. *This table is taken with permission from Kindvall's unpublished report about how to construct the BHI.*

Output map layer	Selection	Input map layers	Source
Habitat	All CadasterENV habitat classes	CadasterENV_AB\AB\Classes\ lc_hr_ab_ogen_3_2.tif	CadasterENV, Metria
Tree Cover		ab_tree_cover.tif	CadasterENV, Metria
Pastures	Land use = ”Pasture”	AB_LandUse.shp, C_LandUse.shp	CadasterENV, Metria
Hard wood trees	All hardwood trees	Several point layers with trees found in different monitoring programs of valuable trees.	The tree portal, Swedish University of Agricultural Sciences, Data from County Administrations of Stockholm and Uppsala
Hollow trees being potential colony sites	Hard wood trees with indications of present hollows.	Several point layers with trees found in different monitoring programs of valuable trees.	The tree portal, Swedish University of Agricultural Sciences, Data from County Administrations of Stockholm and Uppsala
Buildings being potential colony sites	KKOD in (731, 732, 733, 734, 735, 736, 737, 741, 747, 748, 753)	BS_01.shp, BS_03.shp	GSD terrain map (vector), Lantmäteriet
Shorelines	KKOD in (102, 104, 105, 107, 108, 110, 112, 113, 114, 115, 116, 117, 119, 120, 218, 418, 518, 718, 1418, 1518, 1618, 1718, 1819, 1820)	ML_01.shp, ML_03.shp	GSD terrain map (vector), Lantmäteriet
Streams	KKOD in (441, 455, 456)	HL_01.shp, HL_03.shp	GSD terrain map (vector), Lantmäteriet
Highways	KKOD =5011	VL_01.shp, VL_03.shp	GSD terrain map (vector), Lantmäteriet

Appendix 1 continued

Output map layer	Selection	Input map layers	Source
Passage enforcing featurs	Minor roads crossing under highway: KKOD in (5822, 5825, 5829, 5834, 5844, 5851, 5856, 5861, 5871, 5882, 5899), Streams: KKOD in (455, 456) and all other water surfaces.	HL_01.shp, HL_03.shp, VM_01.shp, VM_03. shp, VL_01.shp, VL_03.shp	GSD terrain map (vector), Lantmäteriet

Appendix 2

Appendix 2. Number of recordings per species and box. *Site and recorder were used as random effects factors in all statistical models. Date was used as covariate in all models where sample size was 200, sec refers to the length of the recordings for the corresponding box (measured in seconds) and it was used as covariate in models where it had a significant effect on the response variable. Names are abbreviated as following: Enil* = Eptesicus nilssonii, *Eser* = Eptesicus serotinus, *E* = Eptesicus *sp.*, *M* = Myotis *sp.*, *Mdau* = Myotis daubentonii, *Mdas* = Myotis dasycneme, *Mmys/bra* = Myotis mystacinus/brandtii, *Mnat* = Myotis nattereri, *Nnoc* = Nyctalus noctula, *N* = Nyctalus *sp.*, *Paur* = Plecotus auritus, *Pnat* = Pipistrellus nathusii, *Ppip* = Pipistrellus pipistrellus, *Ppyg* = Pipistrellus pygmaeus, *Vmur* = Vespertilio murinus, *Micro* = *Microchiroptera.*

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
1	P	05-07-17	5	2					2		5	4				4	2			19
1	AC	18-07-17	5	3					2		1	2				1			2	11
1	AC	20-07-17	5	1					1		1	4				1			1	9
1	S	23-07-17	5	3					3			9								15
3	V	03-07-17	3									18				1			1	20
3	AU	10-07-17	3					1			1	15				1				18
3	AT	17-07-17	3								1	3				2		2	1	9
3	AC	23-07-17	5	82				2			5	162							1	252
5	D	03-07-17	3	4					1							2				7
5	V	16-07-17	5	1				1			13									15
5	AC	21-07-17	5						5	4	36					1				46
5	L	26-07-17	5						9	2	2	49								62
6	AT	03-07-17	3	1												2			1	4
6	D	10-07-17	5	3							1					4	1			9
6	D	17-07-17	5	2								1				9				12
6	AA	24-07-17	5	6	1	2	1	1			8	4				18		1		42

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
7	Q	05-07-17	5	15				1				86				6				108
7	V	09-07-17	5	3								51				14				68
7	S	18-07-17	5	8					2		7	192				81		1	3	294
7	P	23-07-17	5	86							5	212				55				358
8	K	03-07-17	3	5				1	1		1	13				2				23
8	O	16-07-17	5	1	36			2	3			85				4		8	4	143
8	AA	21-07-17	5	18	9				1		1	5				3	1	2	1	41
8	D	26-07-17	5		5			6	2	2	1	58				3		3		80
10	AU	04-07-17	3	48				2	6		5	29				1				91
10	F	10-07-17	5	382					5		14	43				39				483
10	S	17-07-17	5	433					4		49	26				8	1		1	522
10	AA	23-07-17	5	111				2	4		24	11				9				161
12	P	04-07-17	5						1			2								3
12	D	09-07-17	5								6	1					1		1	9
12	V	18-07-17	5													2				2
12	V	20-07-17	5																	0
14	O	06-07-17	5	49								6	1			1		1		58
14	O	08-07-17	5	7							1	2		1		2		1		14
14	I	09-07-17	5	6	1							24				1		3		35
14	I	21-07-17	5	6								5				1	1			13
16	L	05-07-17	5	2				2			1	8				83				96
16	W	18-07-17	5	13				1	7	3	5					39				68
16	W	20-07-17	5	13					1	2	2	6				23	1			48
16	P	26-07-17	5	5				5	6	1	41	1				44	1			104

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
17	M	04-07-17	3	1				1	1		1	4						1		9
17	P	09-07-17	5	6					1		3	27						1		38
17	L	22-07-17	5	4					1		1	6							1	13
17	S	26-07-17	5	9								12								21
19	F	04-07-17	3	85	1				2		3	39			3	26				159
19	O	09-07-17	5	72	12						3	8			13	7		2	1	118
19	V	21-07-17	5	5	4				3		15	58			11	123		3		222
19	F	24-07-17	5	4	12			4	4	3	22	127		2	22	85		8	7	300
20	D	05-07-17	5	5								2				8			1	16
20	L	15-07-17	5	13						2	2	6				1	3			27
20	P	18-07-17	5	12							2	2				5				21
20	P	20-07-17	5	13							2	4				3				22
23	K	05-07-17	3																	0
23	V	10-07-17	5	1																1
23	AA	17-07-17	5	5					1											6
23	V	23-07-17	5	4																4
25	I	05-07-17	5																	0
25	W	15-07-17	5	7				2	1		8	5								23
25	P	21-07-17	5	16					2		2	3		1		3				27
25	AC	24-07-17	5	9				1	3		3	5				6				27
26	O	05-07-17	5	4								4				2				10
26	F	15-07-17	5					2	2		5	1				45				55
26	L	18-07-17	5									1								1
26	L	20-07-17	5									2						1		3

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
28	AF	04-07-17	3	1							1			1		1				4
28	L	09-07-17	5	3				2			1	16								22
28	D	21-07-17	5	3							11								2	16
28	P	24-07-17	5	2				3	9		4	1				1	1	1		22
29	AA	18-07-17	5	3								32		1		2				38
29	AA	19-07-17	5	5	2			1			4	32				1		1		46
29	AU	23-07-17	3	19	1			2	4		2	5				2	1			36
29	V	27-07-17	5	39	4			1	1		3	155		1		6		1	1	212
30	AA	04-07-17	3	7	1			3	1		9	72			3	31				127
30	L	12-07-17	5	2							5	118		1		14				140
30	L	14-07-17	5	1							5	55		2		15				78
30	I	22-07-17	5	3				3	1		3	16				9				35
31	AC	04-07-17	3									95						1		96
31	O	18-07-17	5		37				1			181							2	221
31	O	20-07-17	5	9	19			2	17		25	154				2	1	3	1	233
31	AU	26-07-17	3	26	16			3	11		6	633					1	3	4	703
32	H	04-07-17	3						2			4								6
32	D	18-07-17	5	36					4		2	13								55
32	D	20-07-17	5	15	1			1	3		1	2				1	3			27
32	S	24-07-17	5	43	9				1	4	4	175					5	2		243
34	AV	05-07-17	3	1								6								7
34	J	16-07-17	5	3								16								19
34	V	17-07-17	5		1				3			43					1			48
34	V	24-07-17	5	16						2	2	27								47

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
35	AU	06-07-17	3	69												2				71
35	AU	08-07-17	3	18								21						1		40
35	I	16-07-17	5	41					1			6				3	1			52
35	V	26-07-17	5	32			1					5				2				40
36	W	04-07-17	3									8								8
36	D	12-07-17	5	2								46				4				52
36	D	14-07-17	5	2					1		1	7				2				13
36	L	23-07-17	5	5								3								8
38	F	06-07-17	5	6								2				12	3		1	24
38	F	08-07-17	5	4					2			4				2	6		1	19
38	I	15-07-17	5	1				1	1			1				8	3			15
38	AU	22-07-17	3	1				1			1	2				3				8
42	V	06-07-17	5	4						1						1				6
42	V	08-07-17	5	8								1								9
42	V	15-07-17	5	1							1	1								3
42	S	27-07-17	5	4							1	2					1			8
43	F	05-07-17	5	4								23				2				29
43	I	18-07-17	5	1								8								9
43	I	20-07-17	5	1								3								4
43	S	22-07-17	5	1							7	55				2				65
44	L	04-07-17	3	1				1				1								3
44	L	10-07-17	5	5					1		1	18		1		2		1		29
44	L	11-07-17	5	3							1	4		1						9
44	I	23-07-17	5	5				1			3	4		1		1	1			16

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
47	I	03-07-17	3	4	4			3	3		84	5				57			2	162
47	F	09-07-17	5	12				8	25		24	3				19		1	1	93
47	AC	17-07-17	5	13				2	4		22	3				6			1	51
47	I	24-07-17	5	15	17	25		15	11	1	14	3				34	14		1	150
51	V	05-07-17	5	5				1				1				1				8
51	O	10-07-17	5	3							2	28				2			1	36
51	O	17-07-17	5	13								2				1	1		1	18
51	V	22-07-17	5	13						1		25				12				51
57	D	06-07-17	5	2				2			1	22				24				51
57	D	08-07-17	5	37			1	4			2	17				38				99
57	P	15-07-17	5	3				2			3	1				2				11
57	W	24-07-17	5	19				2			12	14				13	1			61
58	I	06-07-17	5	5								1				1				7
58	I	08-07-17	5	9				2				4				4		2		21
58	O	15-07-17	5	11				1								8				20
58	I	27-07-17	5	1	3					1	1	22				2		2	1	33
65	Q	04-07-17	3	2					5			28								35
65	AU	09-07-17	3	26				4	5	1	16	41						6	1	100
65	L	21-07-17	5	34				2	4		3	14		1		2				60
65	F	26-07-17	5	2	1			4	4		4	14				4		1		34
68	AT	05-07-17	3						1	1										2
68	F	16-07-17	5	4					1	1		7								13
68	O	21-07-17	5	9	1				1			14				1				26
68	L	24-07-17	5	1	1				2			21						1	1	27

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
71	AU	05-07-17	3									2								2
71	F	18-07-17	5						1			2								3
71	F	20-07-17	5											1		1				2
71	F	23-07-17	5		1															1
74	P	06-07-17	5									2								2
74	P	08-07-17	5	1								6								7
74	AU	16-07-17	3	2								1					2			5
74	AU	24-07-17	3	6					1		3	8								18
75	L	06-07-17	5	1				3				7						1		12
75	L	08-07-17	5	5						1		1				1				8
75	P	10-07-17	5	1					1		1	1							1	5
75	O	24-07-17	5	47				2	1			15				1				66
78	D	15-07-17	5	19				1		1		1				7				29
78	D	16-07-17	5	13					1	1		8				12			1	36
78	W	22-07-17	5	17				1	1		4	26				6			3	58
78	D	27-07-17	5	132				1	1		3	15				19				171
82	P	12-07-17	5	21				4	3		7	11		1	1	25				73
82	P	14-07-17	5	9				1			1	4		1		14				30
82	P	22-07-17	5	19	2			2	1	1	16	15				6			1	63
82	I	26-07-17	5	11				17			2	12		1		7	1	3		54
84	O	12-07-17	5	1																1
84	O	14-07-17	5	1																1
84	P	17-07-17	5	4												1	1			6
84	F	27-07-17	5	1														1		2

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
85	I	12-07-17	5					3	1		4	13							1	22
85	I	14-07-17	5								5	2				1	1			9
85	F	17-07-17	5						1		2					1	3			7
85	AU	27-07-17	3	1	2			3				6						1		13
89	P	11-07-17	5	2							1	5				6				14
89	AU	18-07-17	3													7				7
89	AU	20-07-17	3	1																1
89	O	26-07-17	5	1								1				2				4
92	V	12-07-17	5					1	1		3					14				19
92	V	14-07-17	5					1	1		3					11				16
92	W	17-07-17	5					1	1							8				10
92	O	22-07-17	5	1												19				20
93	F	11-07-17	5																	0
93	W	16-07-17	5	3						1	1	3				15				23
93	D	22-07-17	5	1					4		9					19				33
93	D	25-07-17	5	4				1	3		9	2				8			1	28
97	I	11-07-17	5													4				4
97	AU	15-07-17	3								5					2				7
97	H	17-07-17	3						2			3				14				19
97	W	26-07-17	5	4	1			1			3					2				11
100	AU	11-07-17	3	258				2	3		3	9				18				293
100	P	16-07-17	5	282				5		1	2	114				75			1	480
100	AA	22-07-17	5	25				7			1	11				9				53
100	AC	26-07-17	5	11				2	2		8	4				5				32

Appendix 2 continued

site	recorder	date	sec	*Enil*	*Eser*	*E*	*Mdas*	*Mdau*	*Mmys/bra*	*Mnat*	*M*	*Nnoc*	*N*	*Pnat*	*Ppip*	*Ppyg*	*Paur*	*Vmur*	Micro	Sum
102	V	11-07-17	5	134					1		1	116				6				258
102	L	16-07-17	5	263							2	236				18				519
102	O	23-07-17	5	447	1			3	8	1	6	31				112		2		611
102	AA	26-07-17	5	916	62			3	2	2	54	696				88		39		1862
104	AU	12-07-17	3					1	7		44									52
104	AU	14-07-17	3						5		11									16
104	L	17-07-17	5	1							6									7
104	P	27-07-17	5						1	2	4									7
106	F	12-07-17	5	1								1				4				6
106	F	14-07-17	5									2				1				3
106	AU	17-07-17	3	15								1				1				17
106	O	27-07-17	5	11				1				4				2				18
108	W	12-07-17	5								1	1								2
108	W	14-07-17	5	1																1
108	I	17-07-17	5						4											4
108	AC	22-07-17	5		1							3								4
Number of recordings				4987	269	27	3	181	275	43	826	5220	1	18	53	1715	64	112	58	

Appendix 3

Appendix 3. Site coordinates and habitat variables. *For each site (n = 50), the distance to the highway E18 was calculated as well as means for the variables bat habitat index (BHI), insect abundance (IA), flight friction (FF) and colony movement (CM). The subscript refers to the radius around the site over which the mean value of each variable was calculated. Coordinates are given in the Swedish coordinate system SWEREF99 TM.*

site	east	north	dist	BHI_{30}	BHI_{170}	BHI_{200}	BHI_{500}	IA_{30}	IA_{200}	IA_{500}	FF_{30}	FF_{200}	FF_{500}	CM_{30}	CM_{200}	CM_{500}
1	709599	6634003	5669	21	16.03	16.14	12.31	5	3.83	3.07	3.9	2.76	3.85	117.75	196.99	261.36
3	690346	6622683	2573	7.55	6.6	6.63	4.66	2	1.56	1.16	15.24	21.34	32.53	214.9	303.15	420.49
5	698021	6613863	8838	10.21	9.35	9.36	8.15	2.45	2.37	2.36	5.03	3.79	4.35	168.41	231.69	397.53
6	689574	6622159	2813	10.79	4.08	4.25	3.59	2.25	0.94	0.89	1	24.41	30.21	62.65	224.99	357.82
7	710054	6631547	3387	5.93	5.01	5.02	5.86	1.28	1.12	1.39	10.93	30.88	19.35	101.78	299.14	287.86
8	702808	6618748	6915	16.43	10.86	10.98	9.92	3.71	2.55	2.45	1.79	3.22	3.02	143.37	173.09	242.91
10	694036	6622703	830	17.86	11.2	11.34	9.84	3.52	2.59	2.59	4.55	9.43	7.11	85.59	229.64	329.07
12	709307	6629063	794	17.96	9.12	9.31	6.91	4.74	2.54	1.79	2.48	13.58	14.33	394.58	450.04	379.49
14	714710	6626668	695	5	5.31	5.32	5.27	1.36	1.85	1.93	14.18	14.5	11.69	557.73	637.68	662.04
16	702826	6629983	1641	5.24	6.5	6.42	9.66	1.1	1.54	2.35	14.41	17.62	7.63	267.69	329.9	254.8
17	711457	6628415	331	5.07	4.55	4.57	5.63	2	1.69	1.77	6.46	4.64	8.53	675.36	603.3	475.61
19	708217	6626086	2226	20.25	15.26	15.37	11.57	3.79	3.51	2.85	1.57	2.24	5.93	59.62	146.15	234.47
20	683899	6626017	9504	22.59	11.94	12.18	9.7	4.79	2.81	2.45	3.07	5.15	7.64	83.95	180.49	302.76
23	693267	6612647	5874	11.33	10.79	10.79	9.6	2.93	2.59	2.35	8.89	8.34	7.95	281.83	254.31	264.96
25	686353	6627323	8692	3.45	4.92	4.89	6.19	2	2.13	2.14	8.14	7.62	9.41	909.04	715.75	517.41
26	686142	6625867	7825	4.24	7.97	7.87	6.87	2.24	2.58	2.41	9.69	5.41	5.36	835.84	522.57	600.6
28	713509	6627060	509	20.69	12.3	12.47	11.03	4.31	2.9	2.94	1.31	4.4	4.16	78.66	159.32	324.74
29	706465	6628053	510	13.07	8.36	8.48	8	3.03	1.9	2.24	6.45	24.29	14.67	135.45	220.42	403.45
30	708263	6627540	791	20.92	15.55	15.65	11.18	5	3.59	2.7	3.62	2.13	5.82	192.21	149.15	256.16
31	706520	6628290	299	12.08	9.51	9.59	3.12	3.12	2.11	1.1	1.85	9.81	22.08	88.56	133.6	559.9
32	705448	6628292	159	11.93	10.34	10.38	10.41	2.59	2.68	2.77	12.17	19.68	10.18	229.89	278.56	339.22
34	687697	6617133	1175	4.52	5.51	5.5	4.45	1.33	1.25	1.14	29.63	22.92	29.18	608.98	337.22	407.36
35	696176	6625590	1813	10.92	8.64	8.68	7.06	1.96	2.01	1.65	3.08	3.52	13.32	52.31	120.14	195.52

Appendix 3 continued

site	east	north	dist	BHI_{30}	BHI_{170}	BHI_{200}	BHI_{500}	IA_{30}	IA_{200}	IA_{500}	FF_{30}	FF_{200}	FF_{500}	CM_{30}	CM_{200}	CM_{500}
36	712466	6627285	602	7.57	6.37	6.4	6.24	2.32	1.58	1.96	12.57	23.43	11.06	305.32	352.12	458.99
38	695129	6627194	3687	21.89	10.19	10.46	8.06	4.79	2.44	2.35	2.29	8.06	10.01	59.34	231.91	464.09
42	684165	6619280	5192	10.5	4.25	4.38	4.25	3.15	1.64	1.63	7.92	21.04	21.15	425.65	620.57	635.47
43	710126	6634039	5803	7.48	10.66	10.6	12.68	1.04	2.31	2.98	16.26	21.96	7.39	106.04	181.73	207.55
44	706044	6622729	5707	4.89	9.25	9.16	5.81	1.21	2.06	1.45	5.04	10.23	23.48	131.51	183.36	345.06
47	697075	6622660	1184	13.35	11.89	11.92	9.83	2.5	2.84	2.52	1.85	6.95	9.09	35.2	240.38	350.23
51	682091	6609571	1230	8.86	5.94	6	5.68	2.04	1.67	2.11	7.14	19.62	14.84	87.39	448.69	566.26
57	685862	6625081	7528	11.39	10.69	10.7	7.8	2.61	2.77	2.43	4.61	8.94	7.97	243.6	347.24	507.69
58	686467	6621326	4400	10.21	14.31	14.22	11.64	2.32	3.33	2.87	4.21	2.63	5.88	122.64	164.2	265.22
65	710789	6628814	705	10.64	3.46	3.62	1.42	3	0.99	0.5	3.25	34.09	44.73	321.09	518.31	609.21
68	687276	6615132	32	4.96	3.86	3.89	3.37	1.86	1.65	1.55	11.61	13.07	12.01	647.84	697.42	768.66
71	706906	6635022	6415	6.39	5.73	5.74	3.76	2	1.87	1.84	8.71	12.75	11.79	468.68	557.41	797.55
74	695470	6619158	2980	6.07	6.42	6.41	5.97	1.89	2.04	1.99	4.21	3.64	7.11	500.94	473.7	517.95
75	693926	6623885	1983	8.07	5.09	5.16	6.6	2.39	1.49	2.04	2.61	20.93	12.41	471.11	583.48	506.11
78	682015	6626997	11511	16.17	7.15	7.36	6.41	3.62	1.74	1.69	1.21	10.34	9.64	89.92	233.99	339.94
82	701944	6621835	3976	17.48	12.3	12.43	9.57	3.48	2.86	2.6	1.14	7.94	9.47	25.98	210.85	409.62
84	691130	6612827	4171	20.31	12.28	12.46	9.99	4.55	2.79	2.64	1.97	3.54	4.96	66.77	121.32	331.96
85	680543	6611108	3307	4.93	5.79	5.77	5.67	2	1.96	1.87	8.07	7.07	8.2	681.74	524.02	476.06
89	706703	6621890	6499	16.96	9.84	9.98	7.42	3.65	2.25	1.92	1.46	11.48	16.18	107.07	194.61	401.16
92	688567	6610696	3827	11.68	11.45	11.45	10.01	3.07	2.91	2.77	2.93	3.01	3.66	227.41	268.05	369.9
93	691954	6618596	1309	20.8	11.39	11.62	8.66	5	2.99	2.31	4.6	14.35	18.23	227.55	371.8	402.81
97	689237	6620255	1653	4.89	7.79	7.72	7.52	0.86	1.72	2	11.82	17.44	12.35	116.61	238.73	370.88
100	692010	6622128	1035	12.89	13.15	13.14	9.91	2.36	3	2.43	2.61	5.06	7.3	67.39	154.68	262.77
102	691911	6619895	430	20.21	13.6	13.76	8.74	4.39	3.29	2.74	2.14	2.58	10.03	135.66	204.07	492.02
104	686303	6610433	1795	8.38	8.57	8.58	7.94	3	2.64	2.35	9.07	9.91	10.22	610.49	509.45	471.27
106	687647	6616191	592	4.41	7.35	7.29	6.96	0.93	1.69	1.83	1	1.82	8.31	107.22	137.89	321.18
108	687652	6614642	576	2.96	4.01	3.99	5.53	2	1.72	1.88	7.11	9.52	8.78	971.37	726.86	588.11