



Norwegian University
of Life Sciences

Master's Thesis 2023 60 ECTS

The Faculty of Environmental Sciences and Natural Resource Management
(MINA)

Identifying Valuable Habitat Types for *Pipistrellus* bat species in Norwegian Boreal Forests

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Acknowledgements

This thesis marks the conclusion of my master's degree in Ecology at the Faculty of Environmental Science and Natural Resource Management (MINA), at the Norwegian University of Life Sciences (NMBU).

I would like to express my utmost gratitude to my supervisors Katrine Eldgegard and Reed McKay for their unlimited support, advice, and feedback throughout the process of this thesis. Their guidance has been invaluable, and I have learnt so much from them both. Thank you for pushing me out of my comfort zone and helping me to develop skills that will undoubtedly contribute to my future within ecology.

I would also like to thank Frøya Rakvaag and Mathilde Klokkesveen Thomle for their constructive feedback and continuous moral support throughout this journey; Fano Grydland for helping me overcome roadblocks with R; Kia Karina Tahmin for her constant comradery over the last two years; and Sangkoret Noe Gansk Annet for providing endless fun and distractions. Finally, a special thank you goes to Endre Eiklid (and the emotional support chickens), for his unwavering support during the writing of this thesis. Thank you for believing in me when I didn't believe in myself, I could not have done this without you.

Jenna Fairchild

14th June 2023

Ås, Norway

Abstract

1. Bats are a substantial component of the forest vertebrate community and provide numerous ecosystem services. Although protected in Norway, bats still face threats to their habitat due to intensive forestry but are rarely considered in forest management plans. Generally, little is known about bat-habitat relationships in Fennoscandian boreal forests, and scientific studies from Norway are particularly scarce. *Pipistrellus* species are especially interesting in regard to their habitat use, as although classified as edge-space foragers, they display substantial echolocation plasticity, meaning that they are able to hunt and manoeuvre in both cluttered environments and open spaces.

2. The goal of this study was to explore characteristics of habitat more highly selected by *Pipistrellus* spp. bats within Norwegian boreal forests. It examines; (1) whether the amount of *Pipistrellus* spp. acoustic activity, i.e., commuting, feeding, and social behaviour, varies between different boreal forest sub-habitats, and (2) how *Pipistrellus* spp. activity i.e., commuting, feeding and social behaviour, is influenced by forest stand density.

3. Data was collected at 12 boreal forest sites in south-eastern Norway during May and June 2021. Sites were classified as “mixed” coniferous-deciduous forests and were located along a forest density gradient. *Pipistrellus* spp. activity was assessed through non-invasive monitoring using acoustic bat detectors, and passes were manually analysed to identify species and behaviour (feeding, commuting, and social). Activity was compared between three different sub-habitats: (1) forest gaps and (2) interior forest at ground-level, and in the (3) forest canopy. Stand level forest density was measured using the total number of stems as a proxy.

4. Among the monitored sites, there was substantial variation in levels of *Pipistrellus* spp. acoustic activity, and across all sites, *P. pygmaeus* was the dominant species identified. Forest gaps displayed the highest amount of both feeding, and social behaviour, whilst the forest interior displayed the least. All habitats displayed low levels of social behaviour. Forest density was negatively correlated with commuting and feeding passes in both forest gaps and the forest interior, although an apparent positive correlation was displayed in the forest canopy.

5. The findings of this study indicate that boreal forests with a more natural dynamic, which contain gaps and a more heterogenic structure, are more valuable habitat for Norway’s *Pipistrellus* spp. than dense, homogenous forest stands. This has implications for future bat conservation decisions in both Norway and other Nordic countries, particularly in regard to forest management practices. Increasing the number of forest gaps, whilst managing and maintaining those that already exist, will likely greatly benefit *Pipistrellus* spp. populations.

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1 Introduction

The intensive management of Norwegian boreal forests is of particular concern for the country's bat populations. Throughout Norway, approximately 91 percent of productive forests are managed via clear-cutting (Bartlett et al., 2020) which typically occurs every 70 – 110 years (NIBIO, 2021). Forests with a (near) natural dynamic are heterogenic and structurally complex, and as such, provide varied 3D habitat containing numerous ecological niches capable of supporting many bat and bird species (Bouvet et al., 2016). Clear-cutting, however, simplifies forest structure and species composition, creating dense and homogenous even-aged stands (Esseen et al., 1997; Savilaakso et al., 2021). In Norway's southern regions, these habitat alterations are particularly pertinent, as previously mixed deciduous-coniferous forests have become dominated by the economically important Norway spruce (*Picea abies*). As spruce trees are planted at especially high concentrations and thinning is not common practice (Allen et al., 2020), the forest density increases associated with clear-cutting are compounded, along with Spruce's monodominance within the landscape.

Constituting 25 percent of the country's terrestrial mammalian taxa, all of Norway's bat species are associated with forests (Artsdatabanken, 2021), which provide important resources for roosting and foraging (Dietz & Kiefer, 2016). As such, increases in forest density, and the resultant decreases in structural complexity, are likely to reduce habitat suitability for many of these species, leaving them vulnerable to population declines (Frey-Ehrenbold et al., 2013; Jung et al., 2012; Milne et al., 2006). Indeed, more than half of Norway's bats are considered threatened by the Norwegian National Red List, and all those considered "Critically Endangered" are forest specialists (Artsdatabanken, 2021). It is therefore important to identify which forest structure types are most valuable to bat species living within Norwegian boreal forests, to better inform management decisions and protect populations.

Members of the *Pipistrellus* genus are good research candidates in this regard. As edge-space foragers, *Pipistrellus* species primarily hunt around the edges of vegetation and buildings (Denzinger & Schnitzler, 2013), capturing and consuming small dipteran insects on the wing via aerial hawking (Bartonička et al., 2008; Kalko, 1995; Krüger et al., 2014; Vaughan, 1997). They also, however, exhibit considerable echolocation plasticity, and are thus able to forage

and manoeuvre both in more cluttered environments, and open spaces (Kalko & Schnitzler, 1993). Additionally, *Pipistrellus* spp. are particularly reliant on tree microhabitats for roosting, which modern forestry has significantly reduced (Borkin et al., 2011). Increasing knowledge of what constitutes valuable habitat for these species is therefore particularly interesting, however, little research exists on the genus within boreal forests. As such, it is important to find out more about their relationships with habitat in order to prevent population declines.

As bats provide many key services which contribute to important environmental processes and help to maintain ecosystem stability (Beilke & O'Keefe, 2023; Jones et al., 2009; Vilas, 2016), their conservation is essential. In Norway, despite their protected status and the challenges they face from habitat degradation and fragmentation, bats are severely underrepresented in both research and conservation efforts and are rarely considered in forest management plans. This is also true throughout Fennoscandia, and most studies concerning bat species found in Norway have been conducted outside of the Nordic region. Due to the unique environmental conditions, it cannot be assumed that the conclusions of studies on conspecific bat species from mainland Europe and the U.K. can be applied to Norwegian populations. Region-specific research and bat monitoring strategies are therefore necessitated, to best ensure their conservation.

One approach commonly used to survey bats is passive acoustic monitoring. In this non-invasive method, bioacoustic detectors are deployed and automatically record ultrasonic bat vocalisations. This approach allows for the collection of large datasets with comparative ease, whilst also being relatively cost-effective, and easier to conduct within forest habitats than traditional techniques such as mist-netting (Froidevaux, et al., 2014). Bats are volant and highly mobile such that they also occupy a 3D space. Nevertheless, most studies deploy just one bioacoustic detector per site, and few have sampled different sub-habitats within the same forest location (Collins & Jones, 2009; Froidevaux et al., 2014). The deployment of multiple bioacoustic detectors within these different environments, however, allows for a more comprehensive view of both bat activity, and how the community utilises forest habitats. Additionally, the majority of studies tend to either disregard behaviour, counting any bat activity as simply a “bat pass”, or exclude passes containing feeding and social behaviour entirely from analysis. Observations of feeding behaviour, however, are a better indicator of valuable habitat than purely “activity” or commuting behaviour (echolocation

only) (Kusch et al., 2004; Scott et al., 2010), as individuals could merely be passing through the area on their way to more important sites.

The aim of this study was to ascertain how the foraging, commuting (echolocation only), and social activity of *Pipistrellus* spp. within Norwegian boreal forests is affected by forest density, and to identify features of valuable foraging habitat. The research questions were:

1. Does the amount of *Pipistrellus* species acoustic activity i.e., commuting, feeding, and social behaviour, vary between different forest foraging habitats?
 - a. Comparing the amount of observed behaviour between Open, Interior, and Canopy habitats for *Pipistrellus* spp.

2. How is the frequency of pipistrelle acoustic activity i.e., commuting, feeding and social behaviour, influenced by forest stand density?
 - a. Relating plot-level forest density proxies within different habitat types with the number of *Pipistrellus* spp. passes observed containing (i) commuting behaviour, (ii) feeding behaviour, and (iii) social behaviour.

2 Methods

2.1 Study Area

This study was conducted within the Ås and Nordre Follo regions of Viken county in south-eastern Norway (Figure 1a), between 14th May – 14th September 2021. Within the research area, boreal forests cover the majority of undeveloped land (Statistisk Sentralbyrå, 2022), in which Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the dominant canopy species (NIBIO, 2023). This area was targeted due to its ease of access to the Norwegian University of Life Sciences (NMBU).

Based on remote sensing data obtained from a combination of SR16 forest resource maps (Astrup et al., 2019) and AR5 land resource maps (1:5000 scale) (Ahlstrøm et al., 2019), 12 non-protected, mixed coniferous-deciduous boreal forest sites were selected (Figure 1b). Chosen sites were comparable across several metrics, including age, height, productivity, and dominant canopy species. Productivity (site index) was defined as the dominant height in meters at 40 years of age (Eid, 2001). During the selection process, only sites that were older than 50 years, with canopy heights greater than 5 m, and productivity above 7, were considered.

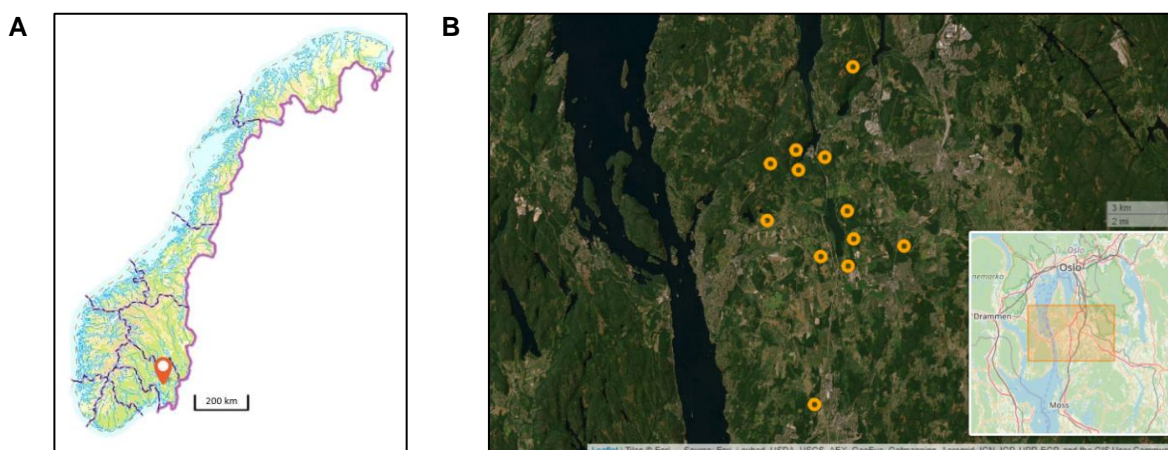


Figure 1. Maps denoting the location of the study area within Norway (A), and each of the 12 study sites (B). Map (A) sourced from Kartverket (2022), map (B) created using the Leaflet package (Graul, 2016) in R Studio (R Core Team, 2021; RStudio Team, 2020). For site coordinates, see Appendix Table A1, and for a map labelled with site numbers, see Appendix Figure A1.

All sites were located within a 40 km² area and were at least 1 km apart, with a maximum distance between any two sites of 17 km. To mitigate edge effects, each site had a buffer distance of approximately 50 m to the forest edge and bodies of water. Age and stand density per hectare were calculated from SR16 map data using model 3 from Eid (2001). Sites were manually selected across a stand density gradient (predicted number of trees per hectare), representing low, medium, and high density, proportional to mixed forest densities found within the study area. Manual site selection also allowed for the assessment of site accessibility, as well as the habitat's suitability for bats.

Within each site, three distinct habitat types were monitored: Open, Interior, and Canopy, following suggestions from Froidevaux et al. (2014). Open habitat plots were situated in areas with forest gaps that were open to the sky. Interior habitat plots were in areas where the forest was dense, whilst still conducive to detector deployment. Canopy habitat plots sampled the forest canopy and were associated with Interior habitat plots. At each site, all habitat plots were located approximately 30 m apart to avoid recording duplication.

2.2 Study Species

Norway is home to 11 recorded species of bat (Table 1), all of which belong to the family of insectivorous microbats, *Vespertilionidae*. Each of Norway's bat species are present in one or more of the nation's southern counties, although more than half are currently classified as threatened by the Norwegian National Red List (Artsdatabanken, 2021) (Table 1). Throughout the rest of their European ranges, all but 1 of these species are classified as of "Least Concern" (IUCN, 2022) (Table 1).

This study focusses on members of the *Pipistrellus* genus, including *Pipistrellus pygmaeus* and *Pipistrellus nathusii*. Both *P. pygmaeus* and *P. nathusii* are common European species with overlapping continental ranges, although *P. pygmaeus* is less widespread (Dietz & Kiefer, 2016). In Norway, both species can be found throughout the southern regions, as far North as Trøndelag county (Artsdatabanken, 2021). Both *P. pygmaeus* and *P. nathusii* are described as predominantly migratory, typically spending the summer months in northern breeding habitats, before moving southwards to hibernation areas in the autumn (Jones & Froidevaux,

2020; Russ, 2020). Observations have, however, been made of *P. pygmaeus* throughout the winter in Norway’s southwest (Frafjord, 2021), indicating that at least some of the population remains year-round. Due to the lack of knowledge surrounding population numbers of *P. nathusii* in Norway, the species was previously “Vulnerable” on the Norwegian National Red List (Henriksen & Hilmo, 2015). In 2021, however, their status was changed to “Near Threatened” due to known breeding populations in neighbouring countries (Eldegard et al., 2021).

Table 1. Norway’s bat species and their current conservation status according to the Norwegian National Red List (Artsdatabanken, 2021), and The IUCN Red List (IUCN, 2022). Asterisks (*) indicate this study’s target species. Abbreviations: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR).

Taxonomic Name	Common Name	Status (Red List 2021)	Status (IUCN)
<i>Myotis brandtii</i>	Brandt’s bat	LC	LC
<i>Myotis mystacinus</i>	Whiskered bat	LC	LC
<i>Myotis daubentonii</i>	Daubenton’s bat	LC	LC
<i>Myotis nattereri</i>	Natterer’s bat	CR	LC
<i>Plecotus auritus</i>	Brown long-eared bat	LC	LC
<i>Barbastella barbastellus</i>	Western barbastelle	CR	NT
<i>Pipistrellus pygmaeus</i> *	Soprano pipistrelle bat	LC	LC
<i>Pipistrellus nathusii</i> *	Nathusius’s pipistrelle	NT	LC
<i>Eptesicus nilssonii</i>	Northern bat	VU	LC
<i>Vespertilio murinus</i>	Parti-coloured bat	NT	LC
<i>Nyctalus noctula</i>	Common noctule bat	EN	LC

It is possible that a third *Pipistrellus* species, *Pipistrellus pipistrellus*, could also be present in Norway. Due to their similar morphology and echolocation structure (Montauban et al., 2021), *P. pipistrellus* and *P. pygmaeus* are difficult to distinguish from one another and were once thought to be the same species. Only after a number of studies were published supporting their differentiation via a variety of metrics (Rachwald et al., 2016), were the two separated in 1999 (Jones & Barratt, 1999). The first instance in which *P. pygmaeus* was described as a distinct, cryptid species, however, did not occur until 2003 (International

Commission on Zoological Nomenclature, 2003). Given the cryptic differences between *P. pipistrellus* and *P. pygmaeus* and the overlap in their habitat use and range (Russ, 2021), it is therefore possible that a Norwegian population exists. In order to ascertain this, however, genetic sampling of *Pipistrellus* spp. across Norway would be necessitated. Whilst the possibility of *P. pipistrellus* occurrences within the study area are therefore acknowledged, the best information available excludes them from the study population.

Pipistrellus spp. are predominantly cavity roosters, making their homes in a variety of small holes and openings. In forest habitats, common roost sites include underneath sloughing bark, in tree holes, and in vertical splits (Jones & Froidevaux, 2020; Russ, 2020). Not all potential roost sites are suitable, however, and roost trees have been found to be consistently tall with large diameters at breast height (DBH), situated in forest stands with high snag densities and open canopies (Kalcounis-Rüppell et al., 2005). Due to intensive forest management practices and land use changes, the number of suitable natural roost sites has been reduced, and many of western Europe's cavity roosting bat species now rely on manmade structures (Dietz & Kiefer, 2016; Kunz & Fenton, 2005). The roosts of *Pipistrellus* spp. can therefore be found underneath the cladding of buildings, in wall cavities and cracks, and in attic spaces, as well as in both bat and bird boxes (Dietz & Kiefer, 2016; Jenkins et al., 1998; Jones & Froidevaux, 2020; Michaelsen et al., 2014; Russ, 2020).

Foraging guilds are one way of categorising insectivorous bats, based on their suitability for foraging in differing levels of clutter (Denzinger & Schnitzler, 2013). One application of foraging guilds is to separate bats within a community into long-, medium-, and short- range echolocators. Medium range echolocating (MRE) species (such as *Pipistrellus* spp.) are those which utilise echolocation well adapted to flying at forest edges and tend to have calls where the most energy is used between 30 kHz – 50 kHz (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2014). The echolocation of *Pipistrellus* spp. also displays considerable plasticity, allowing individuals to change their call characteristics to better suit their surroundings. When echolocating in more cluttered environments, the peak frequency (the frequency at which the amplitude is greatest within the call, FP) of *Pipistrellus* spp. vocalisations will increase, and the inter-pulse interval will decrease, whilst in more open environments, the opposite is true (Kalko & Schnitzler, 1993; Kalko, 1995; Pye, 1980; Russ, 2021). As such, although the preferred foraging locations for *P. pygmaeus* and *P. nathusii* are riparian and riparian

woodland habitats (Jones & Froidevaux, 2020; Russ, 2020), they can also be found in a range of different environments (Rachwald et al., 2016).

2.3 Acoustic Monitoring

Acoustic monitoring was conducted using Song Meter Ultrasonic Bioacoustics Recorders (SM4-BATFS) (hereby referred to as detectors) fitted externally with cardioid directional ultrasonic microphones (SMM-U2). In cases of equipment failure where microphones needed to be replaced and no SMM-U2 microphones were available, detectors were fitted with omnidirectional ultrasonic microphones (SMM-U1). Detectors were programmed to begin recording one hour before sunset, and to cease recording one hour after sunrise. Sunrise and sunset were calculated by the detectors automatically each day based on their GPS location. Recording was triggered by non-ambient, ultrasonic sound activity (for detector settings see Appendix Table A2).

At each of the 12 sites, three detectors were deployed, one in each of the surveyed habitat types. In the Open and Interior habitats, detectors were deployed at ground level by securing them to 1.5 m tall wooden poles, staked 20 cm into the ground (Figure 2a, 2b). To improve recording quality while accounting for differences in habitat type, Open habitat detectors were positioned at least 5 m away from cluttered vegetation, whilst Interior habitat detectors were positioned at least 2 m away from cluttered vegetation. SMM-U2 microphones were deployed at the top of the wooden poles, positioned pointing upwards towards the sky. SMM-U1 microphones were positioned at an approximate 45-degree angle, oriented toward the most open space in the plot, and away from clutter. Canopy detectors were deployed in trees with branches suitable for pulley systems, and where it was possible to reduce vegetation clutter around the microphone whilst still sampling the sites typical canopy. Detectors were attached to chosen trees at breast height (Figure 2c) whilst microphones were hoisted into the canopy via a rope pulley system (Appendix Figure A2). To attach microphones to the detectors, 50 m microphone extension cables were used. All Canopy habitat detectors were placed approximately 30 m from ground level detectors to prevent recording duplication as much as possible. Each detector was locked shut using a combination padlock, and informative signs were placed to deter public interference.

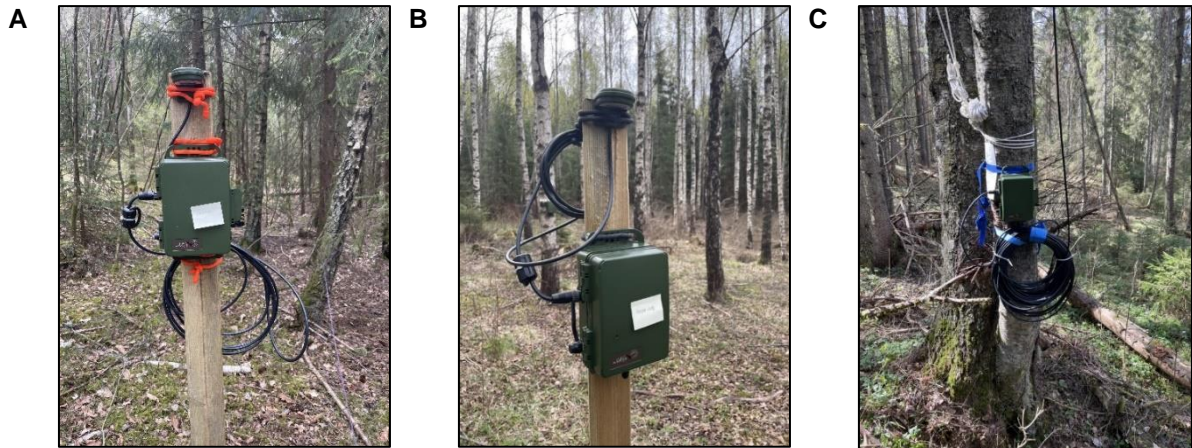


Figure 2. Deployment setup for SM4-BATFS acoustic bat detectors and SMM-U2 microphones at each of the three surveyed habitat types. (A) Interior habitat (B) Open habitat (C) Canopy habitat.

Regular maintenance checks were required throughout the season to ensure equipment functionality and monitor for any technical issues. These checks were performed every 2-3 weeks from deployment until retrieval and were generally carried out by a team of two individuals. During maintenance checks, a standard checklist procedure was followed. Field crews checked each detector's time and date, remaining battery voltage, and available memory card space, and performed microphone calibration tests. All equipment was also checked to ensure that it remained securely in place and had not been disturbed. Batteries and equipment were replaced as necessary, and memory cards were collected and replaced periodically throughout the season depending on the level of site activity.

At every visit a datasheet was filled out for each detector, with information pertaining to the maintenance carried out, and status of the deployed equipment. Retrieved SD cards were checked against the datasheets, and unique SD card ID numbers were recorded at each new deployment. Once all sites had been visited, all information was manually transferred to the project's main Daily Progress Report (DPR). This allowed all team members easy, digital access to datasheets, and provided a backup for the information should the physical sheets become damaged in the field.

2.4 Forest Structure Measurements

A number of forest structure measurements were collected within a 100 m² radius at each of the 36 detector sites (3 in each of the 12 study sites), using both remote sensing data and in-field measurements. The main metric used as a proxy for forest density was the number of stems with a DBH of > 5 cm, counted within the circular 100 m² plot, including live and dead trees as well as snags (Appendix Table A3). Other proxies for forest density were; (1) ground cover, estimated through visual inspection of vegetation, which was then categorised (No, Sparse, Intermediate, Full, Lush), and converted to a score of 1 – 5; (2) relascope sum, sampled from the centre of each 100 m² radius plot, using a relascope; (3) Basal area (BA), calculated by measuring all tree species with a DBH of > 5 cm (living and dead) to establish the average area of each habitat plot occupied by tree stems, expressed per unit of land area (100 m²); and finally (4) predicted number of trees per hectare, calculated using model 3 from Eid (2001), with basal area and crown cover data taken from SR16 forest resource maps (Astrup et al., 2019).

2.5 Acoustic Analysis

Acoustic data was processed from its raw format (.wav files) into standardised bat passes using Kaleidoscope Pro Analysis Software (Wildlife Acoustics, 2022). In this study, a bat pass was characterised as a 5 second triggered recording, processed in Kaleidoscope Pro (Wildlife Acoustics, 2022) to filter noise and estimate species. A 5 second minimum recording was chosen as it allowed bat activity to be quantified in a more cluttered environment, and made recorded bat passes more comparable. For species estimates, Kaleidoscope Pro's automatic classifier "Bats of Europe" (Wildlife Acoustics, 2022) was employed. This classifier matches patterns in recorded files with those from its own database in order to estimate bat species, with identifications limited to taxa found throughout Europe. Included species were further constrained within the classifier to include only those found within Sweden and Norway (Appendix Table A4). The software, however, has limited accuracy, thus, automatic IDs were used only as a baseline, and manual analysis was also conducted. To enable the software to distinguish between bat vocalisations and other noise as much as possible, the signal parameters in Appendix Table A5 were used.

Once the raw acoustic data had been processed, passes identified by the automatic classifier as *P. pygmaeus*, *P. nathusii*, *P. pipistrellus*, *Nyctalus noctula*, and *Nyctalus leisleri*, along with those categorised as “No ID”, were manually analysed and verified through visual inspection in Kaleidoscope Pro (Wildlife Acoustics, 2022). These species IDs were chosen for manual analysis as they were the most likely to contain passes of target species. Those identified as “No ID” were passes in which the automatic classifier recognised bat activity but was unable to make a species determination. Conducting manual acoustic analysis also enabled the identification of passes containing multiple individuals of different species, as well as behaviour; neither of which is possible using the automatic classifier. During manual analysis, each pass was categorised based on three main behavioural groups: commuting, feeding, and social. If a pass contained only echolocation, it was categorised as “commuting”, however if it contained feeding buzzes or social calls, it was labelled as “feeding” or “social” respectively. If a pass contained both feeding and social behaviour, it was identified as both.

2.5.1 Manual Identification

The target species of this study, *P. pygmaeus* and *P. nathusii*, both produce frequency modulated quasi-constant frequency (FMqCF) vocalisations (Appendix Figure A3a), which can be acoustically identified to the species level using several diagnostic parameters. These include FP, inter-pulse interval, and the start and end frequency of vocalisations. In this study, the main parameter used was FP. Typically, echolocation produced by *P. pygmaeus* has an FP range of between 49.8-64.1 kHz, whilst for *P. nathusii*, it is between 35.5-46.1 kHz (Russ, 2021).

Feeding behaviour was assessed in each *Pipistrellus* spp. pass. When *Pipistrellus* spp. capture prey, their echolocation signals change, and they produce a characteristic three-stage vocalisation (Appendix Figure A3b). The three stages are searching, approaching, and a terminal feeding buzz, over which time signal duration decreases and repetition rate increases (Surlykke et al., 2003). In order to be counted as a feeding buzz, a bat pass had to clearly display all three stages.

Pipistrelle spp. produce a range of social calls which vary considerably in their sonographic structure and are categorised as Types A, B, C, and D (Pfalzer & Kusch, 2003). Both Types A

and B are only produced at the roost by stationary individuals, whereas Types C and D are produced during flight (Götze et al., 2020). Of the flight calls, Type C are typically used by one individual whilst flying in tandem to promote cohesion, whereas Type D are used by males in sexual advertisement and agonistic behaviours, as well as in competition during foraging (Appendix Figure A3c) (Barlow & Jones, 1997; Budenz et al., 2009; Chaverri et al., 2018; Götze et al., 2020; Pfalzer & Kusch, 2003; Springall et al., 2019). Although similar, social calls produced by *P. pygmaeus* and *P. nathusii* can be differentiated due to their structural variability (Jahelková et al., 2008; Middleton et al., 2014; Middleton, 2006). In this study, only Types C and D social calls were identified as social behaviour.

2.6 Data Preparation

In preparation for statistical analysis, data was aggregated for night, per detector, per behaviour, per species, using the statistical programme R studio (R Core Team, 2021; RStudio Team, 2020). To create one dataset, the individual .csv files for each of the 36 detector sites were merged. During this process, the data was checked for any duplicate files, and all passes which did not contain target species were removed. In order to compare between all sites, the period containing the least equipment failures was chosen for analysis. This was between 14th May – 28th June 2021. For passes which contained multiple bat species or behaviours, each distinct ID was added to the dataset as a separate pass. Following this, any remaining non-target species were removed, before merging with forest inventory and SR16 map data. The dataset was then aggregated to night, centring the day at midnight rather than noon. As there were nights where the detectors were deployed and active, but no passes were recorded, it was necessary to manually insert zero-activity nights in order to obtain a complete dataset for the target period.

2.7 Statistical Analysis

All data was analysed in R Studio (R Core Team, 2021; RStudio Team, 2020). To ensure the accuracy of regression results, multicollinearity between forest density variables was investigated (Appendix Figure A4). If a variable was found to have a Generalised Variance

Inflation Factor (GVIF) of above 5, it was not used during statistical modelling. All terms included in exploratory analyses had GVIFs under 1.4, indicating low multicollinearity.

The data was also checked for zero-inflation using the R package “DHARMA” (Hartig, 2022), which was found to be extremely high (90 %) (Appendix Figure A5). This was due to many observation bouts containing zero bat passes. It was therefore necessary to model all relationships using Generalised Linear Mixed Models (GLMM’s) fitted with a zero-inflated negative binomial distribution. This allowed for the statistical distinction between “true zeros” and “excess zeros” within the data, accounting for over-dispersion. GLMMs were created using the R package “glmmTMB” (Brooks et al., 2017).

2.7.1 Relationship Between Habitat type and Behaviour

To investigate the relationship between habitat type and behaviour, the GLMM formula used was:

$$\text{Bat passes} \sim \text{Habitat} + \text{Behaviour} + \text{Habitat} : \text{Behaviour} + (1 | \text{Site})$$

The response variable, “Bat passes”, described the number of *Pipistrellus* spp. passes per night, per habitat type at each of the 36 detector sites. “Habitat” and “Behaviour” were the explanatory variables. “Habitat” contained the three different habitat types monitored; Open, Interior, and Canopy, whilst “Behaviour” contained the three bat behaviour categories identified; commuting, feeding, and social. Site number was added as a random effect, to account for the non-independence of observations. After fitting the GLMM, a Type III Wald Chi Square Test was conducted to explore whether the number of *Pipistrellus* spp. passes containing each behaviour was significantly different across habitat types. To obtain the estimated marginal means (EMMs), the R package “emmeans” (Lenth, 2023) was used.

2.7.2 Relationship Between Forest Density and Behaviour

Depending on behaviour identification, *Pipistrellus* spp. passes were organised into three subsets: commuting, feeding, and social. This allowed for the assessment of the effect of

forest density on each behaviour type individually. Due to the low number of passes containing social behaviour, however, it was not possible to conduct statistical analysis for this category. After exploratory analyses, number of stems was chosen as the proxy for forest density, as this variable had the strongest relationship with bat activity.

To examine the effect of forest density on feeding behaviour, the final GLMM formula used after model selection was:

$$\textit{Feeding passes} \sim \textit{Habitat} + \textit{Number of Stems} + \textit{Habitat} : \textit{Number of Stems} + (1 \mid \textit{Site})$$

To examine the effect of forest density on commuting behaviour, the final GLMM formula used after model selection was:

$$\textit{Commuting passes} \sim \textit{Habitat} + \textit{Number of Stems} + \textit{Habitat} : \textit{Number of Stems} + (1 \mid \textit{Site})$$

The response variables, “Feeding passes” and “Commuting passes”, described the number of *Pipistrellus* spp. passes per habitat type at each of the 12 sites, over the duration of the target period which displayed feeding and commuting behaviour respectively. “Habitat” and “Number of stems” were the explanatory variables, and site number was added as a random effect. A Type III Wald Chi Square test was conducted for each model to explore whether the number of passes containing each behaviour across habitat types was significantly affected by forest density (number of stems). Graphical model validation was then carried out to check that the statistical models provided an adequate fit to the data. Diagnostic plots were produced through manual code and the R package “DHARMA” (Hartig, 2022).

3 Results

3.1 Pipistrelle Acoustic Activity

Over 45 sampling nights, 166,809 bat passes were recorded across the 36 detector sites. A total of 48,177 passes were manually analysed, of which 16,447 were identified as *Pipistrellus* spp. Just under 98 percent (16,080 passes) were produced by *P. pygmaeus* (PIPY), whereas 0.1 percent (17 passes) were produced by *P. nathusii* (PINA). The remaining 2 percent (350 passes) were identified as a member of the *Pipistrellus* genus; however, species level identification was not possible. They were therefore labelled with the species code “MR1”.

Between sites, observed levels of *Pipistrellus* spp. activity varied (Figure 3a), as did the relative abundance of passes by each species (Figure 3b). Overall, the most *Pipistrellus* spp. activity was recorded at Site FF08, and the least at Site FF10. This was also true of *P. pygmaeus*; however, the species' relative abundance was highest at Site FF12 and lowest at Site FF04. *P. nathusii* was most active at Site FF09, however, the species made up the greatest percentage of passes at Site FF10. The largest number, and highest relative abundance, of MR1 passes were recorded at Site FF04.

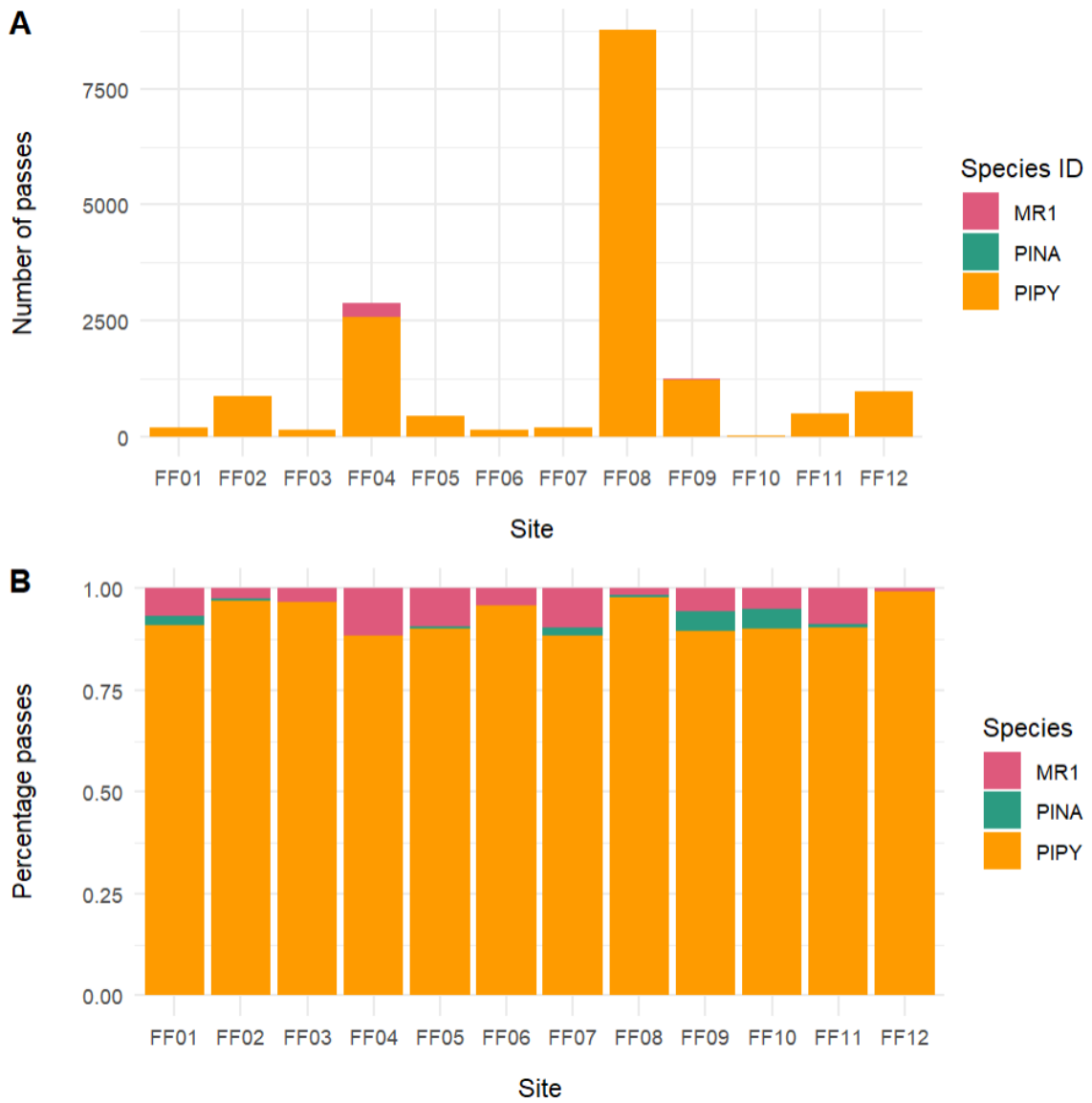


Figure 3. The distribution (A), and proportionate distribution (B) of manually identified *Pipistrellus* spp. passes across the 12 sites. Abbreviations: *Pipistrellus pygmaeus* (PIPY), *Pipistrellus nathusii* (PINA), Unidentified *Pipistrellus* species (MR1). Plots created using the package, ggplot2 (Wickham, 2016) in R Studio (R Core Team, 2021; RStudio Team, 2020).

Owing to the scarcity of *P. nathusii*, it was not possible to perform statistical analysis to ascertain habitat use for each of the target species individually. The raw data, however, suggests that *P. pygmaeus*, *P. nathusii* were most active in Open habitat (Figure 4). *P. pygmaeus* (Figure 4a) was least active in Interior habitat, where the fewest number of MR1 passes were also recorded (Figure 4b), whilst *P. nathusii* (Figure 4c) was least active in Canopy habitat. Due to the small number of observations produced by *P. nathusii*, however, it is not possible to reliably identify trends in the species habitat use, and it is highly likely that those observed here are affected by random variation.

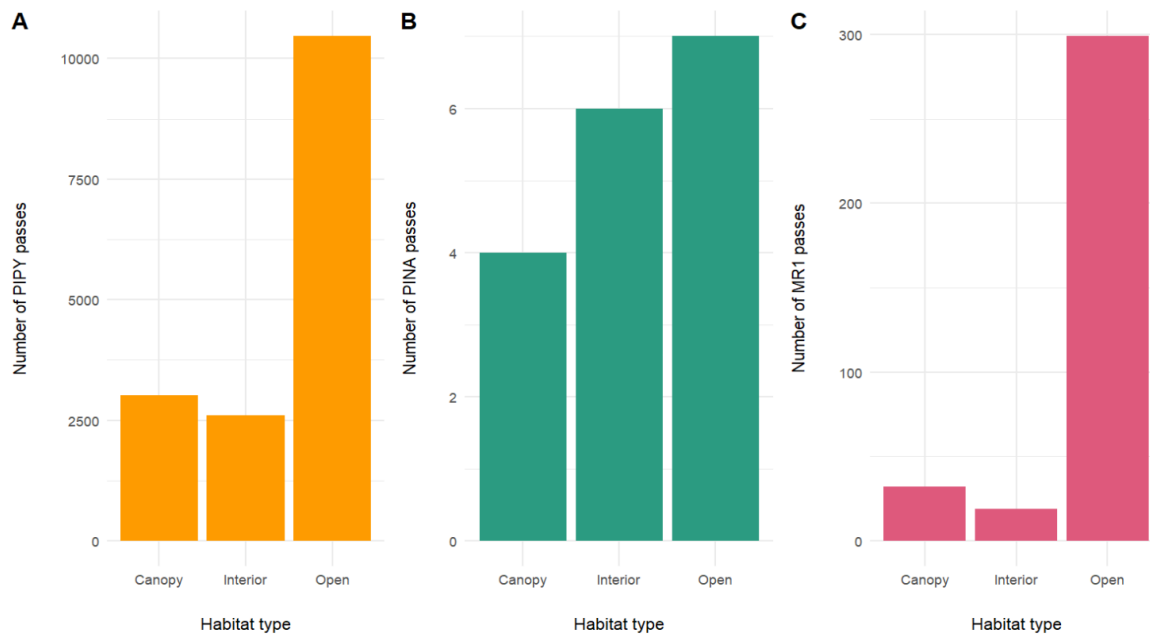


Figure 4. The total number of passes observed per habitat type over the duration of the study (31 nights) manually identified as (A) *P. pygmaeus* (B) *P. nathusii*, and (C) MR1. Due to the extreme differences in the quantity of passes recorded for each species, the Y-axes have been adjusted to fit the data. Plots were created using ggplot2 (Wickham, 2016) in R Studio (R Core Team, 2021; RStudio Team, 2020).

3.2 Influence of Habitat Type

The interaction between habitat type and *Pipistrellus* spp. behaviour was statistically significant ($P = < 0.0001$) (Table 2), implying that behaviour was influenced by habitat type. Between the three behaviours monitored, the relative difference displayed amongst habitat types varied (Figure 5). For all behaviours, activity levels were highest in Open habitat. Interior habitat displayed the lowest activity levels of both commuting and feeding behaviours, whereas levels of social behaviour were equally low in both Interior and Canopy habitat. The relative difference in behavioural activity levels between habitat types was greatest for commuting behaviour, and smallest for social behaviour.

Table 2. Results of a Type III Wald Chi-square test to assess the interaction between the number bat passes and habitat type. The response variable was the number of *Pipistrellus* spp. passes observed per site over the duration of the study (31 nights). The predictor variables were habitat (Open, Interior, and Canopy), and behaviour (commuting, feeding, and social), and site number was added as a random effect to account for non-independence. For summary output tables with Type III Z-test results, see Appendix Table A6.

Variables	Chisq	Df	Pr(>Chisq)
Intercept	1.4393	1	0.2302
Habitat	20.8955	2	2.901e-05
Behaviour	343.7432	2	< 2.2e-16
Habitat:behaviour	54.0795	4	5.065e-11

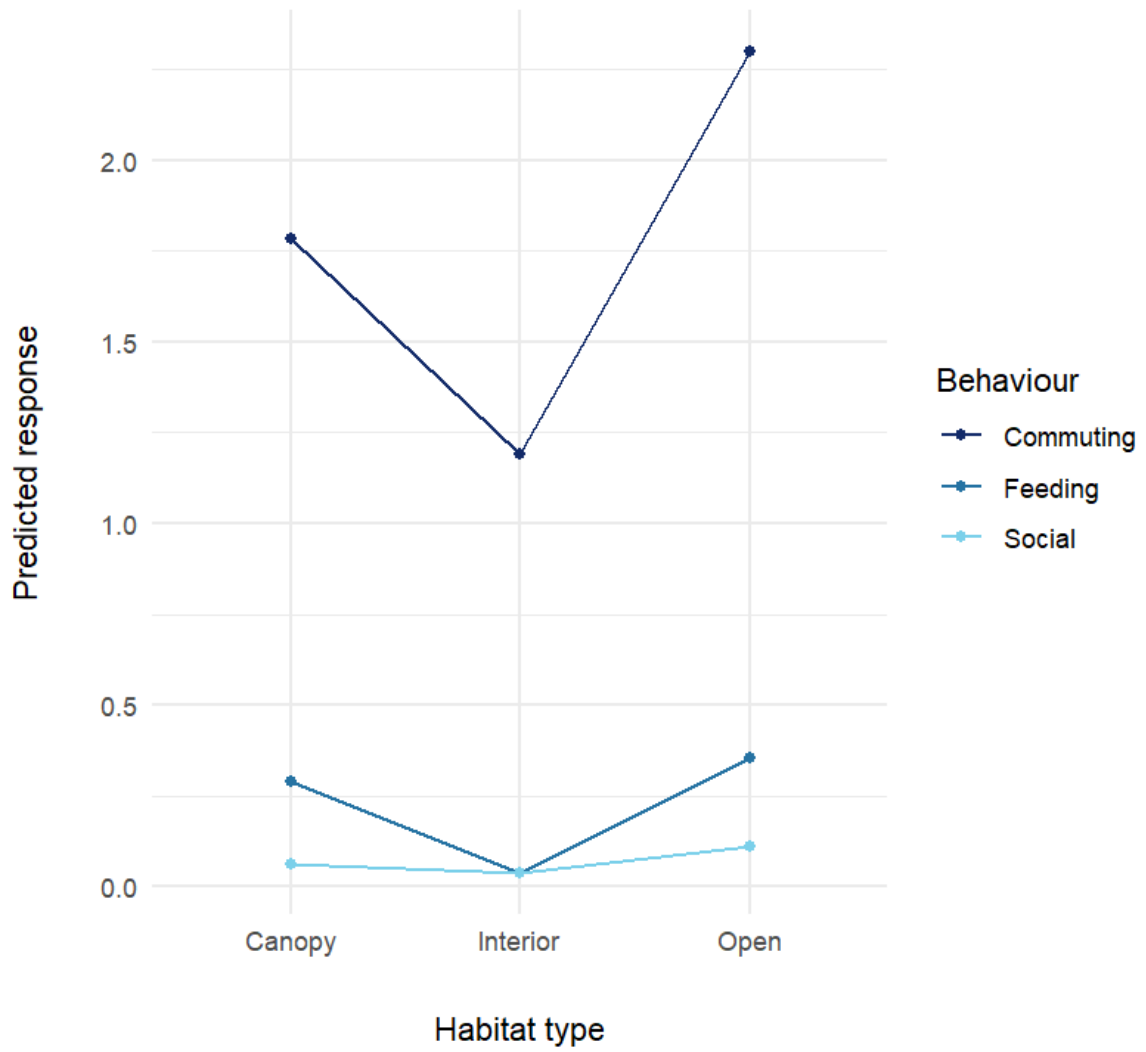


Figure 5. Estimated relationship between *Pipistrellus* spp. behaviour (commuting, feeding and social) with boreal forest habitat type (Open, Interior, and Canopy), based on results of the Type III Wald Chi-square test in Table 2.

The EMMs for each behaviour (Figure 6) show that the confidence intervals for commuting behaviour were extremely wide across all three habitat types. Contrastingly, feeding and social behaviours displayed very narrow confidence intervals, although both behaviours showed more variability in Open and Canopy habitats than in Interior habitat.

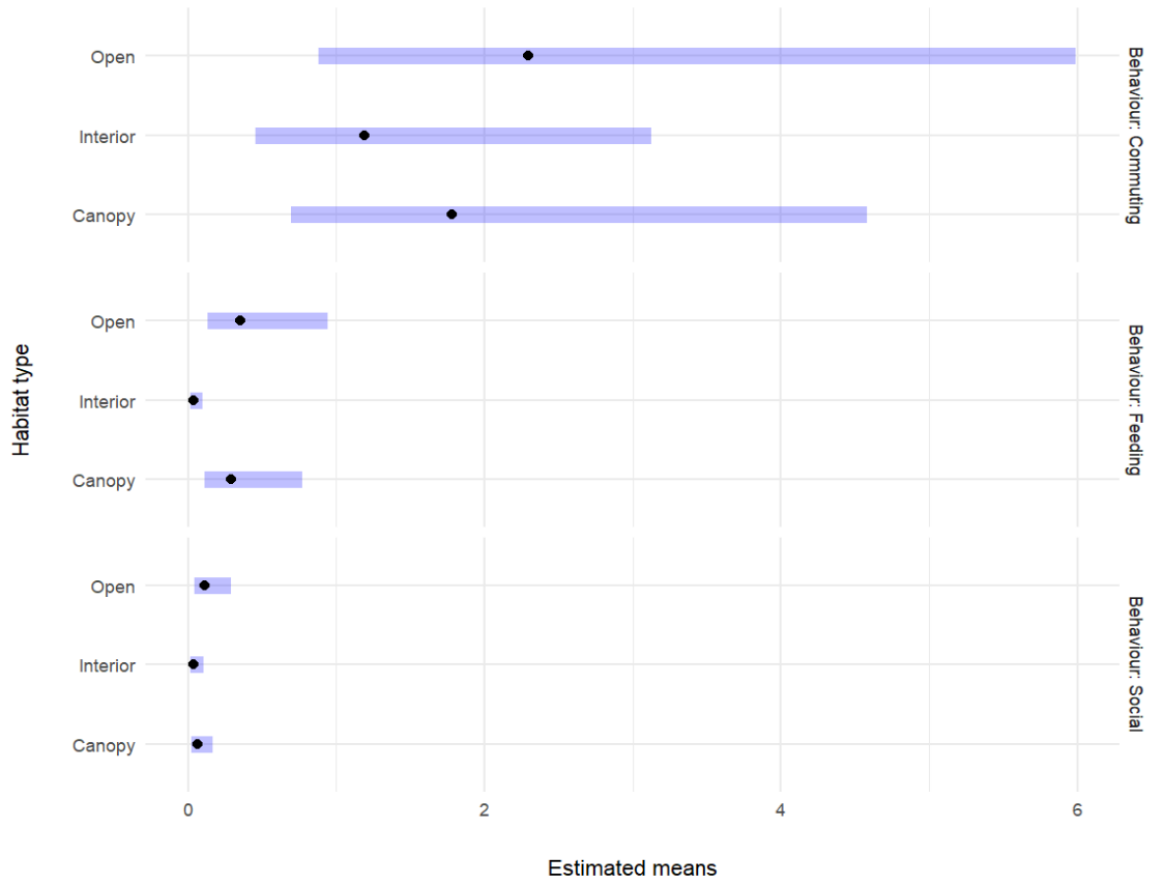


Figure 6. Estimated Marginal Means (EMMs) of *Pipistrellus* spp. behaviour (commuting, feeding, and social) in each of the three habitat types (Open, Interior, and Canopy), and the associated 95% confidence intervals.

3.3 Influence of Forest Density on Feeding Behaviour

The interaction between forest density (number of stems) and habitat type was statistically significant ($P = 0.005705$) (Table 3), indicating that the effect of habitat type on feeding behaviour varied depending on forest density (number of stems). Forest density had a clear negative influence on feeding behaviour, which was most pronounced in Open habitat, but also evident in Interior habitat (Figure 7). In Canopy habitat, however, there is a slight positive influence of forest density.

Table 3. Results of a Type III Wald Chi-square test to assess the relationship between feeding behaviour (the number of *Pipistrellus* spp. passes containing feeding buzzes), habitat type, and forest density (number of stems). The response variable was the number of *Pipistrellus* spp. passes observed per habitat type over the duration of the study (31 nights). The predictor variables were habitat type and number of stems, and site number was added as a random effect to account for non-independence. For summary output tables with Type III Z-test results, see Appendix Table A7.

Variables	Chisq	Df	Pr(>Chisq)
Intercept	4.4878	1	0.034137
Habitat	11.5179	2	0.003154
Number of stems	2.9962	1	0.083459
Habitat : Number of stems	10.3327	2	0.005705

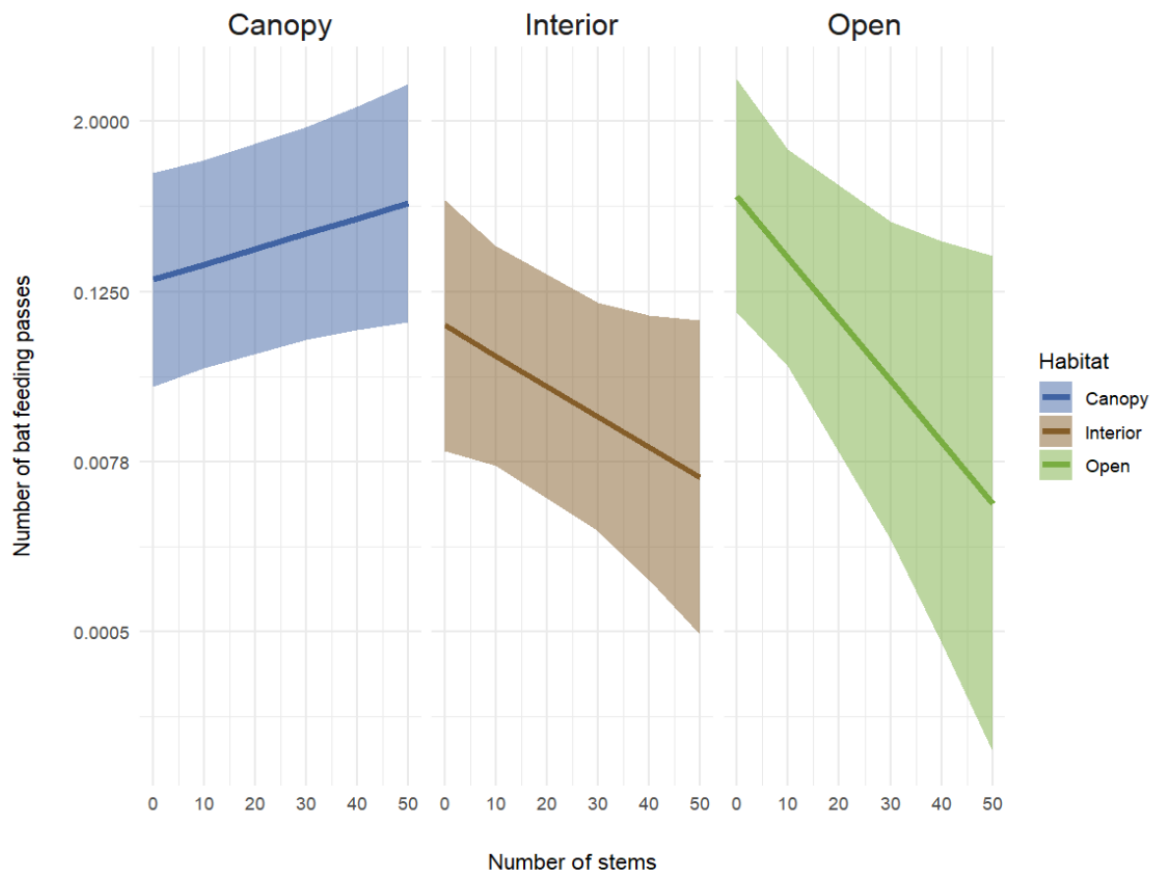


Figure 7. Predicted relationship between forest density (number of stems) and *Pipistrellus* spp. feeding behaviour (number of passes containing feeding buzzes). The predicted relationship is displayed using solid lines, whereas the transparent polygons represent the 95% confidence intervals. Predictions are based on the Type III Wald Chi-square test in Table 3.

3.4 Influence of Forest Density on Commuting Behaviour

The degree to which commuting behaviour was influenced by habitat type was also dependent on forest density (number of stems), as the interaction between habitat type and forest density (number of stems) was statistically significant ($P = 0.002352$) (Table 4). In Open habitat, forest density had a strong negative influence on commuting behaviour, which was also observed in Interior habitat to a lesser extent. In Canopy habitat, however, forest density had an apparent positive influence (Figure 8).

Table 4. Results of a Type III Wald Chi-square test to assess the relationship between the number of *Pipistrellus* spp. commuting passes, habitat type, and number of stems. The response variable was the number of *Pipistrellus* spp. passes observed per habitat type over the duration of the study (31 nights). The predictor variables were habitat type and number of stems, and site number was added as a random effect to account for non-independence. For summary output tables with Type III Z-test results, see Appendix Table A8.

Variables	Chisq	Df	Pr(>Chisq)
Intercept	1.7149	1	0.190346
Habitat	20.5116	2	3.515e-05
Number of stems	5.0843	1	0.024144
Habitat:Number of stems	12.1051	2	0.002352

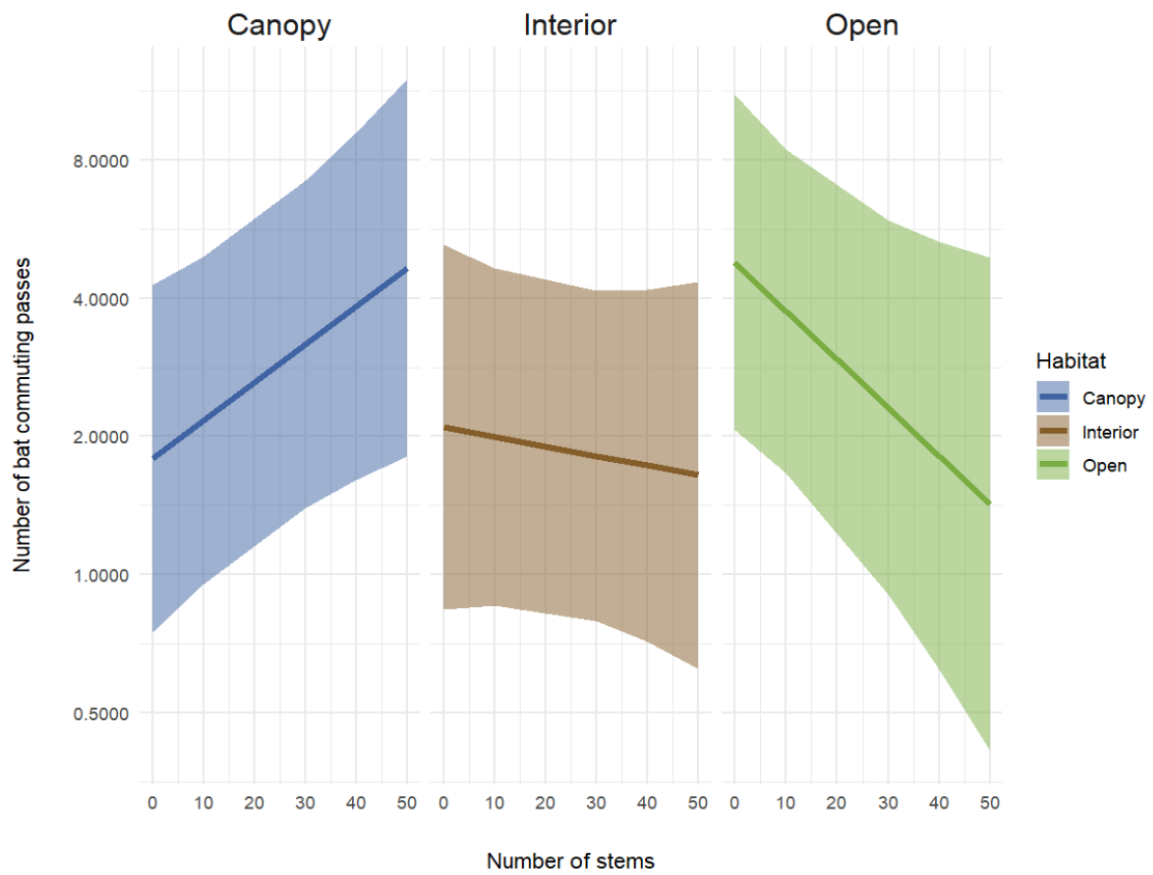


Figure 8. Predicted relationship between forest density (number of stems) and *Pipistrellus* spp. commuting behaviour (number of commuting passes). The predicted relationship is displayed using solid lines, whereas the transparent polygons represent the 95% confidence intervals. Predictions are based on the Type III Wald Chi-square test, in Table 4.

4 Discussion

This study revealed a strong association between habitat type and *Pipistrellus* spp. activity, i.e., commuting, feeding and social behaviour, within Norwegian boreal forests. The findings suggest that Open habitat was the most favourable for *Pipistrellus* spp. activity and displayed the highest levels of feeding and commuting behaviours. Conversely, Interior habitat was the least favourable, and displayed the lowest number of feeding and commuting behaviours. Whilst social behaviour was found to follow similar trends in Open habitat, no clear influence was observed in Interior habitat. Canopy habitat was not utilised to a high extent for any behaviour. Forest stand density (number of stems) was also found to have a modifying influence on activity; negatively influencing feeding and commuting behaviours in Open and Interior habitat, whilst having an apparent positive influence in Canopy habitat. Among sites, large variation was evidenced in activity levels, and *P. pygmaeus* was the dominant species recorded across all sites.

4.1 Influence of Habitat Type on *Pipistrellus* spp. Activity and Behaviour

Pipistrellus spp. activity, i.e. commuting, feeding and social behaviour, was influenced by habitat type. Open habitat generally showed higher utilization compared to Interior habitat, consistent with previous studies (Bartonička & Řehák, 2004; Ciechanowski, 2015; Erasmy et al., 2021; Jung et al., 2012; Kusch et al., 2004; Rachwald et al., 2016; Tena et al., 2020). Across all habitat types, commuting behaviour was the predominant behaviour identified, with the highest number of passes observed in Open habitat, and the lowest in Interior habitat. As *Pipistrellus* spp. are known to move between habitat patches utilising forest edges (Racey & Swift, 1985; Verboom & Huitema, 1997; Verboom & Huitema, 2010), this implies that they may use Open habitat in a similar way, whilst avoiding navigation through Interior habitat (Kusch et al., 2004). Forest gaps are therefore likely to improve habitat connectivity for *Pipistrellus* spp. by facilitating their movement through the landscape. There is, however, high variability in the estimated means for commuting behaviour, indicating the influence of other important factors in addition to habitat type.

Compared with Interior habitats, the amount of *Pipistrellus* spp. feeding behaviour was also markedly increased in Open habitat, further confirming the value of forest gaps. Food is a

limiting factor for bat populations (Kusch et al., 2004; Zahn et al., 2006), and *Pipistrellus* spp. activity has been found to increase in relation to higher densities of dipteran insects (Morris et al., 2010). Typically, forest gaps display increased insect abundances compared with the forest interior (Horn et al., 2005; van Hoesel et al., 2019) due to the higher heterogeneity of 3D structures, and the resultant increase in niche opportunities and insect diversity (Grüebler et al., 2008). Combined with their classification as edge-space, forest gaps are therefore likely to be extremely attractive to *Pipistrellus* spp., as suggested by the high number of feeding behaviours observed in Open habitat.

Although utilised more than Interior habitat, Canopy habitat was not exploited to a large extent, supporting the findings of Plank et al. (2012). The amount of feeding behaviour observed was much lower than in Open habitat, which, given the forest canopy's abundance of insects (Floren et al., 2022; Maguire et al., 2014), and classification as edge-space (Kalko et al., 2008), is somewhat unexpected. In U.K. forests, it has been found that *Pipistrellus* spp. are more active below 30 m (Collins & Jones, 2009), however, the average canopy height within the research area was 23.4 m (Appendix Table A9) (NIBIO, 2023). That *Pipistrellus* spp. also experience high mortality at wind turbine sites (Rydell et al., 2010) further supports that they can, and do, utilise heights within and above the canopy in other areas. There are several potential explanations for the low levels of commuting and feeding behaviours observed. These include high wind speeds (Verboom & Spoelstra, 1999; Verboom & Huitema, 2010), predator avoidance (Lima & O'Keefe, 2013; Verboom & Spoelstra, 1999), niche partitioning between hetero-specifics (Arnett et al., 2007), and temporal shifts in insect abundance (Ruchin & Esin, 2021).

Following the trends observed for commuting and feeding behaviours, social behaviour was found to be highest in Open habitat, although contrastingly, no variance was displayed between Interior and Canopy habitats. Types C and D social calls are known to correlate with increased bat activity (Budenz et al., 2009) and are used only in the presence of conspecifics (Barlow & Jones, 1997; Budenz et al., 2009; Götze et al., 2020; Springall et al., 2019). As such, the small level of variance in activity levels between Interior and Canopy habitat may not have been enough to illicit an increase in social behaviour. This is supported by the low levels also displayed in Open habitat. As this study took place outside the main breeding periods for both *P. pygmaeus* and *P. nathusii* (Bartoničková et al., 2016; Jones & Froidevaux, 2020; Russ, 2020),

Type D social calls were also likely limited to those produced in defence of foraging patches rather than in association with mating activity. Social behaviour may, therefore, display altered trends at different times throughout the season such as during mating, or when juveniles become volant and there is an increased need for in-flight cohesion.

4.2 Modifying Influence of Forest Density on Behaviour

Feeding behaviour displayed a negative correlation with the number of stems in both Open and Interior habitats, although this was far more pronounced in Open habitat. This suggests that as forest density increases, habitat value for *Pipistrellus* spp. decreases, in line with general assessments of bat activity (Humes et al., 1999; Loeb & O'keefe, 2006). Although morphologically adapted to foraging and manoeuvring in higher levels of clutter (Norberg et al., 1997), *Pipistrellus* spp. are intolerant when it comes to overlapping echoes. In cluttered environments, they will only locate and pursue prey from which the returning echoes are distinct from those of environmental clutter, and their own echolocation (Kalko & Schnitzler, 1993). As such, although insect abundances increase in more cluttered habitat (Kalcounis-Rueppell & Brigham, 1995), foraging in these environments likely becomes less attractive for *Pipistrellus* spp., especially if more open areas are available nearby. This is further reinforced by the strength of the estimated relationship between forest density and feeding behaviour in Open habitat. With increased number of stems, feeding behaviour was quickly diminished, likely due to a reduction in canopy gap size, and thus the benefits that they provide. This is supported by the findings of Ford et al. (2005) which links smaller forest gaps with decreased activity of forest bat species.

Commuting behaviour showed a similar decrease in association with forest density both in Open and Interior habitat, implying a preference by *Pipistrellus* spp. for flying in less cluttered spaces. This may be due to the increased energy expenditure required to manoeuvre through clutter, which is particularly pertinent for the study period when females would have been either pregnant or lactating (Jones & Froidevaux, 2020; Russ, 2020). It can therefore be reasonably conjectured that in the presence of more cluttered habitats, that *Pipistrellus* spp. find alternate routes through which to travel, such as above the treetops, in order to conserve energy. It is also likely that denser forests provided less suitable roost habitats (Kalcounis-

Rüppell et al., 2005; Perry et al., 2007), and as such, fewer individuals pass through these areas each night. At higher number of stems, the confidence intervals in Open habitat for both feeding and commuting behaviours were extremely wide, indicating high levels of uncertainty in the estimated relationship. This was likely an artefact of few observations, as limited Open habitat plot types had a high number of stems.

In contrast to the trends observed in Open and Interior habitat, in Canopy habitat there was an apparent positive influence of forest density on commuting and feeding behaviours. This lends support the notion that at increased forest densities *Pipistrellus* spp. will utilise the space just above the treetops, rather than manoeuvring through clutter. Although this is the most likely explanation for the estimated relationship, it may also be possible that with increased numbers of stems, *Pipistrellus* spp. are able to utilise the canopy edge-space more effectively. *Pipistrellus* spp. are known to be less active in areas exposed to high winds (Verboom & Spoelstra, 1999), and thus the addition of stems within the canopy strata may act as a wind buffer, whilst increasing foliage cover may also afford greater protection from avian predators (Lima & O'Keefe, 2013).

4.3 *Pipistrellus* Species Activity and Among-sites variation

Throughout the research area, extreme variation between activity levels of *P. pygmaeus* and *P. nathusii* were observed, as anticipated. Whilst *P. pygmaeus* is one of Norway's most abundant bat species, historically, observations of *P. nathusii* have largely been confined to the species' migration periods in the spring and autumn (Eldegard et al., 2021). Recently, however, increased summer observations have been noted in the country's southern regions (Artsdatabanken, 2023), lending credence to this study's findings of the species during May and June. This is particularly interesting when considered in light of evidence suggesting a recent increase in *P. nathusii*'s continental range (Lundy et al., 2010) and northern activity (Kotila et al., 2023). The low numbers of *P. nathusii* passes recorded (n = 17), however, still suggests vagrant individuals rather than a summer population, which is supported by the fact that all individuals captured during the breeding season in Norway have been adult males (Eldegard et al., 2021). Additionally, it has been found that during the maternity period, when juveniles are not yet volant, high densities of flying individuals can cause *P. pygmaeus* to use

frequencies as low as 44 kHz (Montauban et al., 2021). There is, therefore, some uncertainty attached to the classification of passes identified as *P. nathusii* in this study.

The small number of passes (n = 350) which were unable to be identified to the species level displayed FPs between 46.2 - 49.7 kHz, fitting with *P. pipistrellus* echolocation. In 2007 the species was identified in Stavanger in Norway's southwest through expert analysis of acoustic recordings (Størkersen et al., 2010), although further verified instances have not been documented. It may still be possible, however, that a Norwegian population has been overlooked, and vocalisations misidentified (Michaelsen, 2015). *P. pipistrellus* has known populations in southern Sweden, Denmark, and Scotland (IUCN, 2022), thus, their presence in Norway is not implausible, especially in light of climate-induced species range expansions (Chen et al., 2011). Given the plasticity of *Pipistrellus* genus echolocation and the lack of evidence in favour of a Norwegian population, however, it is most reasonable to assume that these unidentified passes were produced by either *P. pygmaeus* or *P. nathusii*. It has been found that in the absence of *P. pipistrellus*, *P. pygmaeus* will occupy their acoustic niche, producing calls characteristic of their congeneric species (Montauban et al., 2021).

Among the study sites, huge variation in the number of recorded passes was observed. At some sites, activity was extremely low, for instance at Site FF10, where just 22 *Pipistrellus* spp. passes were recorded. Of the locations monitored, this site was situated the closest to a major road, and farthest away from a large freshwater source. As *P. pygmaeus* actively selects riparian habitat (Davidson-Watts & Jones, 2006; Davidson-Watts et al., 2006; Nicholls & A. Racey, 2006), and *Pipistrellus* spp. have been found to select habitat further away from roads (Loeb & O'keefe, 2006), this lack of activity can likely be attributed to the availability of more suitable habitat nearby. In contrast, observations at Site FF08 were more than 3 times higher than at the next most active location, the most reasonable explanation for which is the presence of a nearby roost. During lactation (June – July), *P. pygmaeus* females have been found to return to their nursery roosts approximately 3.7 times per night (Bartonička et al., 2012), with colonies comprising of anywhere between 20 – 650 individuals (Jones & Froidevaux, 2020).

The extreme level of among-site variation illustrates the importance of monitoring sufficient sites during bat surveys, to best represent populations and build the most accurate picture

possible of their status and habitat use. All study sites were manually assessed and determined to be good quality potential bat habitats, thus the level of variation observed implies nuanced, species-specific habitat selection (Kusch & Schmitz, 2013). As *Pipistrellus* spp. are known to roost switch frequently throughout the season (Bartonička et al., 2012), many sites may experience changes in activity levels during different periods. Short-term monitoring of too few sites is therefore likely to misrepresent *Pipistrellus* spp. populations, and lead to incorrect assessments of habitat value.

In terms of bat monitoring programmes, under-representation can lead to the incorrect assumption that within certain areas, some species do not occur. In such instances, anthropogenic activities are not obliged to take such species into account, and potentially vulnerable populations may face increased threats to their habitat. Similarly, over-representation of bat species with high-conservation status may lead to masking of population declines for “common” species and hinder the implementation of necessary conservation measures. As different bat species utilise 3D habitats in different ways, employed monitoring strategies therefore need to take species-specific variations into consideration, and employ appropriate long-term monitoring of various forest sub-habitats, in multiple locations. Due to the increased accessibility of acoustic bat detectors, long-term, broad scale, coordinated studies are feasible, as demonstrated by Kotila et al. (2023).

Traditionally, threatened species have been the primary focus for conservation biologists, however, declines of previously “common” species is of growing concern. One of the characteristic species of the Fennoscandian boreal forest is the willow tit (*Poecile montanus*). Whilst classified as of “Least concern” in 2015 by the Norwegian National Red List, the species is now listed as “Vulnerable” due to a drastic decline in population numbers, with similar trends in Sweden and Finland (Artsdatabanken, 2021). This illustrates the importance of conservation strategies for all species, even those that are considered “common”, and confirms the importance of regular monitoring initiatives. The decline in willow tit abundance is especially pertinent to bat conservation due to their occupancy of similar ecological niches. As such, the threats that have resulted in the willow tits decline are also likely to threaten many of Norway’s bats. As Norwegian bat monitoring programmes are still severely lacking, information gathered on insectivorous forest birds could therefore provide insights which may positively impact bat conservation and management decisions.

4.3.1 Limitations of Acoustic Monitoring

Although passive acoustic monitoring is an extremely valuable survey method, it does come with limitations. Due to the nature of echolocation, detectability varies between species and habitats, based on vocalisation frequencies, and the amount of clutter present (Dietz & Kiefer, 2016). Low intensity, high frequency calls, for instance, travel shorter distances than high-intensity, low frequency calls (Lawrence & Simmons, 1982), whilst higher levels of clutter are progressively effective at blocking sound waves. Variance in microphone sensitivity may also result in reduced detectability, although using current technology this is unavoidable (Adams et al., 2012; Agranat, 2014; Frick, 2013; Kunberger & Long, 2023). In order to represent the most complete picture possible of bat activity, detector placement is therefore a key consideration (Frick, 2013).

When dealing with large datasets, automatic classifiers can be helpful tools, however their accuracy varies and does not compare to trained human analysts (Russo & Voigt, 2016). Of the passes automatically identified as *Pipistrellus* spp. in this study, 1,162 were manually identified as “noise” as they did not contain bat activity. In order to obtain reliable identifications, manual analysis is therefore necessitated, however, accuracy is still never guaranteed due to human error. Factors such as the environmental conditions, the presence of con- and hetero- specific, and the level of ambient noise, can all affect recording quality, complicating species level identification. In the case of *Pipistrellus* spp., different environments also provoke changes in echolocation structure (Kalko & Schnitzler, 1993; Kalko, 1995; Pye, 1980; Russ, 2021), which, when combined with a poor-quality recording, can result in misidentification.

5 Management Implications

By studying species-specific sub-habitat relationships within the same forest location, responses to structural changes within these environments may be better understood and predicted. With the prevalence of intensive production forestry in Norway this is especially important, as large-scale habitat alterations are frequent within the landscape. The findings of this study show that boreal forests with a more natural dynamic, containing canopy gaps and a more heterogeneous structure, are valuable habitat for *Pipistrellus* spp. populations. Whilst many would argue that the space between forests and clear-cuts could provide beneficial forest gaps, research has found that due to foraging strategy diversity among bat species, clear-cuts can have both positive and negative impacts (Patriquin & Barclay, 2003). Smaller forest gaps, however, have been evidenced to benefit both open-adapted, and clutter adapted bat species (Loeb & O'Keefe, 2011). Promoting forest gaps within production forests, and maintaining and managing those that already exist, could therefore help to maintain bat species richness both in Norway, and throughout Fennoscandia.

6 References

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7 Appendices

Table A1. Coordinates for the location of each habitat type, by site.

Site Number	Habitat Type	Longitude	Latitude
FF01	Canopy	59.67172	10.75566
	Interior	59.67155	10.75560
	Open	59.67187	10.75553
FF02	Canopy	59.69589	10.75455
	Interior	59.69598	10.75425
	OB	59.69581	10.75481
FF03	Canopy	59.75812	10.75956
	Interior	59.75831	10.75945
	Open	59.75810	10.76001
FF04	Canopy	59.72195	10.71130
	Interior	59.72193	10.71168
	Open	59.72206	10.71096
FF05	Canopy	59.71337	10.71386
	Interior	59.71311	10.71392
	Open	59.71359	10.71314
FF06	Canopy	59.71643	10.68881
	Interior	59.71653	10.68875
	Open	59.71617	10.68890
FF07	Canopy	59.68034	10.80425
	Interior	59.68042	10.80441
	Open	59.68042	10.80361
FF08	Canopy	59.67624	10.73215
	Interior	59.67614	10.73172
	Open	59.67603	10.73217
FF09	Canopy	59.69189	10.68572
	Interior	59.69236	10.68561
	Open	59.69151	10.68621
FF10	Canopy	59.61194	10.72722
	Interior	59.61177	10.72689
	Open	59.61200	10.72681
FF11	Canopy	59.68329	10.76040
	Interior	59.68348	10.76080
	Open	59.68359	10.76067
FF12	Canopy	59.71892	10.73546
	Interior	59.71857	10.73563
	Open	59.71893	10.73600

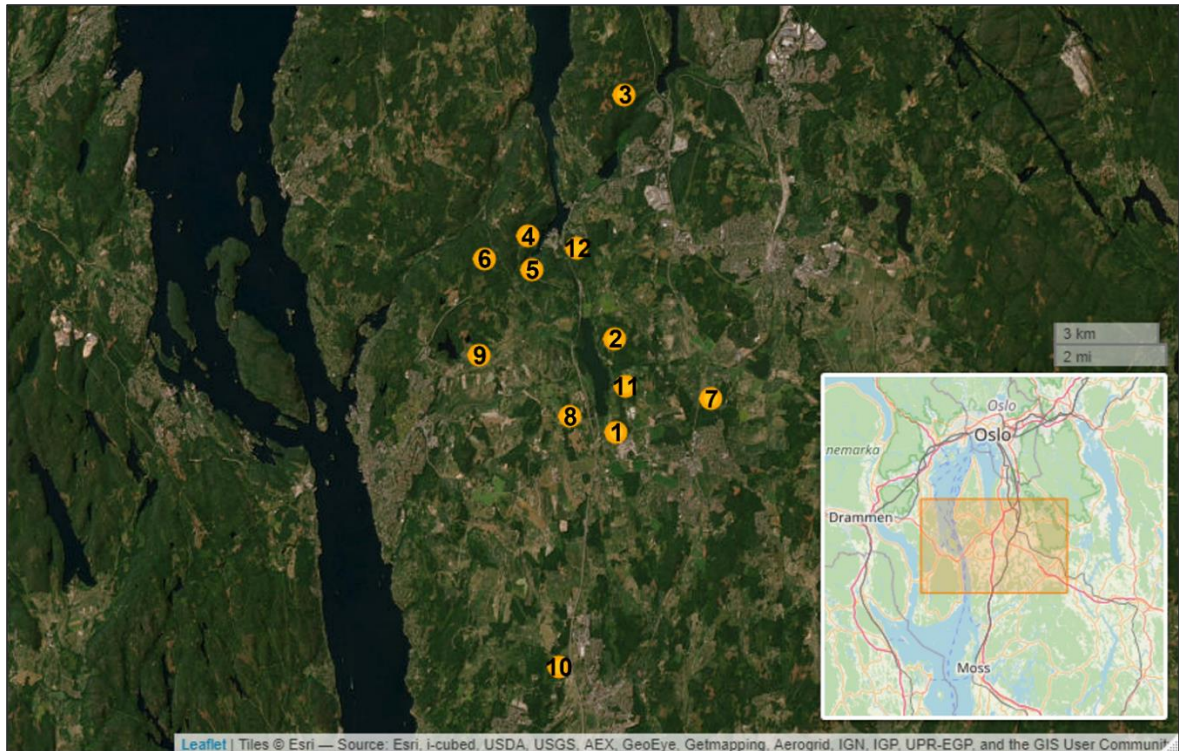


Figure A1. Map denoting the location of each of the 12 study sites, labelled with site numbers. Created using the Leaflet package (Graul, 2016) in R Studio (R Core Team, 2021; RStudio Team, 2020).

Table A2. Settings & Firmware for Song Meter SM4Bat Bioacoustics Recorder.

Firmware: 2.4.1

UTC	+2:00
Gain	12 dB
16k high filter	Off
Sample rate	256 kHz
Min duration	1.5 ms
Max duration	None
Min trigger frequency	12 kHz
Trigger level	12 dB
Trigger window	3 s
Max length	15 s
Compression	None

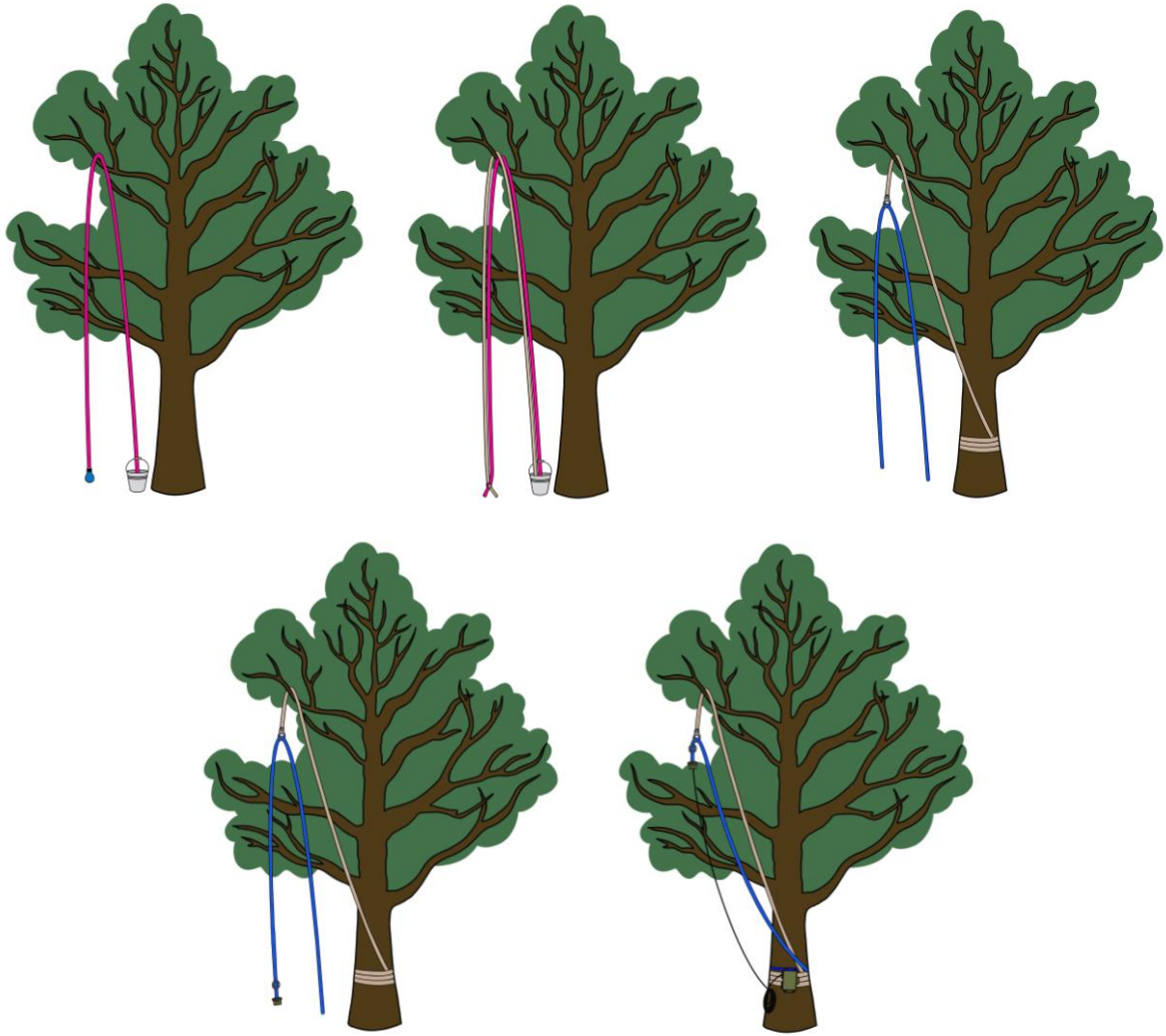


Figure A2. Steps of deployment for microphones in Canopy habitat via a pulley system.

Table A3. Number of stems measured within 100m² plot, at each detector site.

Site number	Habitat type	Number of stems
FF01	Canopy	6
	Interior	23
	Open	12
FF02	Canopy	5
	Interior	8
	Open	9
FF03	Canopy	23
	Interior	28
	Open	28
FF04	Canopy	11
	Interior	9
	Open	3
FF05	Canopy	22
	Interior	19
	Open	0
FF06	Canopy	39
	Interior	49
	Open	2
FF07	Canopy	10
	Interior	18
	Open	10
FF08	Canopy	10
	Interior	17
	Open	8
FF09	Canopy	49
	Interior	31
	Open	5
FF10	Canopy	43
	Interior	54
	Open	38
FF11	Canopy	20
	Interior	15
	Open	10
FF12	Canopy	17
	Interior	24
	Open	7

Table A4. Bats species included in the automatic classification process and whether they are found in Norway or Sweden. During manual acoustic analysis, only bat species known to reside in Norway were found.

Species	Resident country
<i>Barbastella barbastellus</i>	Norway, Sweden
<i>Eptesicus nilssonii</i>	Norway, Sweden
<i>Eptesicus serotinus</i>	Sweden
<i>Myotis alcathoe</i>	Sweden
<i>Myotis bechsteinii</i>	Sweden
<i>Myotis brandtii</i>	Norway, Sweden
<i>Myotis dasycneme</i>	Sweden
<i>Myotis daubentonii</i>	Norway, Sweden
<i>Myotis myotis</i>	Norway, Sweden
<i>Myotis nattereri</i>	Norway, Sweden
<i>Nyctalus leisleri</i>	Sweden
<i>Nyctalus noctula</i>	Norway, Sweden
<i>Pipistrellus nathusii</i>	Norway, Sweden
<i>Pipistrellus pipistrellus</i>	Sweden
<i>Pipistrellus pygmaeus</i>	Norway, Sweden
<i>Plecotus auritus</i>	Norway, Sweden
<i>Plecotus austriacus</i>	Sweden
<i>Vespertilio murinus</i>	Norway, Sweden

Table A5. Signal parameters used to distinguish between bat calls and noise files in Kaleidoscope Pro Analysis Software (Wildlife Acoustics, 2022).

Minimum/maximum frequency range	8-120 kHz
Minimum/maximum pulse length	2-500 ms
Maximum inter-syllable gap	500 ms
Minimum number of pulses	2

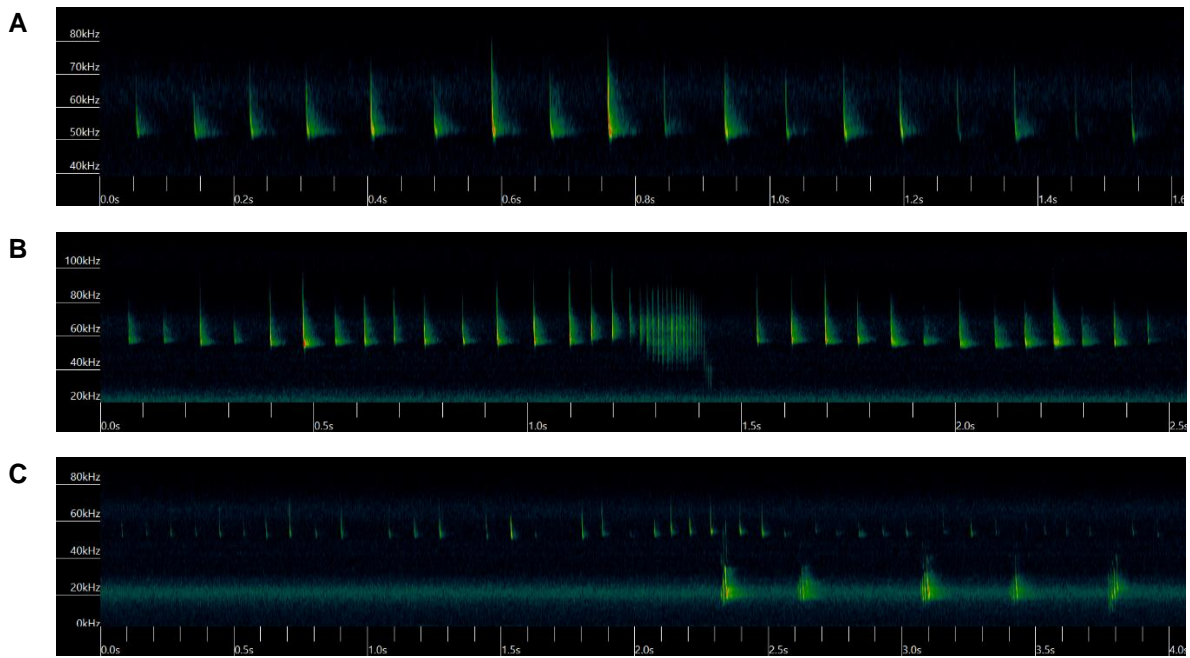


Figure A3. Examples of *Pipistrellus* spp. behaviour displayed on a spectrogram viewed in Kaleidoscope Pro (Wildlife Acoustics, 2022). Example species = *Pipistrellus pygmaeus*. (A) Commuting behaviour. Evenly distributed FMqCF echolocation pulses, with FP > 50 kHz (B) Feeding behaviour. A feeding buzz containing the three distinct stages; searching (0.0 s – 1.1 s), approaching (1.1 s – 1.2 s), and terminal feeding buzz (1.25 s – 1.45 s). (C) Social behaviour. Echolocation, with intermittent Type D social calls (2.3 s – 3.9 s). All examples were taken from the study data.

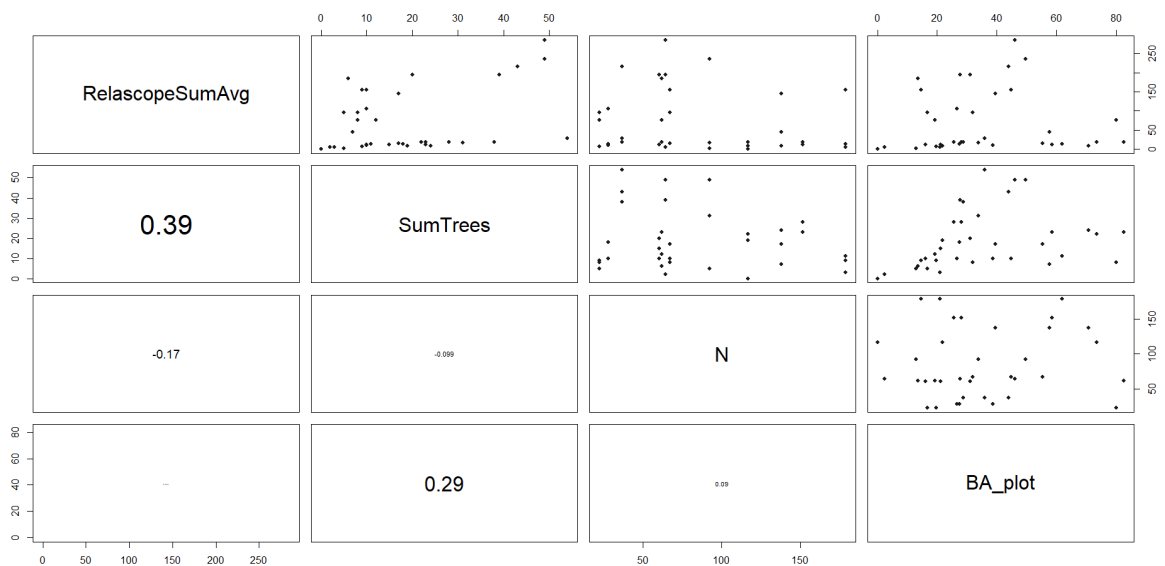


Figure A4. Results from multicollinearity test performed for different proxies for forest density. Proxies included were: relascope sum, the predicted number of stems, number of stems, and basal area.

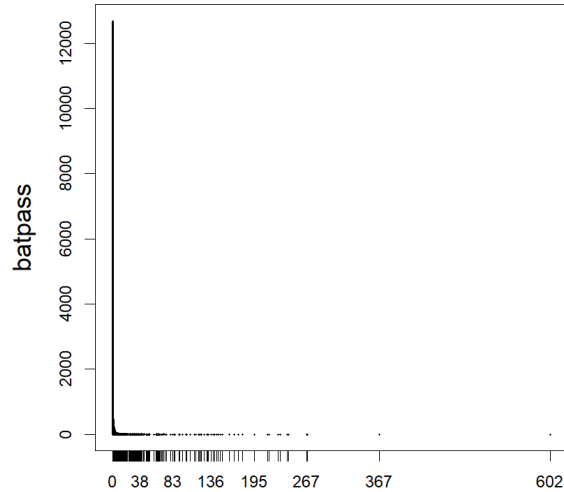


Figure A4. Results of zero-inflation test. Zero-inflation was found to be 90 %, due to many observation bouts containing zero bat passes.

Table A6. Summary output of Type III Z-test results for the estimated relationship between *Pipistrellus* species behaviour (commuting, feeding, and social) and habitat type (Open, Interior, and Canopy).

	Estimate	Std. Error	Z	P
Intercept	0.57802	0.48179	1.200	0.23025
Interior habitat	-0.40383	0.14732	-2.741	0.00612
Open habitat	0.25404	0.14350	1.770	0.07669
Feeding behaviour	-1.81577	0.15617	-11.627	< 2e-16
Social behaviour	-3.34195	0.18929	-17.656	< 2e-16
Interior habitat : Feeding behaviour	-1.64388	0.25209	-6.521	6.99e-11
Open habitat : Feeding behaviour	-0.05769	0.21139	-0.272	0.78492
Interior habitat : Social behaviour	-0.11286	0.28225	-0.400	0.68928

Table A7. Summary output of Type III Z-test results for the estimated relationship between *Pipistrellus* spp. feeding behaviour and forest density (number of stems). The three habitat types were Open, Interior, and Canopy.

	Estimate	Std. Error	Z	P
Intercept	-1.88513	0.88986	-2.118	0.0341
Interior	-0.75076	0.61101	-1.229	0.2192
Open	1.36431	0.54320	2.512	0.0120
Number of stems	0.02488	0.01438	1.731	0.0835
Interior : Number of stems	-0.07448	0.03083	-2.416	0.0157
Open : Number of stems	-0.12538	0.05027	-2.494	0.0126

Table A8. Summary output of Type III Z-test results for the estimated relationship between *Pipistrellus* spp. commuting behaviour and forest density (number of stems). The three habitat types were Open, Interior, and Canopy.

	Estimate	Std. Error	Z	P
Intercept	0.581782	0.444259	1.310	0.19035
Interior	0.157453	0.244394	0.644	0.51941
Open	0.983620	0.229053	4.294	1.75e-05
Number of stems	0.019105	0.008473	2.255	0.02414
Interior : Number of stems	-0.023924	0.009873	-2.423	0.01539
Open : Number of stems	-0.043376	0.013758	-3.153	0.00162

Table A9. Canopy heights for each study site in decimetres, and the associated standard deviation. 1 dm = 10 cm. Information gathered from SR16 map data (NIBIO, 2023).

Site Number	Canopy Height (dm)	SD
FF01	243.22	±25.91
FF02	207.80	±24.48
FF03	214.02	±25.28
FF04	311.41	±28.25
FF05	245.08	±25.90
FF06	209.22	±25.61
FF07	197.68	±24.42
FF08	253.13	±25.41
FF09	219.25	±27.71
FF10	194.79	±24.88
FF11	227.40	±25.82
FF12	281.33	±27.3



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