Norwegian University of Life Sciences
Faculty of Environmental Sciences
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Philosophiae Doctor (PhD)
Thesis 2024:29

Drivers of bat activity and habitat use in boreal forest

Drivere for flaggermusaktivitet og habitatbruk i boreal skog

Reed April McKay

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For the bats

and all the hopeless romantics who chase them in the North

Cover image: Photo captured by an insect camera trap in Frogn municipality in the summer of 2021.

BatLab
Norway

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I went to a lecture on songbird and insect migration given by a visiting scholar when I was a bachelor's student at Indiana University. I had been working with bats for about 2 years at this point and was eager to ask the scholar about the methods they had just presented on and how it could be applied to bat migration research. At the end of the lecture, I approached the scholar to ask my questions. I have thought of the scholar's response often in the twist and turns of my career throughout the years that have followed: **"Bats are a lost cause. Study something else."**

My pursuit to learn more about bats, share this knowledge with others and find ways to put it to use has been a sometimes frustrating, often delightful – absolutely wild adventure. The *adventure* has certainly come with challenges which forced me to learn new skills, to fortify my personal character, and to accept failures. It has not at any point felt like a lost cause. That is because at every step in my career, I have found myself amongst a vibrant and passionate community of naturalists, ecologists, poets, friends, and family who have inspired and supported me. Even so, I am grateful to that scholar from years ago and their bad advice because I have really enjoyed proving them wrong.

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[1] *(sjef)*

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1 List of papers

Paper I

McKay, R.A.; Johns, S.E.; Bischof, R.; Mathews, F.; van der Kooij, J.; Yoh, N. and Eldegard, K. (2023), Wind energy development can lead to guild-specific habitat loss in boreal forest bats. Wildlife Biology e01168. https://doi.org/10.1002/wlb3.01168

Paper II

McKay, R.A.; Yoh, N.; Mathews, F.; Bischof, R.; Eldegard, K. Differences in sub-habitat use throughout the summer for forest specialist bats in mixed boreal forest. Manuscript.

Paper III

Eldegard, K. & **McKay, R.A.;** Thomle, M.K.; Fairchild, J.K.; Sætre, V.; Mathews, F.; Bischof, R. Predatory-prey dynamics in the boreal forest: *Myotis* bat foraging activity depends on insect abundance and forest density. Manuscript.

Paper IV

McKay, R.A., Hoelzl, F., van der Kooij, J., Sørås, R., Ørka, H.O., Smith, S., Stawski, C., Eldegard, K. Foraging ecology of two morphologically similar sympatric bat species. Manuscript.

The following publications and unpublished documents are supporting, but not core elements, of this PhD dissertation.

Choiński, Mateusz; Zegarek, Marcin; Hałat, Zuzanna; Borowik, Tomasz; Kohles, Jenna; Dietzer, Melina; Eldegard, Katrine; **McKay**, **R. A.,** Johns, Sarah E. and Ruczyński, Ireneusz. "Insect Detection on High-Resolution Images Using Deep Learning." In *Computer Information Systems and Industrial Management*, edited by Khalid Saeed, Jiří Dvorský, Nobuyuki Nishiuchi, and Makoto Fukumoto, 225–39. Lecture Notes in Computer Science. Cham: Springer Nature Switzerland, 2023. https://doi.org/10.1007/978-3-031-42823-4_17.

McKay, R.A.; Mathews, F. Eldegard, K. 'Bats and Wind Turbines Onshore and Offshore. Norwegian national guidelines for monitoring surveys, assessments, and mitigation.' The Norwegian Environment Agency. Submitted: September 2023. Unpublished.

McKay, R.A.; van der Kooij, J.; Mathews, F.; Eldegard, K. 'Bats and wind energy infrastructure in Norway. Recommended pre- and post-construction monitoring protocol guidelines.' The Norwegian Environment Agency. Submitted: December 2020. Unpublished.

Sørås, R.; **McKay, R.A.** van der Kooij, Jeroen; Eldegard, K. "Recaptured Myotis Brandtii Carried Glue-on Radio-Tag for 10 Months: Does Time from Tagging to Shedding Depend on Timing of Annual Moulting?" *Barbastella* 13, no. 1 (March 1, 2020): 60–65. https://doi.org/10.14709/BarbJ.13.1.2020.11.

2 Abstract

Bat species in Fennoscandia make up approximately 20% of the terrestrial mammal wildlife and are all reliant on forest habitats to some extent throughout their annual cycle. However, there is a lack of knowledge on ecological responses of bat species to changes in their environment in this region. All bat species found in Fennoscandia are insectivores; with each individual bat consuming thousands of insects every night that they are actively foraging. The links between bats, their prey, and the habitat that both require to fulfil basic needs are critical knowledge for making informed decisions about monitoring and management. For example, it is important to take bat-insect-forest dynamics into consideration as concerns about maintaining biodiversity in boreal forests throughout Fennoscandia increase. In this thesis, I investigate how bats within boreal forests across three study areas in Southeastern Norway respond to habitat conditions and prey availability throughout the summer and early autumn.

In **Paper I,** I found evidence that bats belonging to the short range echolocator (SRE) foraging guild lost foraging habitat to wind turbine infrastructure whereas long range echolocator (LRE) bats remained highly active at sites located on wind energy infrastructure as well as in undeveloped “natural” habitats. As LRE bats are amongst those most vulnerable to colliding with wind turbines and include several threatened and migratory species, this study further highlights the importance of monitoring bats at active wind farms in Fennoscandia. I also found a new location for the forest specialist Western Barbastelle bat, *Barbastella barbastellus*, which is critically endangered in Norway. In this study we were also able to synchronously monitor bat feeding activity and insect presence/absence using a novel combination of ultrasonic passive acoustic detectors and insect camera traps.

In **Paper II** and **Paper III,** I studied how SRE bats within mixed boreal forests responded to different types of forest density throughout the summer by simultaneously monitoring three sub-habitats (open, interior and canopy) continuously across 12 forest sites of varying density and similar age, heights, productivity, and composition across two seasons. Findings from **Paper II** provide insights for what types of forest density are valuable foraging habitat for SRE bats, that is *Myotis* species and *Plecotus auritus*, the brown long-eared bat, throughout the season. I found a non-linear relationship between increasing SRE bat activity and forest density, marked by a decrease in bat activity when density approaches upper and lower thresholds. Furthermore, the results from this paper support previous studies which show the value of monitoring multiple sub-habitats in tandem over long periods to sample the bat community effectively. These findings lend more

evidence for the importance of managing forests to have varying density to support biodiversity. Furthermore, findings in this study emphasize the value of including bats in efforts to conserve biodiversity in boreal forests.

In **Paper III,** I further developed the insect camera trapping techniques used in **Paper I** and use a subset of the data collected from open sub-habitats in **Paper II** to study how *Myotis* bat commuting and feeding activity are modified by canopy openness and insect abundance. I found that forest gaps of moderate openness where there was also substantial insect activity captured had the highest levels of *Myotis* feeding activity. These findings indicate that even within mixed boreal forest gaps, which are typically considered highly valuable SRE bat foraging habitat, bats may be inhibited in their ability to forage by too high or too low forest density. The implication of this paper further supports the findings from **Paper II**, that habitats of varied forest density are important for SRE bats.

I accounted for differences in behavior (commuting, feeding and social) in all manual acoustic analysis included in this thesis. Differentiating between acoustic behaviors allowed me to identify differences in foraging habitat use between guilds (**Paper I**) as well as in the magnitude of effect that habitat structure (**Paper II** and **Paper III**), period in season (**Paper II**) and insect abundance (**Paper III**) had on *Myotis* feeding and commuting activity. It is not feasible to distinguish *Myotis* species found in Fennoscandia from acoustics alone in most cases, and therefore these have been grouped within sonotypes in the first three papers which rely on acoustic monitoring methods. However, it is important to account for species-specific ecological differences in many management, conservation, and research contexts. *Myotis brandtii*, the Brandt's bat and *Myotis mystacinus*, whiskered bat, are morphologically very similar in addition to using very similar echolocation calls. Therefore, in many studies where these species co-exist, they are grouped together. Thus, there is limited information on the distinct habitat use and foraging ecologies of *M. brandtii* and *M. mystacinus* where their ranges overlap. This is especially true within Fennoscandia, although both *M. brandtii* and *M. mystacinus* are common species throughout most of Norway, Sweden, and Finland.

In **Paper IV,** I used a combination of tracking data from radiotelemetry surveys and habitat description derived from aerial laser scanning metrics along with diet analyses from genetic metabarcoding methods to describe differences and similarities in the foraging ecologies of *M. brandtii* and *M. mystacinus.* I found that both bat species were highly associated with forest habitats of diverse heights near water and that bat species was a strong predictor of differences in alpha and beta diversity of the arthropod prey found in the bats' diets. Furthermore, *M. brandtii* selected more so for mature, continuous forest habitats whereas *M. mystacinus* was more generalized in habitat use, indicating that whereas *M. mystacinus* could utilize the smaller forest patches within the cultural landscape in the study area. We found opposite responses in how the two bat species used habitats in relation to increasing canopy density. *M. brandtii* exhibited a strong selection for forest with low canopy density while *M. mystacinus* more generally selected for forests with higher density. This findings further supports the results presented in **Paper II** and **Paper III** that varied forest density is important for SRE bats in boreal forest of Fennoscandia.

Together the findings from this thesis provide evidence for how variation in forest habitat structure, especially density, are important for supporting thriving bat communities. Furthermore, the methods and findings presented in this thesis can inform future studies on bats in similar systems as well as bat and boreal forest management in Fennoscandia.

Sammendrag

Flaggermusartene i Fennoskandia utgjør omtrent 20% av de landlevende pattedyrene. Alle disse flaggermusartene er avhengige av skogshabitater i løpet av sin livssyklus, men i varierende grad. Det mangler imidlertid kunnskap om hvordan flaggermusartene responderer på habitatendringer i denne regionen. Alle flaggermusene i Fennoskandia er insektetere; hver enkelt flaggermus spiser tusenvis av insekter hver natt den er ute og jakter. Kunnskap om sammenhengen mellom flaggermus, byttedyr og miljøet som både flaggermus og byttedyr er avhengige av, er nødvendig for å kunne treffe kunnskapsbaserte beslutninger om overvåking og forvaltning. For eksempel er det viktig å ta hensyn til dynamikken mellom flaggermus, insekter og habitategenskaper i boreale skogøkosystemer Fennoskandia, der det er en økende bekymring for at moderne skogbruk fører til redusert biologisk mangfold. I denne avhandlingen undersøker jeg hvordan flaggermus i boreale skoger i studieområder i Sørøst-Norge responderer på endringer i habitatforhold og tilgjengelighet av byttedyr gjennom sommeren og tidlig høst. Jeg har studert både enkeltarter og grupper av arter. Flaggermusartene i den boreale skogen kan deles inn i tre hovedgrupper basert på typen ekkolokalisering som de bruker for å jakte og navigere; short (SRE), medium (MRE) og long range (LRE) 'echolocators'.

I **Paper I** påviste jeg at utbygging av landbasert vindkraft kan føre til tap av jaktområder for SRE-flaggermus, mens LRE-flaggermus var svært aktive både på steder med vindenergiinfrastruktur og i ikke utbygde "naturlige" habitater. Fordi LRE-flaggermus er blant de mest sårbare for kollisjoner med vindturbiner, og inkluderer flere truede og migrerende (trekkende) arter, understreker denne studien viktigheten av å overvåke flaggermus ved aktive vindfarmer i Fennoskandia. Jeg fant også en ny lokalitet for den kritisk truede skogspesialisten bredøre, *Barbastella barbastellus*, i Norge. I denne studien klarte vi også å gjennomføre synkron overvåking av flaggermusens jaktadferd og forekomst/fravær av insekter, ved å kombinere ultrasoniske passive akustiske detektorer og kamerafeller for insekter.

I **Paper II** og **Paper III** studerte jeg hvordan SRE-flaggermus i boreal blandingsskog responderte på ulik grad av skogtetthet. Jeg gjennomførte kontinuerlig akustisk overvåking av 12 lokaliteter med lignende alder, høyde, produktivitet og treslagssammensetning, men med ulike skogtettheter, gjennom to sommersesonger. På hver lokalitet gjennomførte jeg samtidig overvåking av tre ulike delhabitater; inne i sluttet skog, i trekronehabitat, og i en åpning i skogen. Resultatene fra **Paper II** gir innsikt i hvilke typer skogtetthet som er verdifulle jaktområder for SRE-flaggermus, nærmere bestemt flaggermusarter i slekten *Myotis* og for arten brunlangøre *Plecotus auritus*, gjennom sommersesongen. Jeg fant et ikke-lineært forhold mellom

aktiviteten av SRE-flaggermus og skogtetthet, med en tydelig nedgang i flaggermusaktivitet når skogtettheten ble for høy og for lav. Videre støtter resultatene fra denne studien tidligere studier som viser verdien av å overvåke flere delhabitater samtidig over lange perioder for å få et representativt bilde av flaggermussamfunnet. Disse funnene gir ytterligere bevis for viktigheten av å forvalte skogen for å oppnå variert tetthet for å opprettholde biodiversiteten. Videre understreker funnene i denne studien viktigheten av å inkludere flaggermus i innsatsen for å bevare biologisk mangfold i boreale skoger.

I **Paper III** videreutviklet jeg teknikken for overvåking av insekter med kamerafeller som ble brukt i **Paper I** og brukte en del av dataene samlet inn fra åpne delhabitater i **Paper II** for å studere hvordan forflytning og jaktadferd hos *Myotis*-flaggermus endres med graden av åpenhet i kronesjiktet og mengden av insekter. Jeg fant at middels åpne habitater der det også var betydelig insektaktivitet, hadde høyest nivåer av *Myotis* jaktktivitet. Disse funnene indikerer at selv i små åpninger i skogen, som vanligvis anses som svært verdifulle jaktområder for SRE-flaggermus, kan flaggermusenes i evne til å jakte bli redusert ved for høy eller for lav skogtetthet, og at det er størst jaktaktivitet ved middels skogtettheter. Disse funnene støtter ytterligere resultatene presentert i **Paper II**, at habitater med variert skogtetthet er viktige for SRE-flaggermus i boreale skoger i Fennoskandia.

Jeg skilte mellom ulike typer atferd (forflytning, jaktadferd, sosial adferd) i all manuell akustisk analyse som er inkludert i denne avhandlingen. Differensiering mellom ulike typer akustisk atferd gjorde det mulig å identifisere forskjeller mellom ulike flaggermusgrupper sin bruk av jakthabitat (**Paper I**) samt hvilken påvirkning habitatstruktur (skogtetthet) (**Paper II** and **Paper III**), sesong (**Paper II**) og mengde insekter (**Paper III**) hadde på henholdsvis jaktadferd og forflytningsadferd hos *Myotis*-arter. Det er i de fleste tilfeller ikke mulig å skille mellom *Myotis*-arter som forekommer i Fennoskandia kun basert på akustistiske data, og derfor ble disse artene gruppert sammen i sonotyper i de første tre artiklene som er basert på akustisk overvåking. Imidlertid er det viktig å ta hensyn til artsspesifikke økologiske forskjeller i mange sammenhenger knyttet til forvaltning, bevaring og forskning. *Myotis brandtii*, skogflaggermus, og *Myotis mystacinus*, skjeggflaggermus, er morfologisk svært like og i tillegg utviser de svært lik ekkolokaliseringsadferd. Derfor blir de ofte gruppert sammen i studier fra områder der disse artene sameksisterer. Dermed er det begrenset informasjon om den distinkte habitatbruken og økologiene til skogflaggermus og skjeggflaggermus fra regioner der utbredelsesområdene til disse to artene overlapper. Dette gjelder spesielt i Fennoskandia, selv om både skogflaggermus og skjeggflaggermus er vanlige arter i store deler av Norge, Sverige og Finland.

I **Paper IV** brukte jeg en kombinasjon av sporingsdata fra enkeltindivider utstyrt med radiosender, habitatbeskrivelser basert på målinger fra flybåren laserskanning, og diettanalyser fra genetiske metabarkodingsmetoder for å beskrive forskjeller og likheter i furasjeringsøkologen (matsøk) til skogflaggermus og skjeggflaggermus. Jeg fant at begge artene var sterkt knyttet til skogsmiljøer med variasjon i vegetasjonshøyde, nærhet til vannforekomster, og at art var en viktig variabel for å forklare forskjeller i alfa- og beta-diversiteten av byttedyrrester i flaggermusenes ekskrementer. Videre brukte skogflaggermusene i stor grad eldre, sammenhengende skogsmiljøer, mens skjeggflaggermus var mer allsidige i sin habitatbruk, noe som indikerer at skjeggflaggermus kunne utnytte mindre skogspartier innen kulturlandskapet i studieområdet. De to flaggermusartene responderte også ulikt på skogtetthet. Skogflaggermus viste en sterk preferanse for skog med lav kronetettet, mens skjeggflaggermus generelt valgte skog med høyere tetthet. Disse funnene støtter ytterligere resultatene presentert i **Paper II** og **Paper III**, som viste at variert skogtetthet er viktig for SRE-flaggermus i boreale skoger i Fennoskandia.

Samlet sett viser denne avhandlingen at varierte i skogsmiljøer, spesielt med tanke på tetthet, er viktig for å sikre robuste flaggermussamfunn. Videre kan metodene og funnene presentert i denne avhandlingen informere fremtidige studier av flaggermus i lignende systemer, samt forvaltning av flaggermus og boreale skoger i Fennoskandia.

3 Synopsis

All images were taken by Reed April McKay unless otherwise indicated.

3.1 Introduction

Bats are overlooked in discussions on biodiversity in the Fennoscandian boreal forest system, which focuses almost exclusively on birds, arthropods, vascular plants, lichens, fungi and game species (Pettersson et al. 1995; Angelstam 1998; Hanski et al. 2000; Larsson and Danell 2001; Angelstam et al. 2004; Hanski 2008; Stokland et al. 2012; Hedwall et al. 2013; Dufour-Pelletier et al. 2020; Felton et al. 2021; Hanzelka et al. 2023; Hekkala et al. 2023; Löfroth et al. 2023; Virkkala et al. 2023). The Fennoscandian region, defined in this context to include Norway, Sweden and Finland, encompasses the northern range limits of 19 bat species (Tidenberg et al. 2019; De Jong et al. 2020; Eldegard et al. 2021) which all rely on forest habitats to some extent throughout the year. Boreal forests cover between 38 – 60% of the land area in Fennoscandian countries (Eggertsson et al. 2008) where bat species, as well as their critical habitat are protected. Norway, Sweden, and Finland are all parties to EUROBATS, an extension of the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention; CMS). EUROBATS parties are expected to uphold and promote bat conservation and research (United Nations 2001) and are party to an agreement which "*…provides a framework of co-operation for the conservation of bats throughout Europe…*" (UNEP/EUROBATS 2024). Even so, limitations in general knowledge on the abundance, distribution, and region-specific ecology of bat species in Fennoscandia have stunted the development of bat monitoring and management efforts necessary to rigorously monitor and protect bat populations (Gaultier et al. 2020).

Bat research in Fennoscandia spans back to before the 10th edition of Systema Naturae (Linné and Salvius, 1758), especially in Sweden where several prolific bat ecologists have produced a number of pivotal studies (Racey et al. 2021; ORCID 2024; SLU Artdatabanken 2024). However, much of the knowledge on bats from across Fennoscandia is in reports and gray literature, often in the local language, that are not easily accessible/and or available to the broader scientific community (Isaksen et al. 2009; Tidenberg et al. 2019; De Jong et al. 2020). Nevertheless, there has been an increase in bat research and conservation in Fennoscandia over the last decades, leading to many exciting studies (a non-exhaustive list: Frafjord 2021; 2013; Michaelsen 2017; de Jong et al. 2021; Blomberg, Vasko, Salonen, et al. 2021; Vasko et al. 2020; Gaultier et al. 2023; 2020; Kotila et al. 2023; Suominen et al. 2023; Vesterinen et al. 2018; Wermundsen and Siivonen 2008; Wood, Lindborg, and

Jakobsson 2017; Blomberg, Vasko, Meierhofer, et al. 2021; Sørås et al. 2022; Fjelldal 2023; Sørås 2023; Skåra et al. 2021; Apoznański et al. 2021) and conservation efforts (Dyrebeskyttelsen Norge 2017; Bergenholtz-Foglander 2021; Lundberg et al. 2021; BatLife Sweden 2024). There is a large potential to develop bat monitoring and conservation as well as a strong bat research environment in Fennoscandia to meet and exceed international standards. Fennoscandian countries are home to a rich and growing community of bat workers which is expected to expand as these regions are faced with a combination of important bat conservation and ecological issues that are becoming increasingly apparent such as the influences of wind energy development (Rydell et al. 2010b; Apoznański et al. 2018; Gaultier et al. 2020, 2023; de Jong et al. 2021) and artificial lights (Rydell 1992; Rydell et al. 2021).

Many of the bat species found in Fennoscandia can also be found throughout mainland Europe, the British Isles, Western Asia and Northern Africa (Dietz and Kiefer 2016). However, the Fennoscandian peninsula is distinct from surrounding regions; characterized by a combination of low human population density, extensively forested areas, abundant water resources, extreme shifts in daylength throughout the year and a relatively wet and cold climate (Seppä et al. 2009; Kuosmanen et al. 2018). Furthermore, the last glaciation event in Europe covered most of the area of Fennoscandia with long-term impacts for the flora and fauna (Nota et al. 2022). Thus, studies on the same bat species from more southern latitudes may not necessarily reflect the ecological conditions of bats living in Fennoscandia. Knowledge of the ecological responses of bats to their environment with appropriate regional context is key for advancing bat monitoring and conservation practices.

Historically, mainland Europe has experienced a severe depletion in the amount of landmass covered in forest since the Bronze Age (Roberts et al. 2018), while the amount of forest in Fennoscandia has remained relatively consistent (Kouki et al. 2001). Before the late 17th century, most of the forestry practices in Fennoscandia were small-scale or replicated natural disturbance regimes i.e. using burning techniques (Kuuluvainen 2002; Pennanen 2002). It was at this time that sawmilling became an industry in Norway, Sweden and Finland which led to the first large scale harvesting of trees in Fennoscandia (Sejersted 1972; Östlund et al. 1997; Kunnas and Borsari 2021). The forestry industry in Fennoscandia would revolutionize after World War II to optimize forest management for wood product production (Kouki et al. 2001; Kuuluvainen et al. 2012; Svensson et al. 2019). In the time the term “ecology” has been in use (Haeckel 1866), forestry practices in Fennoscandia have nearly removed all forest older than 200 years old (Svensson et al. 2019; Ahlström et al. 2022; Määttänen et al. 2022). Today, the forests in Norway, Sweden and Finland are some of the most intensively managed production forests in the world, supporting an immense forestry and biofuel industry (Blattert et al. 2023). The results of these industrial processes have led to forests in the Fennoscandian region becoming simplified in age, structure and composition (Esseen et al. 1997; Kuuluvainen 2009) with cause for alarm on the broadscale impacts on biodiversity (Angelstam 1998; Larsson and Danell 2001; Kuuluvainen 2009; Hjältén et al. 2023).

Nearly half of the threatened species in Norway, and approximately 30% of those in Finland and Sweden, rely on forest habitat (Anon 2019; SLU Artdatabanken 2020; Artsdatabanken 2021). Even so, less than 10% of the forest in Norway, Sweden and 17% of the forests in Finland are protected, with the remaining subject to intensive forestry management or for building and infrastructure (Hannerz and Ekström 2023). The cost of habitat loss from harvesting, fragmenting and homogenizing boreal forest in Fennoscandia has been thoroughly studied for taxa such as arthropods and birds (Pettersson et al. 1995; Van Wilgenburg et al. 2001; Felton et al. 2021; Hanzelka et al. 2023; Virkkala et al. 2023). However, the link between the loss in insects and the impacts on bats in this region, which are all insectivorous predators, is poorly understood. This is an unfortunate oversight because it is likely that bats perform important ecosystem services modifying herbivorous insect populations in forests (Beilke and O'Keefe 2023). Additionally, bats make up approximately 20% of the terrestrial mammals in Fennoscandia, making them an integrally important element of biodiversity. Most studies on the connection between insect population dynamics and bats in Fennoscandian boreal forest, have been done in relation to wind energy infrastructure (Rydell et al. 2010b; de Jong et al. 2021).

The development of wind farms in forest is commonplace in Fennoscandia (Gaultier et al. 2020) as well as other parts of Europe (Barré et al. 2022a; Ellerbrok et al. 2022; Ellerbrok 2023) but goes directly against EUROBATS recommendations (Rodrigues et al. 2015). Wind energy infrastructure is likely to appear increasingly in forests in Northern Europe to support the immense growth in wind energy planned for the coming decades (Enevoldsen 2016; Nordic Energy Research 2021). While wind energy is an important part of the shift away from fossil fuels, there is a huge amount of concern for the impacts that the land use change associated with wind energy infrastructure has on biodiversity (Voigt et al. 2019) and in particular for bats (Kunz et al. 2007; Arnett et al. 2016). Bat populations can be negatively impacted by wind energy through direct impacts i.e., fatalities (Box 1; Rydell *et al.*, 2010) and loss of roost sites, as well as indirect impacts on bat populations through avoidance effects, which have already been documented in Northern Europe (Ellerbrok et al. 2022; Ellerbrok 2023; Gaultier et al. 2023). However, one of the major areas of bat conservation and research in Fennoscandia that is lagging behind the rest of mainland Europe is the issue of addressing the "green-green" dilemma (Gaultier et al. 2020; Straka et al. 2020).

Box 1. Carcass searches to estimate bat mortality at wind farms

It is highly challenging to evaluate bat fatalities at wind farms from bat acoustic monitoring alone (Solick et al. 2020) though tools for mitigation are advancing (Barré et al. 2023). The most effective way to quantify bat fatalities at wind farms is to carry out thorough carcass search surveys (Kunz et al. 2007). To account for bat carcasses missed due to searcher error and the natural removal of carcasses by scavengers, carcass searches should be done in parallel with searcher efficiency trials and carcass removal trials (Bernardino et al. 2013). Carcass search crews led by dog-handler teams are more effective than human only search teams in terrain with tall vegetation or rugged substrate (Arnett 2006; Mathews et al. 2013). A formidable amount of effort and skilled workers are required to carry out all these elements of carcass searches. To date, carcass searches for bats at wind farms are very rarely carried out in Fennoscandia. However, there is increasing attention on the negative impacts that wind farms may have on bats in Norway, Sweden and Finland (Rydell et al. 2017b; Apoznański et al. 2018; Gaultier et al. 2020, 2023) which is leading to changes in policies and regulations which could make these surveys more common place in the near future.

Carcass searches, including searcher efficiency and carcass removal trials, were carried out at Marker Wind Park in the summer and autumn of 2020 by search team Pacho and Reed McKay (left image, photo: Sarah Johns). Two bat carcasses (right image) were detected during these surveys, both parti-coloured bats (*Vespertilio murinus).* Prior to these findings, only one bat carcass collected from under a wind turbine in Norway had ever been reported (Follestad et al. 2007). No manuscript could be generated from these results alone, but the findings will be included in a future publication with other findings that have since emerged regarding bat carcasses collected at wind farms in Norway.

In this thesis I investigated how bats on the community, species, and local population levels respond to various kinds of land use and forest attributes at three main study areas throughout Southeastern Norway (Figure 1). I used a variety of methods for monitoring bats as well as their arthropod prey and their habitat selection to study dynamic interactions. In **Paper I**, I described how activity across the bat community differs between previously forested areas cleared for wind turbine infrastructure and nearby natural habitats at a wind farm within a boreal forest. Furthermore, I explored how bat activity responded to insect presence using a novel camera trapping approach. In **Paper II**, I studied how bat species that are well adapted to hunting inside forest respond to differences in forest density across different sub-habitats within a mixed boreal forest. In **Paper III**, my collaborators and I further developed techniques for insect monitoring first used in **Paper I** and focused on a subset of the bat acoustic data used in **Paper II.** This allowed me to study how *Myotis* species feeding activity responded to insect abundance and canopy openness in open sub-habitats. In **Papers I, II**, and **III,** findings on bat activity and habitat use were mainly informed by acoustic monitoring data and related to insect presence or abundance without taxonomic information for arthropods. In **Paper IV**, I used data collected from capturing, radio-tagging, and tracking bats in combination with diet analyses from genetic metabarcoding to study the foraging ecology of *Myotis brandtii* and *Myotis mystacinus*. The findings from this thesis are intended to inform future research on bat ecology in the boreal forest system and provide guidance for management strategies related to boreal forest biodiversity and monitoring bats in similar environments.

3.2 Methods

3.2.1 Study area

Field work to collect the data in this thesis occurred at several locations in Southeastern Norway between the spring of 2017 and the autumn of 2022 (Figure 1). Data for **Paper I** was collected in the summer and autumn of 2020 at Marker Wind Park in Ørje, Norway, near the Swedish border. Data collection for **Paper II** and **Paper III** took place at 12 sites found in Ås, Vestby and Frogn municipalities between May and October in 2021 and 2022. The field work associated with **Paper IV** was collected in Nittedal municipality in the spring and summer of 2017 and 2018.

Figure 1. Map of the different study areas in Southeastern Norway where field work for each paper in this thesis took place. Data collection occurred between spring 2017 – autumn 2022. The Norwegian-Swedish border is the thick gray line that runs along the point next to "Paper I".

3.2.2 The bat community

There are 11 species currently recorded in Norway (Eldegard et al. 2021). However, there are an additional 8 recorded in neighbouring Sweden (de Jong et al. 2021) which includes the 13 species found in Finland. The findings from this thesis are primarily discussed in the context of Fennoscandian systems within the boreal zone which pertains to all 19 species found in Fennoscandia (Table 1). These species can be organized into foraging guilds (Denzinger and Schnitzler 2013) based on similarities in their behavior and characteristics of their echolocation (Frey-Ehrenbold et al. 2013; Froidevaux et al. 2016).

I chose to work with three established foraging guilds: short, medium, and long range echolocators (SRE, MRE, LRE). This enabled me to compare my findings to other studies which have used similar survey designs to my own (Frey-Ehrenbold et al. 2013; Froidevaux et al. 2016). A limitation of this approach is that some of the nuances in the responses between bats species is lost. There can also be differences in how studies choose to define these guilds depending on which characteristics are prioritised for grouping. For example, I defined SRE bats to include *B. barbastellus, Myotis* species and *Plecotus* species. *B. barbastellus, Myotis* species and *P. auritus* found in Norway use a low intensity echolocation which makes their detection range short and these species are highly associated with forested habitats (Wermundsen and Siivonen 2008; Russ 2021). Other foraging guild approaches would place *B. barbastellus* and *Myotis* species with *Pipistrellus* species given these species can be well adapted to flying in edge space habitats (Erasmy et al. 2021). I prioritised echolocation structure over behavior as I needed to account for differences in detectability between species in my research. I was also primarily focused on forest-specialist bats, which made the SRE, MRE, LRE foraging guilds a practical tool in this case.

Table 1. Overview of the bat species found in Sweden, Finland (underlined) and Norway (bold) along with their English name and conservation status on the Norwegian National Red List (Eldegard et al. 2021). NA = not listed (in Norway), LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

Bat species and foraging guilds	English Name	Status
Short range echolocators		
Myotis alcathoe	Alcathoe whiskered bat	NA
Myotis bechsteinii	Bechstein's bat	NA
Myotis brandtii	Brandt's bat	LC
Myotis dasycneme	Pond bat	NA
Myotis daubentonii	Daubenton's bat	LC
Myotis myotis	Greater mouse-eared bat	NA
Myotis mystacinus	Whiskered bat	LC
Myotis nattereri	Natterer's bat	CR
Plecotus auritus	Brown long-eared bat	LC
Plecotus austriacus	Gray long-eared bat	NA
Barbastella barbastellus	Western barbastelle bat	CR
Medium range echolocators		
Pipistrellus pygmaeus	Soprano pipistrelle	LC
Pipistrellus nathusii	Nathusius' pipistrelle	NT
Pipistrellus pipistrellus	Common pipistrelle	NA
Long range echolocators		
Eptesicus nilssonii	Northern bat	VU
Eptesicus serotinus	Serotine bat	NA
Vespertilio murinus	Parti-coloured bat	NT
Nyctalus leisleri	Leisler's bat	NA
Nyctalus noctula	Common noctule	EN

3.2.3 Sampling bats

3.2.3.1 Acoustics

The concept of using acoustics to study bats has experienced a radical evolution in a relatively short period of time. The term “echolocation” did not even exist 100 years ago (Griffin 1944) and yet today there are dozens if not hundreds of tools associated with recording, analyzing and interpreting the sounds produced by bats (Browning et al. 2017; Lim et al. 2021). In this thesis, I used only bat acoustic data collected from passive acoustic detectors, all of which were Wildlife Acoustics song meter SM4-BATSFS acoustic detectors (hereafter, detectors) (Wildlife Acoustics Inc., Maynard, MA, USA). Detectors were programmed to record for the whole night (from one hour before sunset until one hour after sunrise) and left out for multiple weeks or months at a time. A key advantage of using detectors to monitor bats for my research was the ability to monitor multiple places simultaneously over long periods of time in a standardized format. This is of course made possible by the ability to store large amounts of data in ways that were not possible even 20 years ago (Computer History Museum and Laws 2024). Furthermore, passive acoustic monitoring is non-invasive and nearly eliminates observer bias from the data collection process. It is generally quite easy to standardize data collection within a single project, but it can be challenging to compare results between studies due to all the variation in how bat acoustic data is collected, analyzed, and interpreted. Therefore, it is important to be transparent in the methodological approaches taken when using acoustic monitoring to sample bats, or any taxa, as the steps taken throughout these processes will influence the results.

The choice of equipment (detector, microphone, etc.) used for passive acoustic monitoring of bats as well as the methods of how the equipment is deployed, which settings and recording schedules are used will all influence and therefore bias the data collected (Adams et al. 2012; Rydell et al. 2017a; Gibb et al. 2019; Nocera et al. 2019). Ground level detectors were deployed on 1.5-2m tall wooden poles staked into the ground, with a cardioid ultrasonic SMM-U2 microphones or omnidirectional SMM-U1 microphone (hereafter U2 or U1 microphones) attached at the top (Figure 2). In most cases, detectors were fitted with U2 microphones which are more sensitive than U1 microphones. For **Paper I**, I was interested in recording bat activity above the tree line and within the rotor sweep zone at a wind farm. I did not get permission to deploy our equipment on the wind turbines directly but did receive permission to deploy two microphones on a nearby meteorological tower instead. In this case, a U1 microphone was a better fit because we could direct the cone of detection on the microphone in such a way to reduce number of recordings of mechanical noise (Figure 3).

I took care to site detectors in locations away from cluttered vegetation to improve the recording environment but also to avoid recording the types of echolocation that bats must use to navigate tight clutter, which can be challenging to interpret (Russ 2021). Even so, I was curious about the bats that were highly adapted to navigating those environments, so I also detectors closer to clutter and up into forest canopy (Figure 3). The study design used to collect bat acoustic data in **Paper II** and **Paper III** was inspired by the work of Jeremy Froidevaux (Froidevaux et al. 2014, 2016) which used a sampling design of monitoring three forest sub-habitats simultaneously to capture how the whole bat community optimizes forest structure. Although sampling in the interior forest and in the canopy is a more challenging recording environment, sampling these spaces allowed us to look at differences in how bats utilize habitats of varying density throughout the summer (**Paper II**). Collecting bat acoustic data in the forest canopy is especially challenging in terms of avoiding vegetation clutter (Adams et al. 2009; Froidevaux et al. 2016). However, we felt that it was important to capture habitat use that accounted for the vertical stratification of bat activity in the forest. The system we used for deploying the bat acoustic detector microphones in the canopy for **Paper II** was developed in collaboration with Maya Bruun Farmelo, an arborist. To deploy the microphone in the canopy, we only needed two ropes, a few small pieces of hardware and a throw line weight and moderately technical skills (Figure 3, bottom right). This system made it possible to deploy and maintain our equipment for months at a time as well as target specific points in the canopy to avoid overly cluttered environments safely and securely.

Then there is the issue of interpreting the data, for which there is a wide range of techniques. It is common for bat workers analyzing acoustic data to use a combination of automatic processing tools and manual checks of the recordings. The automatic processing stage most often includes a “scrubbing” phase in which filtering is used for removing noise files (López-Baucells et al. 2019). That is, files that are not likely to have bat recordings, or at least not high-quality ones which could be identified to species level. Automatic processing tools using machine learning will also often then be used to classify bat recordings to species level. One of the primary challenges of working with acoustic data, whether automatically or manually, is that it is not always possible to identify recordings to species level confidently and so functional groups that reflect similarities in echolocation (sonotypes) and/or foraging strategies (foraging guilds) are often used instead (Denzinger and Schnitzler 2013). In my research, I first used automatic tools to classify my files using only bat species found in Norway (**Paper I**). Later, I included all the species found in Sweden (**Paper II** and **Paper III**). Initially, I did this to account for the possibility that these species could also be in my study area, even though I did not believe that it was possible to make that assessment from acoustic recordings alone. I then found that there was a benefit of including the additional seven species in the automatic classifier settings as this separated my acoustic recordings into more nuanced “bins” which helped me to structure my manual acoustic analyses.

Quantifying bat activity from acoustic data is inherently challenging because there is currently no reliable way to identify individual bats from acoustic monitoring alone. It is common for echolocating bats to circle an area repeatedly while foraging, which if done near an active acoustic detector can generate many recordings in a short time by a single individual. Therefore, the amount of bat pulses, recordings, or time that bats are recorded from stationary passive acoustic monitoring is not necessarily a proxy for the number of individuals in an area. Bat acoustic data can be used to quantify bat activity, but to do so it is necessary to identify a unit of bat activity. There are many different approaches to this, but in my research, I have used “bat pass” which in this thesis has two slightly different definitions between papers. In **Paper I,** a bat pass was defined as any recording with at least two consecutive pulses with less than one second of separation between them (Fenton et al. 1973), with a range of 2-15 seconds per bat pass recording length. This approach is widely used and worked well but I found it challenging to manually analyze files of varying lengths. In **Paper II** and **Paper III**, I used a similar definition, but standardized bat passes to five seconds. This approach is also common (Millon et al. 2015; Appel et al. 2017; Torrent et al. 2018; López-Baucells et al. 2019) and allowed me to be more efficient during manual acoustic analysis.

In some cases, acoustic recordings can also provide information about bat behavior as well as overall activity. Bats produce social vocalizations that can be identified from recordings and, in some cases, can be associated with specific species as well as distinct functions like breeding (Russ 2021; Middleton et al. 2022). Many bat species also produce a terminal feeding buzz when they have, or have very nearly, captured prey (Ratcliffe et al. 2013). In all my manual acoustic analyses, I followed guidelines for identifying species described in Russ (2021) and differentiated between bat passes that only contained echolocation (“commuting”), bat passes that included social vocalizations (“social”) and bat passes that contained a complete feeding buzz (“feeding”).

Bioacoustic methods were integral to approaching the research questions in this thesis. I, along with my crew mates, deployed and managed bat acoustic detectors at 85 different locations recording data across 9,099 detector nights (24.9 years) over 3 field seasons. The data collected from these detectors generated over 226,000 recordings of bats, of which, 128,427 I manually identified as bat passes. This allowed me to identify a new location for a critically endangered bat species, (**Paper I**), to explore how feeding activity varied between within a single genus of bats (**Paper II, Paper III**), to study changes in habitat use across the season for forest specialist bats (**Paper II**), and between foraging guilds (**Paper I**) within boreal forest.

Figure 2. Examples of bat acoustic detectors deployed at ground level sites in this thesis. In **Paper I**, we monitored turbine pad sites (top left) paired with nearby natural site (top right) across Marker Wind Park in Ørje, Norway. In **Papers II – III**, we monitored bats in three different forest sub-habitats including interior (bottom left) and open areas such as gaps (bottom right) in Frogn, Ås and Vestby municipalities, Norway. The top the bottom right image was taken by Mathilde Klokkersveen Thomle.

Figure 3. Images depicting different techniques used in this thesis for deploying ultrasonic microphones attached to bat acoustic detectors at heights: on a meteorological tower (top right; **Paper I**; Image: Tommy Rambøl) and in the forest canopy (**Paper II** ; left, bottom right: using a throw line attached to a 500 g weight for deploying the first in a series of two ropes required for the set up; photo: Katrine Eldegard). The final location of the microphone in the forest canopy detector on the left is indicated with a white circle.

3.2.3.2 Bat captures

Bats were captured as part of the field work in **Paper II** and **Paper IV** using primarily mist net surveys (harp traps were occasionally used during field work for **Paper IV**). Mist net surveys are carried out by deploying fine mesh nets designed specifically for capturing wildlife, most often passerines and bats (Kunz and Parsons 2009). The benefit of capturing bats using such methods is that it is then possible to collect detailed information about individual bats (age, sex, morphometric data, reproductive status, body condition, etc.) as well as to identify species that are not feasible to detect from acoustics alone (O'Farrell and Gannon 1999; Kunz and Fenton 2005). There is a variety of equipment and approaches for capturing bats, but none are cheap, and all are reliant on highly skilled workers (Kunz and Parsons 2009). Mist net surveys must be led by a highly skilled person who holds the necessary permits, often with several crew members assisting throughout the process. These surveys are technical and time consuming, and they do not guarantee the capture of bats. If bats are captured, how many, and which species are collected can be highly variable and difficult to predict. Furthermore, the amount of effort used during mist net surveys (net hours, number of nets, etc.) is not necessarily correlated with survey effort (see supplementary materials, **Paper II**). Most essential, these surveys, when successful, subject bats to the stress of capture and handling. Therefore, bat capture surveys should be restricted to when there are no alternatives available to address research or management needs.

Capturing bats is usually an essential pre-requisite for radio-tagging and tracking bats (4.2.3.3), which can provide information about spatial movements by individuals as well as roost locations and foraging behavior. In the summer of 2018, I worked with a crew to capture *M. brandtii* and *M. mystacinus* to radio tag females and compare the foraging ecology (**Paper IV**) as well as the roost selection (Birkeland 2019)and physiological responses (Skåra et al. 2021) of these species. It is not recommended to use acoustics monitoring alone to distinguish between *M. brandtii* and *M. mystacinus* where their ranges overlap, given their similarities in echolocation calls (Russ 2021). Therefore, capturing bats was essential to compare differences in foraging activity between the two species. I carried out three nights of mist net surveys at each of the twelve sites associated with **Paper II** and **Paper III** where we were conducting acoustic surveys to gather information about species composition within the bat community. This made it possible to describe changes in the phenological cycle (i.e., reproduction status) of bats within our study area and to identify the presence of short-range echolocating bats that are difficult to sample and distinguish from acoustics alone.

An important advantage of carrying out mist net surveys is that collecting certain biological samples is relatively easy and non-invasive once a bat has already been captured. During field work for this thesis, we collected fecal samples directly from bats captured at mist net sites which were later analysed using genetic metabarcoding techniques (4.2.4.2) which allowed us to verify our ability to identify cryptic bat species as well as to study the diet of the bats captured (**Paper IV)**.

Figure 4. Images from mist net surveys for capturing bats. While processing bats, standard measurements such as the length of the right forearm were collected (top left: a northern bat, *Eptesicus nilssonii;* top right: backlighting a bat's wings to check for parasites or damage and to evaluate the age of the individual. Photos: Torleif Bækken). Mist nets can be deployed over many kinds of habitats to capture bats, though most often they are placed over flyways such as over forested paths and creeks, as well as over water bodies (bottom right, photo: Jarle D. Haukeland).

3.2.3.3 Radiotelemetry

I worked with a team to track the foraging movements of 9 female *M. brandtii* and 11 *M. mystacinus* captured in Nittedal municipality in the summer of 2018 (**Paper IV**). To compare the foraging habitat use of these two species, it was necessary to capture and tag bats to sample the target species and follow them using Very High Frequency (VHF) radiotelemetry. VHF radiotelemetry is a standard technique for tracking spatial movements and behavior which has been used for a wide range of wildlife (Baratchi et al. 2013; Whitney 2022). This technology is relatively simple compared to more modern tools, such as using GPS tags (i.e., transmitters). However, the smallest GPS tag currently available is still approximately 1 g (Recio et al. 2011; Stantial and Cohen 2020; Wild et al. 2022); which if following the 5% rule (Aldridge and Brigham 1988) is too large for any bat smaller than 20 g. Therefore, VHF radiotelemetry is typically the tool used to study the spatial movements and roost selection of bats (O'Mara et al. 2014). Even so, it is considered invasive to affix a transmitter to a bat. It is generally agreed that radio tagging bats using an appropriate weight transmitter that has been affixed properly does not hinder the ability of the bat to fly and will typically fall off after a few weeks with limited long-term impact (O'Mara et al. 2014). However, a bat captured during the field work for **Paper IV** was later recaptured 306 days after the bat had been tagged, representing the longest retained VHF-tag record known for bats (Sørås et al. 2020). Therefore, care must be taken to only carry out these surveys when no other alternatives exist and to mediate the amount of stress subjected to animals while tagging.

There are three basic types of surveys associated with using radiotelemetry to study bats: daytime tracking to locate roost, foraging telemetry to track bats while they are foraging at night, and roost monitoring surveys (Figure 5), to study how and when bats emerge from roosts. Using radiotelemetry to study bats is inherently "high risk, high gain". A bat must first be acquired or captured (3.2.3.2) to affix a transmitter to the back of the animal. Even if this is accomplished, it is common for radio transmitters to fail or the signal on a transmitter can disappear shortly after tagging a bat (Amelon et al. 2009). Then, the signal from an active transmitter affixed to a bat, can be difficult to continuously monitor and it can still be extremely challenging to track bats while they are foraging or to find roost sites (Amelon et al. 2009). These surveys are all resource intensive techniques which requires expensive equipment, permits for capturing and tagging wildlife, as well as skilled crew.

Figure 5. Top left: Reed McKay carrying out a daytime search for roosting locations of Brandts' bats (*M. brandtii)* and whiskered bats (*M. mystacinus) (*Photo: Karoline Manneråk Birkeland). Top right: image of a whiskered bat, *M. mystacinus*. Bottom left: A telemetry tower built by deploying a 5 element YAGI antenna on an approximately 7 m tall pole to track bats long distance. Bottom right: Rune Sørås searching for signal on a bat during a foraging telemetry survey.

3.2.4 Sampling arthropods

3.2.4.1 Camera traps

The method used for measuring arthropod presence/absence and abundance in this thesis was inspired by the work presented in Ruczyński *et al.*, (2020). An important advantage of using this method is that it does not rely on killing arthropods. Another key advantage of this method is that it was possible to identify and measure the number of arthropods near camera traps paired with bat acoustic detectors such that we could relate insect abundance to bat feeding activity (Figure 6). However, the camera traps we used were energy intensive to maintain and were subject to technical complications. We experienced issues related to having an adequate power supply to operate the cameras over multiple days (see Johns, 2021; Sætre, 2022; Thomle, 2023 for more information about equipment failures) and during periods of rain or high humidity, the images would be of too poor quality to inspect for arthropods. In **Paper I,** we could only relate bat acoustic activity to insect presence/absence instead of abundance on account of the equipment failures leading to a small dataset. We were able to overcome some of the technical issues with the camera traps by improving the design of the trap. In **Paper II**, we were able to collect enough data to compare *Myotis* feeding and commuting activity with insect abundance measured from camera traps.

In collaboration with Ronny Steen at the Norwegian University of Life Sciences, we developed our own design for a similar camera trap for the research described in **Paper I**. We used Ricoh WG-6 Digital cameras (Model R02050 2019) for all camera traps in this thesis, but the housing around the camera evolved from **Paper I** to **Paper III** (Figure 7). During field work in the summer of 2020 for **Paper I**, insect camera traps were powered by a 12V 45 Ah car battery which needed to be connected to a power inverter, which was encased by a plastic box with holes for ventilation and power cables. The casing around the camera was a store-bought picture frame which was guerilla taped to the camera, with a tripod and a gear tie used to attach this unit to the top of a wooden pole (see Johns (2021) for information about this camera trap design). Through collaboration with the EIK lab at NMBU, we were able to modify a waterproof box that was specially fitted for the cameras and compatible with a larger tripod for data collected in 2021 and 2022 (**Paper III**). After 2020, we switched to using 12V 19- or 21-Ah motorcycle gel batteries which required a smaller power inverter, were easier to charge and carry into the field as well as being less prone to technical failures. We also focused our efforts using the camera traps to sample period when the weather was warm and dry to avoid collecting images that were impaired by condensation or water droplets.

Images collected from the camera trap were all manually annotated by myself or other members of our research group (Sarah Johns, Vilde Sætre, Mathilde Klokkersveen Thomle). Manually annotating images is time intensive and can introduce bias with differences in detection of arthropods between analysts. Choiński *et al.*, (2023) created a deep learning tool for automatically annotating these images. However, it is not clear how well this tool can be used when deploying camera traps with vegetation or clutter in the background, which can make insects difficult to detect.

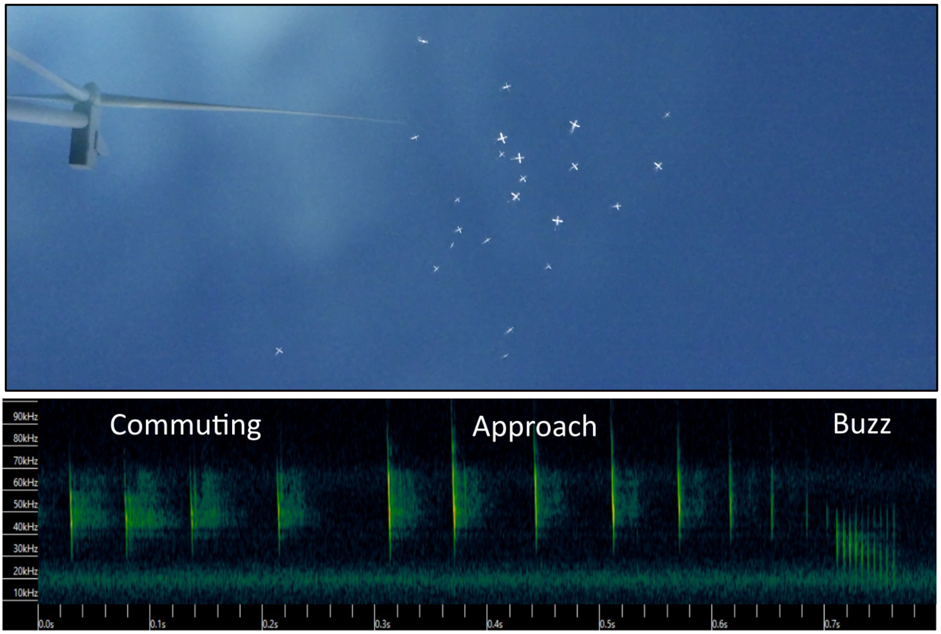

Figure 6. Top image: examples of a camera trap image containing insects, captured at Marker Wind Park (**Paper I**). Bottom image: example of a *Myotis* species feeding buzz, preceded by commuting and approach echolocation, captured using a stationary bat acoustic detector.

Figure 7. Evolution of the insect camera trap between **Paper I** (top images; photos: Sarah Johns and **Paper III** (bottom images; photos: Mathilde Klokkersveen Thomle):

3.2.4.2 Genetic metabarcoding

Genetic metabarcoding, hereafter metabarcoding, is a technique wherein DNA of a target taxa are extracted and then amplified, typically using a polymerase chain reaction (PCR), before being identified using high throughput sequencing (HTS) (Liu et al. 2020). DNA Metabarcoding has become increasingly affordable and widely used over the past 20 years especially within ecology and measuring biodiversity (Zinger et al. 2019; Compson et al. 2020). One of the primary advantages of metabarcoding is that it can produce a huge volume of data from even very small biological samples in a relatively short period of time. Before this tool was available, bat diet studies relied on inspecting bat feces manually and searching for body parts of prey items. Macro and microscopic inspection of feces to detect diet lends an obvious bias toward prey items which are difficult to digest and easy for the human eye to detect. Additionally, manually inspecting feces in this way is an extremely time consuming and technical task, which is typically resulted limited to only Order or Family level information about the prey consumed (Schattanek et al. 2021). Studying bat diet from feces using metabarcoding is less influenced by human observer bias but there are other forms of bias that can be introduced at nearly every stage in lab work as well as in how the DNA sequences are identified into taxa (Zinger et al. 2019). Furthermore, it can be challenging to quantify taxa detected through metabarcoding because DNA is not uniformly amplified and sequenced (Deagle et al. 2019). Therefore, it is very important to be transparent when describing the methods involved with collecting and analyzing data for metabarcoding analyses. To account for differences in how taxa are detected and DNA sequences are amplified in metabarcoding, it is recommended to represent findings using a combination of presence/absence with a measure of abundance that accounts for unequal detection (Deagle et al. 2019).

Lab work for the data analysed in this thesis took place at the Konrad Lorenz Institute for Ethology in Vienna through collaborations with Steve Smith and Franz Hoelzl between autumn 2019 – summer 2020, with delays caused by the COVID-19 pandemic.

3.2.5 Sampling forest habitat features

3.2.5.1 Coarse habitat categories

In this thesis, I used coarse categorical descriptions in **Paper I** and **Paper II** to describe bat habitat. One of the main advantages of using this approach to describe bat habitat is that it is simple to do and easy to communicate. However, using this approach, habitat definitions. are inherently subjective. To account for this, I took great care to be consistent with our sampling approaches within each study area. One way I accounted for subjectivity in sampling sub-habitats in **Paper II** was to combine coarse habitat descriptions with in-field measurements of forest structure (3.2.5.2). In **Paper I**, I compared bat activity sampled at detectors deployed at gravel crane auxiliary pads next to active wind turbines (turbine pad sites), paired with a detector deployed at a nearby "natural" habitat that had not been developed for wind farm infrastructure. The distance between the turbine and the acoustic detectors within a site-pair was similar but the area surrounding the detectors was consistently distinct: turbine pads were further from forest edges and water bodies on average, and directly next to roads; natural sites were in wetlands and/or near forest edges. This allowed us to study the differences in habitat use by bats regardless of disturbances caused by the noise and presence of the turbines. In **Paper II**, I sampled three sub-habitat types within mixed boreal forests: open, interior and canopy, following similar methods to Froidevaux *et al.*, (2016). Sampling the forest using these three sub-habitats made it possible for us to investigate how bats responded to forest density across vertical and horizontal scales within the forest.

3.2.5.2 In-field forest measurements

In **Paper II** and **Paper III**, my collaborators and I collected a combination of in-field measurements of forest structure and habitat characteristics in the same study area (Figure 8). The advantage of using these methods is that they are widely used in ecological and forestry research, making our findings easy to communicate and compare with other studies. Additionally, the surveys associated with these measurements are relatively cheap and easy to carry out and were targeted to cover the area directly around the acoustic detectors. For each detector location sampled in **Paper II**, we measured a combination of metrics including the diameter at breast height (DBH, that is 1.35 m above the tree's base) of all trees with a DBH greater than 5 cm, the basal area, and descriptions of understory vegetation in 100 m^2 plots. For all open sub-habitats sampled, we also took hemisphere images of the forest canopy to measure canopy openness which was used to describe bat and arthropod habitat use in **Paper III.**

3.2.5.3 Remote sensing: Aerial laser scanning (ALS)

In **Paper IV**, I collaborated with Hans Ole Ørka from the Norwegian University of Life Sciences to compile a habitat description dataset from aerial laser scanning data for foraging locations of *M. brandtii* and *M. mystacinus.* This research is the first to our knowledge that combines ALS data with bat foraging locations gathered from radiotelemetry surveys. This combination of techniques allowed us to describe differences in how two cryptic species select for habitat use on a 3-dimensional and wall-to-wall full high resolution spatial coverage. Gaining a perspective on the 3 dimensional structure of habitat is an important advantage of working with remote sensing data for studying bat foraging ecology which several previous studies have championed using (Froidevaux et al. 2014; Müller et al. 2018; Rauchenstein et al. 2022; Hermans et al. 2023) and roost monitoring (Carr et al. 2018) methods. Using remote sensing data, it is also possible to sample at multiple spatial scales, which can be important for testing how wildlife respond to different types of environmental changes (Carr et al. 2018; Ciuti et al. 2018). However, finding a suitable scale to compare spatial characteristics with wildlife observations can be difficult to determine (Wright et al. 2022). One of the challenges associated with using ALS to describe wildlife habitats is that many of the variables extracted from these tools can be collinear, both structurally and in how animals respond to them. Therefore, it can be challenging to determine which variables to include in analyses. The interpretation of results from models that use ALS metrics as explanatory variables can also be more difficult to communicate to broader audiences compared to more coarse categorical descriptions. Therefore, it is important to link the findings using ALS to ecological processes in a way that all relevant stakeholders can easily understand.

Figure 8. Examples of in-field measurements collected during this thesis**.** We measured the diameter at breast height of mature stems within 100 m^2 plots surrounding acoustic detector locations in **Paper II** (bottom left; photo: Katrine Eldegard) and collected hemisphere images (top; bottom right: example of how photos were taken in the field; photo: Katrine Eldegard) which were used for calculating canopy openness in **Paper III.**

3.2.6 Data management and statistical analyses

Open science practices are integral to my philosophy as a researcher. My data science skills as well as my knowledge of open science tools and practices, have evolved as part of my PhD journey. I am committed to continuing to develop my protocols around data collection, management, and analysis so that my work is transparent and accessible to others. I initially gained more of an appreciation for data stewardship through working with bioacoustic data. All the original and processed bat acoustic data used in this thesis, along with the relevant metadata, are backed up on highly secure servers hosted by the Norwegian University of Life Sciences, as is required for PhD research data. This data will be made publicly available for future research upon the publication of the manuscripts in this thesis and once I find an appropriate repository. Workflows associated with the analyses carried out in this thesis are available on GitHub with separate repositories for the data associated with each study area (links to relevant repositories provided within each paper).

In this thesis, I primarily used general additive mixed models (GAMMs; **Paper I**, **Paper III**) and generalized mixed-effect models (GLMMs; **Paper II, Paper IV**) to explain relationships between bat acoustic activity or foraging locations, their environment and available prey. In all datasets, I had to account for random effects such as detector locations, differences between years or differences between individual bats. Therefore, mixed effect models were necessary. GAMMs were a practical tool for addressing non-linear relationships that are common in bat acoustic data, especially when investigating responses to seasonal effects and weather conditions. GLMMs were more suitable for inspecting categorical explanatory variables such as differences between sub-habitats and periods in season (**Paper III**), or between bat species in a resource selection model (**Paper IV**). I also used a variety of other multivariate analyses such as PERMANOVA to test differences in beta diversity of the diet between *M. brandtii* and *M. mystacinus* (**Paper IV**) and a variety of ordination techniques, including Non-metric Multidimensional Scaling (NMDS), and Principal component analysis (PCA), and Principal Coordinate Analyses (PCoA). These ordination techniques made it possible for me to visualize and define complex relationships between bat foraging activity, their environment, and their prey, as well as to describe forest structure and deal with collinearity between explanatory variables.

3.3 Results and discussion

3.3.1 Identifying important habitat features in boreal forest for bats

I investigated how bats respond to their environment using a range of different bat classifications depending on taxonomy and between bat functional groups. I also investigated bat responses over different spatial scales. The overarching findings from my four papers indicate the importance of providing diversely structured, mature, and intact forest habitats for bats within the SRE guild (Figure 9) living in boreal forest systems. I consistently found that forest density had a strong influence on SRE bat activity, providing further evidence for the importance of managing boreal forests to have varied densities that wildlife can benefit from (Hedwall et al. 2019; Felton et al. 2021). I also provide evidence for the importance of sampling across the entire bat community using a combination of methods to account for the differences in foraging ecologies and detectability of different bat species in relation to monitoring approaches. Furthermore, I have documented the value of accounting for differences in behavior from bat acoustic recordings to understand how bats respond to their habitat.

In **Paper I**, I found that SRE bats at a wind farm in Norway rarely foraged at locations where turbine pads and supporting infrastructure had been erected within a boreal forest. Natural habitat sites were far more open i.e., far removed from vegetation clutter than those sampled in **Paper II** and **Paper III** where I found that even within forest gaps, *Myotis* avoided commuting and feeding in too low-density forest habitats. The findings from **Paper I** indicate that wind energy infrastructure located in forests removes foraging habitat for SRE bats that are not well adapted to foraging in highly exposed habitats. Conversely, LRE bats, which include species such as *E. nilssonii* and *V. murinus,* which are highly vulnerable to colliding with turbines (Rydell et al. 2010a; Box 1), remained highly active across the different habitats sampled, and were consistently recorded from above the tree line at the wind farm. These results on LRE bat activity provide evidence for the importance of carrying out carcass searches at windfarms in Fennoscandia, and especially at wind farms near valuable bat habitat such as forests. Our findings that SRE bats are losing foraging habitat due to loss of forest habitat at wind farms concurs with several recent studies carried out in other parts of the world (Barré et al. 2018, 2022b; Ellerbrok 2023) but is one of the first of its kind for Fennoscandia (Gaultier et al. 2020, 2023).

In **Paper II,** I found that *P. auritus* optimized low-density forest sub-habitats throughout the summer at mixed boreal forest sites. I was also able to describe how *Myotis* activity at open, interior and canopy sub-habitats shifts throughout the season in relation to forest density. Surprisingly, I found that *Myotis* avoided the open sub-habitats (i.e., forest gaps) of low forest density in the early period of the summer. It is well documented that SRE bats in Fennoscandia are highly associated with forest habitats and avoid flying in highly open areas (Jones and Rydell 1997; Stone et al. 2015; Spoelstra et al. 2017; Apoznański et al. 2021), but gaps within forest were expected to be highly valued foraging habitat for these species, as other studies have found (Froidevaux et al. 2016; Tena et al. 2020). Our findings that overly open habitats are avoided by *Myotis* during the early period of the season are similar to the findings of Wood et al. (2017) who also documented a decrease in forest specialist bat activity in wood pastures of low tree density.

I found similar trends in *Myotis* feeding activity and commuting activity across the differences in the sub-habitats sampled in **Paper II**, but there were different magnitudes of the effect of forest density and the period in season between behaviors. Most notably, *Myotis* feeding activity increased more in the canopy than what was found for *Myotis* commuting activity in the mid-period of the season (late June to early August). One possible reason for Myotis to feed more in the canopy during this period could be due to the summer canopy vegetation. Such developed foliage would provide habitat and shelter for both herbivorous arthropods and for Myotis to forage on these prey species. In **Paper III**, I explored *Myotis* feeding and commuting activity from open sub-habitats (i.e., forest gaps) and in relation to insect abundance and canopy openness. I found that *Myotis* feeding activity was highest at intermediate levels of canopy openness and when insects were somewhat abundant, whereas *Myotis* commuting activity was much less sensitive to different levels of canopy openness and insect abundance. These findings generally agree with other studies which have found that overly dense and overly open habitats are challenging for *Myotis* species to utilize (Aldridge and Brigham 1988; Brigham et al. 1997; Froidevaux et al. 2016). However, all the data from **Paper III** was collected in mixed forest gaps, which are considered highly suitable habitat for many forest vertebrates in the boreal system (Hekkala et al. 2023). Therefore, our findings show that even in “ideal” bat foraging habitat, providing varied vegetation structure is important to avoid limiting bat foraging opportunities with areas that are overly dense or too open.

In Paper IV, my collaborators and I were able to look at more species-specific responses to habitat structure by capturing and tracking *M. brandtii* and *M. mystacinus.* These two species are often grouped together in ecological studies because it is challenging or not feasible to distinguish them unless they are observed in hand by someone trained to recognize their species diagnostic features (Berge 2007; Dietz and Kiefer 2016; Budinski and López-Baucells 2023). While both of these species are considered forest specialists in Fennoscandia (Wermundsen and Siivonen 2008), we found that *M. brandtii* was more associated with mature, continuous forest habitats whereas *M. mystacinus* foraged in more varied habitat including forest patches bordering cultural landscapes. Notably, we found that *M. brandtii* selected foraging habitat in more dense boreal forest, while we found the opposite effect for

M. mystacinus. Both species were highly associated with forest habitats near water and of varying height, providing further evidence for the importance of diversely structured forest for SRE bats in Fennoscandian boreal forest systems.

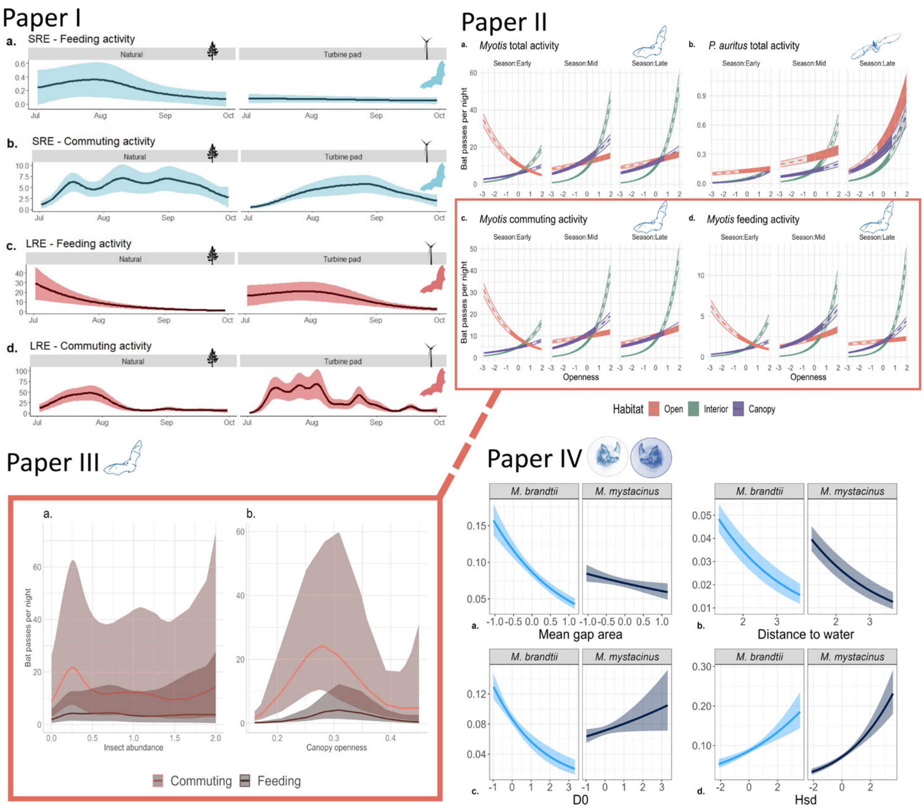

Figure 9. A composite of the main results related to bats and their habitat use from the four manuscripts in this thesis. The data from **Paper III** are a subset of the *Myotis* activity recorded at open sub-habitats from the research presented in **Paper II.** In the figure for **Paper I** (top left), the y axis is the number of bat passes per night; SRE (short range echolocators); LRE (long range echolocators). In the figure for **Paper IV** (bottom right), the y axis is the predicted probability of a location being used by a foraging bat; "D0" and "Hsd" are ALS metrics describing canopy density and canopy height heterogeneity, respectively.

3.3.2 Bat and arthropod dynamics

I found links between bat activity and insect presence and abundance using a novel combination of bat acoustic monitoring and insect camera traps (Figure 10). In **Paper I,** I show that bat feeding activity is correlated with insect occurrence. In **Paper III**, my collaborators and I further developed this method and were able to look at how *Myotis* feeding activity responded to insect abundance in relation to varying canopy openness. Thereby, we found that *Myotis* feeding activity was highest when insect abundance increased, and canopy openness was moderately high. In **Paper IV**, I used genetic metabarcoding techniques to describe the diet of *M. brandtii* and *M. mystacinus* living within the same study area in addition to also studying the habitat selected for foraging. There were 66 and 126 unique prey taxa identified in the diets of *M. brandtii* and *M. mystacinus,* respectively. I found that *M. brandtii* was more associated with mature and coniferous forest habitats, both in terms of diet composition and the top prey taxa in the diet of bats as well as from the results of a resource selection function analysis of bat foraging locations. The findings from **Paper IV** further illustrate that there may be some form of niche partitioning between *M. brandtii* and *M. mystacinus,* as I consistently found that bat species was a strong predictor of differences in alpha and beta diversity of the species found in our diet analyses. Our findings collectively indicate the value of monitoring prey species alongside efforts to monitor insectivorous bats and their habitat to better understand key mechanisms explaining their foraging behavior.

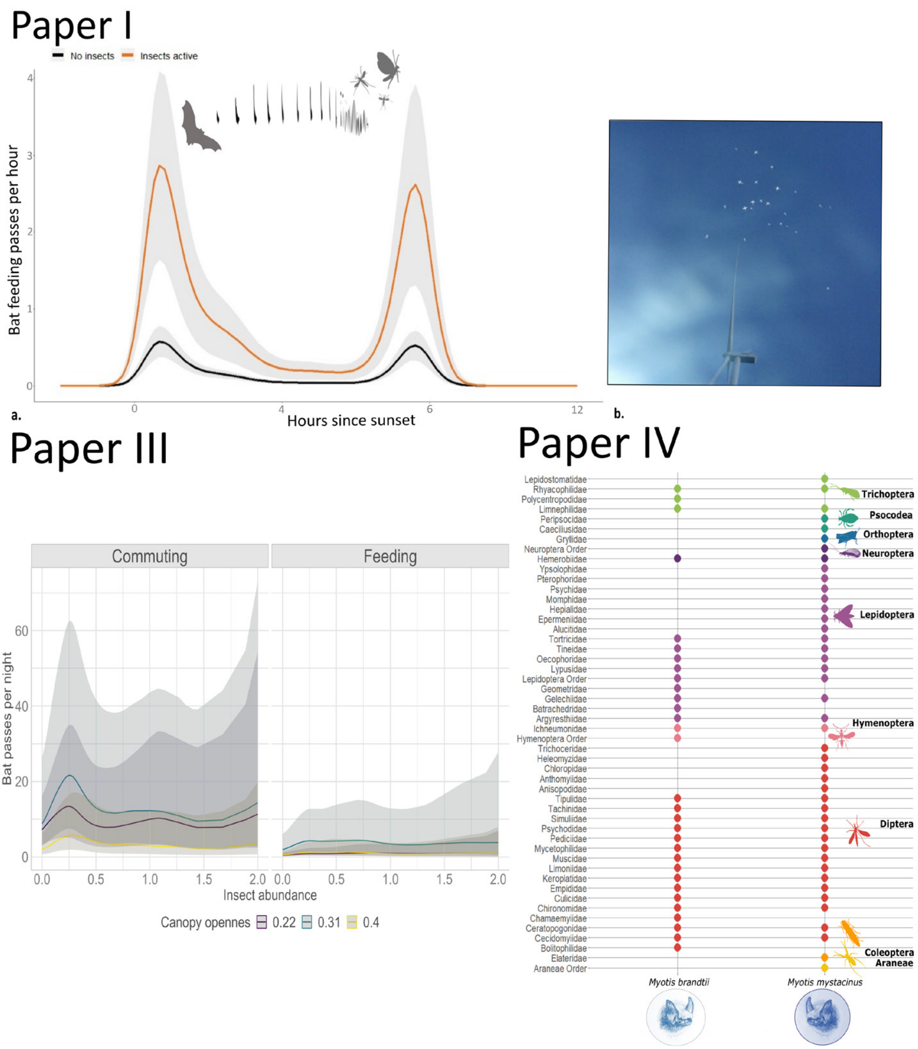

Figure 10. Composite of main findings related to bat -insect dynamics from **Paper I**, **Paper III**, and **Paper IV**.

3.4 Identified gaps for future studies

In this thesis, I focused on studying how bats responded to their environment across three locations in Southeastern Norway. The research in this thesis also focused on bat activity during the summer and early autumn which encompasses the main breeding period of the year for bats, but it is important to further document the full phenological cycles of bat species throughout their range in Fennoscandia (Blomberg et al. 2021a; Kotila et al. 2023). Findings from this thesis, and the corresponding data, can be used to inform future studies, monitoring, and management on broader spatial and temporal scales. Understanding precisely what kinds of environmental conditions benefit bats at critical phenological periods such as during migration, hibernation, and breeding is necessary to inform bat conservation and management. This is especially pertinent as we can expect the ranges of bats to shift as the climate progressively changes, which can prove fatal for species already living at the extreme edge of their environmental tolerance. Simultaneously, we may expect to see species previously associated with more southern latitudes to be forced northwards (Rebelo et al. 2010; Jones and Rebelo 2013; Festa et al. 2023). Thus, studies on bat ecology that cover broader spatial scales and that include year-round monitoring will be of great value in Fennoscandia moving forward.

Governments in Norway, Sweden and Finland share ambitions to increase the amount of protected forests to foster more biodiversity (Angelstam et al. 2023; Klima og miljødepartementet 2023; Räty et al. 2023). As a large proportion of the threatened species in these countries are closely associated with forest habitats (Kuuluvainen 2009; Artsdatabanken 2021; Angelstam et al. 2023). Identifying which types of forest and forest structure are most important to the bat community is critical but this knowledge must be placed in the context of the greater forest ecosystem. Little to no consideration is given to bats or other small mammals for that matter, despite bats being overrepresented as threatened species in Norway, Sweden, and Finland relative to other terrestrial mammals. Future studies should investigate how well current conservation efforts in Fennoscandian forest management effectively protect bat populations. There are several important aspects of forest structure I did not focus on in this thesis. For example, I did not study how the amount and quality of deadwood in boreal forests was related to bat activity. The link between deadwood and diverse bird communities, especially threatened species, has been well documented in Fennoscandia (Lindhe et al. 2005; Dufour-Pelletier et al. 2020; Martin et al. 2021; Löfroth et al. 2023). However, it is likely that this is another important characteristic of forests that influences bat habitat use in Fennoscandia. as many bat species would also benefit from the increased arthropod abundance and roost site availability associated with dead wood (Tillon et al. 2016). As I was interested in forest bats as a community, I also did not target monitoring for specific, rare bat species in Norway. However, in the future, it would be valuable to focus more efforts on monitoring highly threatened species, such as the critically endangered *B. barbastellus* to determine what types of forest habitats support this species, given there is limited data in northern Europe (Apoznański et al. 2018, 2021).

The longest days of the year from mid-June to early July coincide with peak periods in the maternity season of most bat species in Fennoscandia, when mothers are either about to give birth or are lactating. Several studies done in Southeastern Norway on SRE bats have highlighted the importance of understanding what kinds of physiological responses bats must master to survive living at far northern latitudes (Skåra et al. 2021; Fjelldal 2023; Sørås 2023). Fjelldal (2023) found that *P. auritus* that were pregnant or lactating living in Southeastern Norway would leave roosts approximately 25 minutes earlier than non-reproductive bats, despite their intense light aversion, presumably to meet their high energy demands. In this thesis, I indicate how our findings may be influenced by a bat's physiology, phenological events (such as reproduction) and the influence of shifting daylength. However, it was not within the scope of this thesis to study those responses directly. The potential influence that the short, summer nights have on bat habitat use and behavior in Fennoscandia, and on SRE bats in particular, has so far received little attention and requires further study. In my future research, I plan to explore bat activity patterns at more detailed temporal scales, such as diel activity. I intend to return to the data collected in **Paper II** to further analyse bat acoustic data outside of the SRE guild so that I can investigate how the larger bat community responds to seasonal effects in more detail.

In this thesis, I address the link between bats, arthropods, and the boreal forest system. However, insectivorous birds are also likely to play an important role in the interactions within this system. I collected bird acoustic data in parallel with bat acoustic data collection for the research described in **Paper II** and **Paper III** but ultimately was not able to analyse this data within the scope of this thesis. I intend to work with collaborators to secure the resources to revisit this data to further explore the relationship between insectivorous bats and birds with arthropods within boreal forests. Studying insectivorous birds and bats can provide a detailed lens into the richness of arthropod communities that would otherwise be energy-intensive to do by sampling arthropods directly. Insectivores benefit from thousands or even millions of years of evolution in their ability to sample insects which those interested in biodiversity can benefit from studying.

3.5 Conclusion

In this thesis I have presented evidence for the value of considering how bats in boreal forest habitats interact with their environment and respond to changes. These findings indicate the importance of mature boreal forest with diverse structure and density to support foraging opportunities for bats in Fennoscandia. The results from these studies can inform forest management strategies which aim to promote species conservation in Norway and elsewhere in Northern Europe. By presenting novel, complementary methodological combinations, I have demonstrated how non-invasive approaches can inform future studies investigating predator-prey interactions in relation to habitat characteristics. Moreover, the extensive data collected during this thesis has the potential to address many more unanswered questions relating to bat and insect ecology within Fennoscandia and to inform boreal forest management more broadly.

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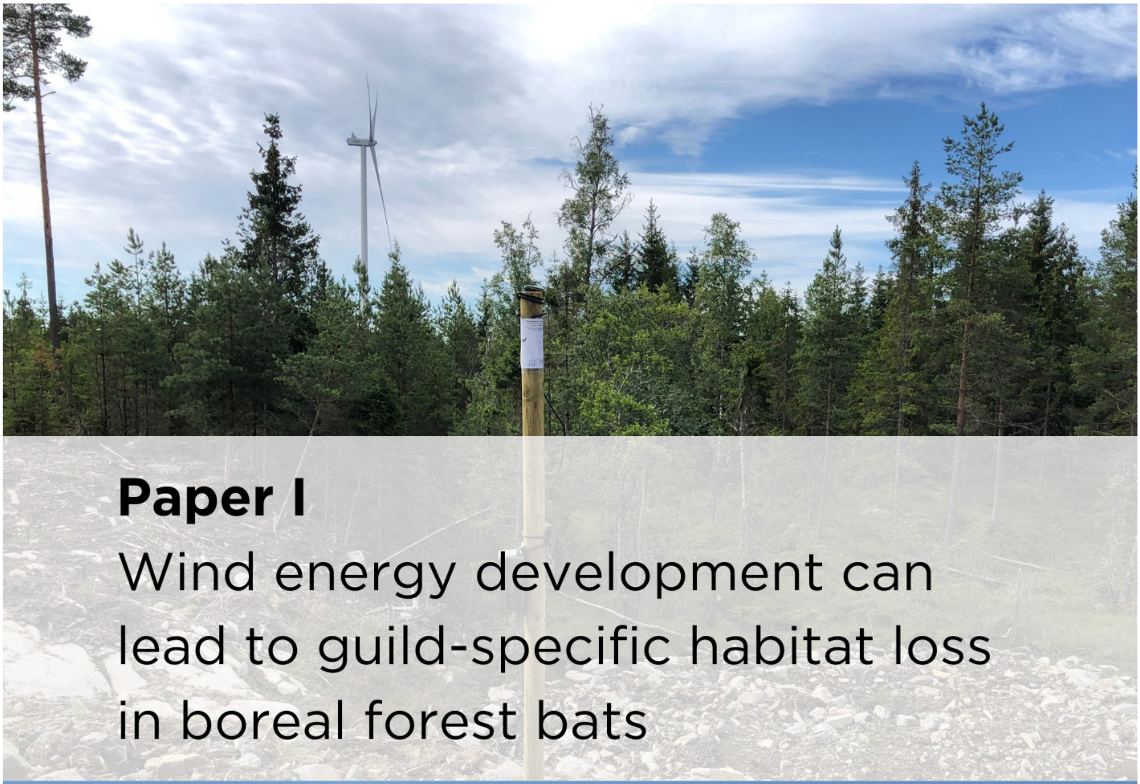
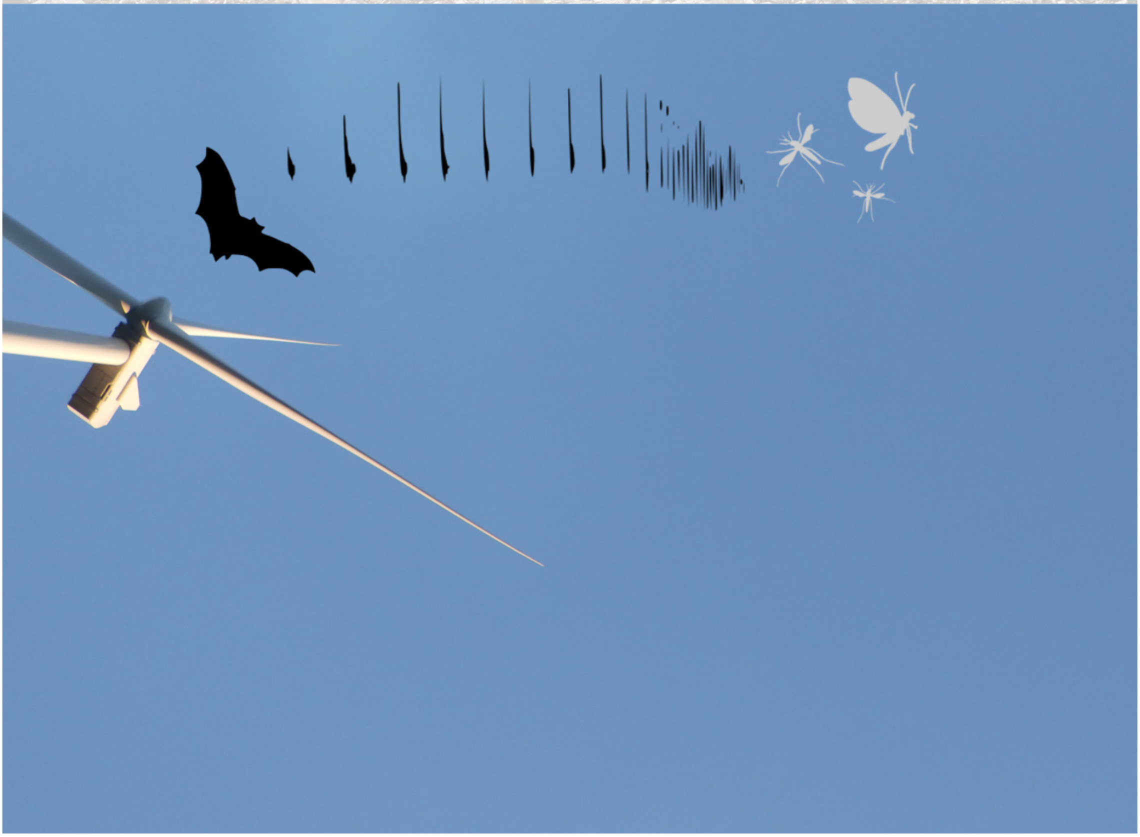


Paper I

Wind energy development can lead to guild-specific habitat loss in boreal forest bats



WILDLIFE BIOLOGY

Research article

Wind energy development can lead to guild-specific habitat loss in boreal forest bats

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Forest management rarely considers protecting bats in Fennoscandian regions although all species rely on forest habitat at some point in their annual cycle. This issue is especially evident as wind parks have increasingly been developed inside Fennoscandian forests, against the advice of international bat conservation guidelines. In this study, we aimed to describe and explain bat community dynamics at a Norwegian wind park located in a boreal forest, especially to understand potential avoidance or attraction effects. The bat community was sampled acoustically and described using foraging guilds (short, medium, and long-range echolocators; SRE, MRE, LRE) as well as behavior (commuting, feeding and social calls). Sampling was undertaken at two locations per turbine: 1) the turbine pad and 2) a paired natural habitat at ground level, as well as from a meteorological tower. We used a recently developed method for camera trapping nocturnal flying insects synchronously with bat acoustic activity. Our results reveal trends in feeding and general bat activity across foraging guilds in relation to insect availability, habitat type, wind, temperature, and seasonality. We show how seasonal patterns in behavior across guilds were affected by habitat type, temperature, and wind. We found that SRE commuting and especially feeding activity was highest in natural habitats, whereas LRE overall activity at habitats more season dependent. We found that nocturnal insect availability was positively correlated with total bat feeding activity throughout the night. Our results provide evidence for both direct and indirect risks to bat communities by wind parks: SRE bat habitat is lost to wind energy infrastructure and LRE bat may have an increased risk of fatality. Our findings provide important insights on seasonal and spatial variability in bat activity, which can inform standardizing monitoring of bats acoustically in boreal forests, at wind parks, and in combination with non-invasive insect monitoring.

Keywords: acoustic monitoring, avoidance effect, bat - insect monitoring, boreal forest, foraging guilds, wind turbine

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Introduction

As Fennoscandian countries strive to meet zero-emission goals, there are high demands to use forests for renewable energy (Enevoldsen 2016, Searchinger et al. 2018, Neumann et al. 2022). Boreal forests play a vital role in supporting global biodiversity (Bradshaw and Warkentin 2015) and sequestering carbon (Pan et al. 2011). In Europe, most of the boreal forest is in Fennoscandian countries where it dominates the landscape, covering 38–68% of the land area (Nordic Co-operation | Nordic Council and Nordic Council of Ministries. 2008, Framstad et al. 2013). Boreal forests are some of the most heavily exploited types of land-cover in these countries (Zhou et al. 2021). The rapid expansion of onshore wind energy infrastructure in Nordic countries in the Fennoscandian region (Norway, Sweden, Finland) is expected include substantial installation in forests (Högbom et al. 2021). Rehbein et al. (2020) found that large wind parks already overlap with key biodiversity areas such as forests, and will continue to be developed in such areas, in Fennoscandia. Wind energy development in the Nordic region has increased by 14% between 2005–2019 (Nordic Energy Research 2021) and, as of 2020, makes up 15% of total energy production (Nordic Energy Research 2021, Wråke et al. 2021). The Nordic Clean Energy Scenarios project (NCES) predicts that Nordic wind energy, will increase to as high as 65% of total energy production by 2050 (Wråke et al. 2021). The balance between managing forests for economic productivity, biodiversity and with consideration to carbon stocks requires a synergistic strategy to effectively balance the needs to industrial productivity and safeguarding ecological stability (Dinesen et al. 2021).

Wind energy infrastructure has the potential for direct, indirect, as well as cumulative adverse impacts on wildlife, especially bats (Laranjeiro et al. 2018). Both local populations and transient/migratory populations can be at risk from wind turbine development and operations (Kunz et al. 2007, Roscioni et al. 2013, Arnett et al. 2016). Wind energy may also affect predator–prey interactions (Rydell et al. 2010b, Voigt 2021). In spring and summer, the local movements of migratory bats may correspond with activity of high-flying insects (Reynolds et al. 2017), both of which can suffer mortality when colliding with or flying near turbines. Rydell et al. (2010b) and Jansson et al. (2020) provide arguments along with some evidence for the theory that a portion of the bat fatalities at wind turbines in Europe are caused by migrating bats feeding on insects during late summer and autumn migration. Residential populations of insects and bats at the ground level will have their habitat radically changed by the development of turbines, especially in forest. In some cases, the development of turbines may improve the habitat suitability for species that thrive in open or edge environments (Kirkpatrick et al. 2017). Such development can also displace species that require forest cover and/or are sensitive to the sounds and presence of turbines by degrading the habitat, resulting in broad cascading effects (Barré et al. 2018, Roemer et al. 2019). Ellerbrok et al. (2022) and Gaultier et al. (2023) both recently found that bats, especially those adapted to flying in cluttered habitat, were deterred by the presence of wind turbines in northern Europe. These studies emphasize the importance of acknowledging habitat loss from wind turbines as a risk to bats. However, neither study evaluated how bat behavior i.e. feeding activity, may be influenced by the presence of wind turbines differently from overall activity. Furthermore, the studies were not designed to distinguish if the observed effects were from sound/noise disturbance or habitat degradation. Understanding the specific drivers of wind turbine effects on bats is essential for making informed decisions regarding mitigation as well as the placement and development of energy infrastructure.

Norway, Sweden, and Finland are all member states of EUROBATs, an extension of the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention; CMS), and The Agreement on the Conservation of Populations of European Bats. EUROBATs has provided a series of publications informing best practices in bat monitoring, management, and conservation for party states to follow as guidelines. Rodrigues et al. (2015) describes the most recent EUROBATs guidelines for monitoring bats for wind energy projects which include recommendations for pre- as well as post-construction monitoring and mitigation measures at wind parks. Unfortunately, there are many examples of party states failing to follow these guidelines (Barré et al. 2022). A resolution to the EUROBATs guidelines for managing bats in relation to wind parks has since been published which urges parties to implement national bat monitoring programs at wind parks in accordance with the existing guidelines, and that the guidelines will be updated to reflect advances in research and conservation practices since 2015 (EUROBATs 2022). Bat species associated with boreal regions are expected to be the most impacted by climate change (Jones and Rebelo 2013) and many European migratory bat species ranges are predicted to move northward in response to climate change (Rebelo et al. 2010). The Fennoscandian and Baltic countries are especially limited in this capacity with little to no monitoring of bats at wind parks (Gaultier et al. 2020), in part due to knowledge gaps in general bat ecology and how to implement broadscale monitoring programs in this region. Addressing such knowledge gaps through developing international bat conservation strategies in Fennoscandian boreal regions is critically important for conserving European mammalian biodiversity.

There are national bat monitoring guidelines for most EUROBATS party states (Battersby 2010, Barova and Streit 2018). Effective monitoring to evaluate bat populations on a large scale require a variety of surveys but increasingly acoustic monitoring is becoming an integral tool. Acoustic monitoring of bats has rapidly advanced in the last few decades, as the technology available for collecting and analyzing bat calls becomes more sophisticated, affordable, and accessible (Sugai et al. 2019). Passive acoustic monitoring provides a non-invasive and standardizable means of monitoring wildlife over broad time and spatial scales and is expected to continue to expand in playing a vital role in how bats are monitored in the future (Browning et al. 2021). Echolocating bats have a wide range of call types that can also be flexible in structure, such that the effectiveness of identifying bat species acoustically varies across taxa and is heavily influenced by recording conditions (Kershenbaum et al. 2016). An alternative to species level analysis of bat acoustic data is to categorize the passes into sonotype defined foraging guilds that group bat species based on similarities in their echolocation which tend to reflect morphological, taxonomic, and ecological traits (Aldridge and Rautenbach 1987, Denzinger and Schnitzler 2013, Frey-Ehrenbold et al. 2013, Müller et al. 2013, Froidevaux et al. 2016, Erasmy et al. 2021). We have combined manual acoustic analysis to species level with foraging guild categorizations and evaluated for behavior to capture complexity in the bat community while acknowledging the limitations of species level analysis.

We address knowledge gaps in the seasonal activity patters and habitat use of bats in Fennoscandian boreal forest using acoustic monitoring and camera trapping to investigate differences in bat activity and behavior at a wind park located in a boreal forest. This study aims to 1) describe seasonal patterns in bat acoustic activity including response to wind and temperature 2) compare bat acoustic activity (guild and behavior) between undeveloped 'natural' forest habitats and habitat modified by wind energy infrastructure ('turbine pads'), and 3) test if prey availability was related to bat feeding activity. Our results are discussed in the context of future management and monitoring strategies for bats in boreal forests as well as at forested wind parks.

Materials and methods

Study area

Data were collected between 1 July and 29 September 2020 at BKW/Scanergy AS Marker wind park located in Ørje, Norway within Viken (Østfold) county (turbine 5 (North): 59°30′58.1″N, 11°43′12.1″E, turbine 12 (South): 59°27′52.7″N 11°45′15.8″E, Fig. 1). This period was selected because late summer and early autumn have been identified as peak period for bat fatalities at wind parks in northern Europe by several studies (Rydell et al. 2010a). We could only collect data over one field season due to a change in

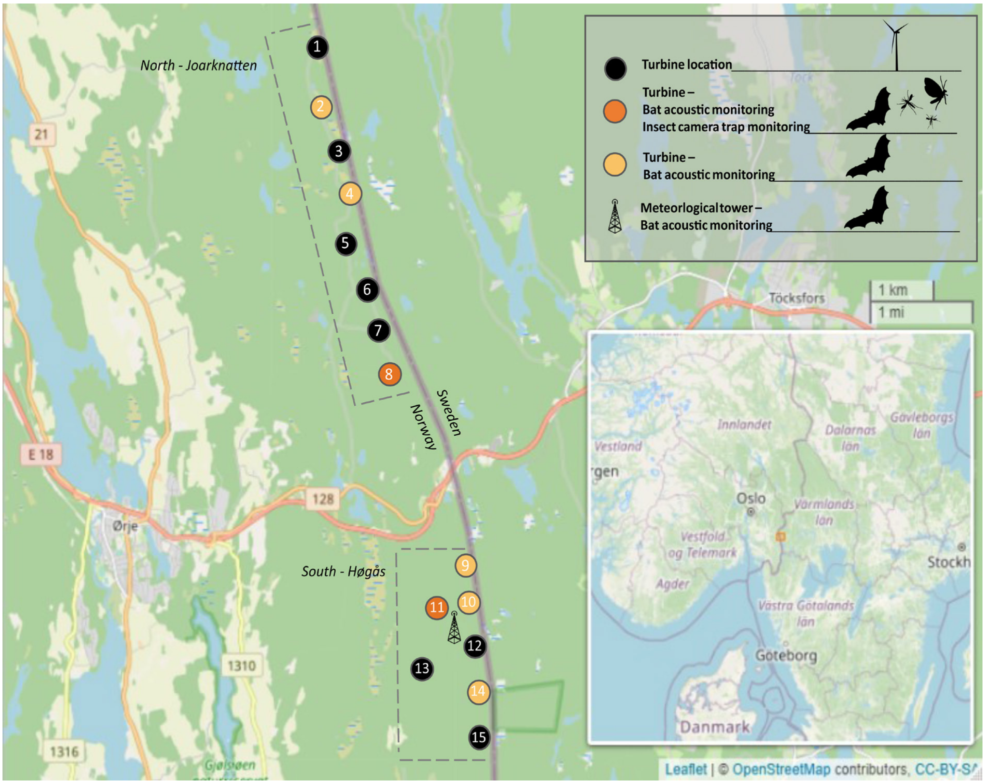

Figure 1. Map of Marker wind park in southeast Norway and the sampling locations. Internal map of the wind park in relation to Oslo, the capital of Norway. The thick gray line east of the wind turbines is the Norwegian – Swedish border. Thin, gray dashed line indicates the North (Joarknatten) and South (Høgås) facilities. The location of the meteorological tower is indicated in the south facility. Data collection was in the summer and autumn of 2020. Meteorological tower image: https://www.pngwing.com/en/free-png-tacee.

ownership of the wind park which entailed uncertainty and challenges around access to the wind park and weather data. Additionally, due to the COVID-19 pandemic, travel within Norway was made challenging and limited the ability to do field work.

The entire wind park in 2020 included 15 Vestas V136 3.6 MW turbines that are 142 m tall at the nacelle with 68 m long blades. The turbines are installed at two facilities, Joarknatten and Høgås, which we refer to as the north and south facility respectively (Fig. 1) and collectively as the wind park. Each turbine, within each facility, were between 500 m and 1 km apart. The distance between the two closest turbines from the north and south facility is approximately 3 km. The wind park and supporting infrastructure covers an area of approximately 8.6 km^2 of cleared land (Wiersdalen Karlsen 2017), located in a boreal production forest dominated by *Picea abies* and *Pinus sylvestris*, containing several small lakes and wetlands. The weather for this area during the summer and autumn is warm and mild, with average daily temperatures ranging between 7 and 20°C, with average monthly rainfall between 76–81 mm (http://weatherspark.com). Temperature and wind speed data were collected approximately once every 10 min from the nacelles of the turbines at the wind park throughout the study period and were made available for analysis.

Bat acoustic monitoring

Bat acoustic monitoring took place from 1 July to 29 September 2020 at seven wind turbines (three in the northern facility and four in the southern facility; turbines 2, 4, 8, 9, 10, 11 and 14). Wildlife Acoustics Song-Meter4-BATFS detectors (hereafter detectors) combined with either SMM-U2 or SMM-U1 microphones (hereafter U2 or U1 microphones) were deployed at ground-level in pairs at 7 turbines (14 detectors in total) and two detectors were deployed a meteorological tower 'at height', above the forest canopy and within the rotor sweep zone.

At each turbine locality where bat acoustic monitoring took place (Fig. 1), two different habitat types were sampled: a turbine pad site and a natural habitat site. The turbine pad sites were located on crane auxiliary pads, between 45–110 m from the base of the nearest turbine. Each turbine was surrounded by a large, flat gravel pad that had been developed for installing and maintaining the turbine. Crane auxiliary pads, the location of turbine pad sites, were within or directly adjacent to the gravel pad surrounding turbines. Natural sites were closer to forest edge and sampled habitat that had not been physically altered by development and were located between 80 and 115 m from the base of the turbine. This design ensured that disturbance from light or sound produced by the turbines were as similar as possible between the two different habitat types. The design enabled us to quantify how changes in physical habitat due to development, regardless of light and sound disturbance, impacted the activity patterns and behavior of bats. At ground level detector sites, detectors were affixed to wooden poles approximately 2 m high, with either U2 or U1 microphones. Turbine pads and natural sites at each turbine locality were monitored simultaneously. Ground level detector sites were monitored for 20 days out of every 30. The 7 turbines localities were split into two monitoring groups which had a 10 day overlap (turbines 2, 8 and 10 in one group, turbines 4, 9, 11 and 14 in the other) such that at least one turbine from both the northern and southern facility were actively being monitored.

Two detectors were deployed at height continuously between 16 July and 23 September on a meteorological tower (met tower detectors) located in the southern facility (Fig. 1). Both met tower detectors were deployed with U1 microphones oriented slightly upward and stationed at approximately 45 (sampling above the forest canopy, hereafter referred to as Met 45) and 95 (sampling within the turbine rotor sweep zone, Met 95) m high, directed toward north and east, respectively.

Detectors collected 16-bit resolution full spectrum .wav files, programmed to become active from one hour before sunset to one hour after sunrise, triggered to ultrasonic activity, with a 256 kHz sampling rate, 12 kHz minimum trigger frequency and maximum recording length of 15 seconds. Detectors were checked approximately once a week while deployed for regular maintenance checks and to collect data.

Bat acoustic analysis

Bat acoustic data were processed using Kaleidoscope Pro (ver. 5.1.9i, Wildlife Acoustics). We defined a bat pass in the study as a recording which contained at least two pulses, with less than 1 second of separation between them (Fenton et al. 1973), otherwise files were classified as noise and not included in further analysis. All passes identified as 'NoID' by the classifier were treated as bat passes and manually analyzed Bat pass duration varied between 2–15 seconds long. These recordings were then classified using the Bats of Europe Classifier (ver. 5.2.1) auto ID function. The species list was specified as only those species found in Norway according to the 2015 Norwegian Red List (Henriksen and Hilmo 2015), excluding *Eptesicus serotinus* (conservation status Not Applicable). In 2021, *Pipistrellus pipistrellus* was designated as 'Not Applicable' on the Norwegian Red List (Eldegard et al. 2021) and thus this species was reclassified as unknown pipistrelle species due to similarities in call structure with other *Pipistrellus* spp. (Montauban et al. 2021).

All bat passes were manually analyzed by one analyst (Author1, n = 19 438). Forty-five passes were found to be noise files and were subsequently removed. During manual verification, bat passes were classified to two-tiers: 1) subguild or species level, following parameters from Russ 2021 and 2) guild-level. For guild-level analysis, we used three foraging guilds to describe the bat community: short range (SRE; grouping *Myotis* species, *Plecotus auritus, Barbastella barbastellus*), medium range (MRE, grouping *Pipistrellus* species), and long range echolocators (LRE; grouping *Eptesicus nilssonii, Vespertilio murinus, Nyctalus noctula*). Grouping species in this way provided a robust method for comparing trends within foraging guilds which may encompass rarer species or species with overlapping call structures (Denzinger and Schnitzler 2013). We chose to identify bat passes to sub-guild, genus, or species to provide more detailed taxonomic data for forest management. Where a bat pass could not be assigned to species with confidence, these were classified into sub-guilds: *E. nilssonii* or *V. murinus* (LR1) and *V. murinus* or *N. noctula* (LR2), *Myotis* species (SR1), *Pipistrellus* species (MR1). Bat passes that were not feasible to classify confidently to any of these categories were classified as 'NoID'. Comparisons between the results of the manual acoustic analysis and the automatic acoustic analysis can be found in the Supporting information. Behavior was also recorded for each pass: commuting, feeding (feeding buzz), or social (Middleton et al. 2014, Russ 2021). Feeding buzzes were prioritized over social calls where both occurred such that a pass containing both would be categorized as a feeding pass but otherwise passes with social calls were classified as social passes.

Insect camera trapping

Insect camera traps were deployed in pairs (combined with the bat acoustic natural and turbine pad sites) at one turbine locality in the north and one in the southern facility (turbines 8 and 11, respectively, Fig. 1) to monitor the abundance of flying insects. The camera trap survey period was paired with bat acoustic detectors between 16 July 2020–28 September 2020 however, due to equipment failures, sampling effort was uneven across sites (Supporting information). The camera traps were designed to closely follow the methods described in Ruczyński et al. (2020) and consisted of a digital camera (Ricoh WG-6 Waterproof 20 m / 65.6 ft; Model R02050 2019) oriented skyward, in protective water-resistant housing, attached to an external battery power source and programmed to take images (JPG, 5184 × 3888 pixels) every 10 min with flash. Only photographs taken between 2 h (accounting for differences in how the bat acoustic detectors calculated sunset and calculations in R) before sunset and 1 h after sunrise were included in the analyses such that the dataset was comparable with bat acoustic recordings. Photographs were manually annotated using VGG annotator (Dutta and Zisserman 2019) to identify the number of flying insects as well as to describe the quality of the photo (viable = high quality image or unviable = poor quality image). Insect abundance was quantified as the sum of insects identified in each image per night.

Data preparation

We prepared seven datasets (Supporting information): 1) unaggregated bat passes for each site, 2) ground level nightly aggregated total summed bat activity per site 3) ground level nightly aggregated SRE bat feeding activity per site, 4) ground level nightly aggregated SRE bat commuting activity per site, 5) ground level nightly aggregated LRE bat feeding activity per site, 6) ground level nightly aggregated LRE bat commuting activity per site, 7) insect abundance and total (all guilds) bat feeding (social and commuting passes excluded) activity combined aggregated to hour per site (only turbines 8 and 11, when both cameras and acoustic detectors were active) combined with weather data and, 8) insect counts and bat feeding passes per site per hour for turbines 8 and 11 when both cameras and acoustic detectors were active. Additional variables per detector location were included in all datasets such as detector site (14 ground level detector sites and 2 met tower detector sites, n = 16) and locality (7 turbines and one met tower locality, n = 8) as well as habitat type (turbine pad, natural or meteorological tower). Data from the meteorological tower was only included in dataset 1. The variable 'hours since sunset' was calculated for hourly aggregated data. The variable 'night' was created by adjusting the true date and time by 12 h centered at noon to conceptualize bat activity on a nightly scale. The variable Julian night was also included, which is the Julian day (the sequential number of the day in the year) applied to night rather than day.

For datasets 2–6 (nightly aggregated datasets), relevant bat activity was represented as the sum of bat passes per night per site. The nightly mean wind speed as well as temperature averaged across the whole wind park was included. Weather data were collected from the turbine nacelles approximately every 10 min, but there were missing hours or nights for some turbines, so weather data were aggregated, and the mean was taken across the whole wind park. For hourly and nightly aggregated datasets (2–8), zeroes values were inserted for nights when a detector or camera trap was present and functioning but did not record any bat or insect activity.

Statistical analysis

We applied negative binomial generalized additive models (GAMs) with restricted ML (REML) using the R package 'mgcv' ver. 1.8-41 (www.r-project.org, Wood 2011) to model bat acoustic activity in response to habitat, temporal, and environmental variables. This model approach was selected to account for the non-linear patterns in seasonality that were detected in exploratory analyses, and which were too complex to be adequately captured by including second-order polynomials as predictors. A set of five different model groups were explored to explain patterns of total bat acoustic activity, SRE feeding, SRE commuting, LRE feeding and LRE commuting activity separately (Table 1). We analyzed these subsets of the data separately rather than fitting one complex model with several interaction terms, to make it easier to interpret model outputs, but also to improve model fit. The predictor variables for these models were: locality, habitat, the interaction between Julian night and habitat (allowed for separate shapes of relationships with Julian night for each habitat), mean nightly wind speed, and mean nightly temperature. Locality was treated as a random effect using a smooth ('re'). A Gaussian process smooth was applied to the interaction between Julian night and habitat to address temporal autocorrelation, and a thin plate regression spline smooth was applied to average nightly wind speed. Temperature was treated as a

Table 1. Model specifications for the generalized additive models of bat acoustic activity for total bat activity and four subsets of guild (short range and long range echolocators) – behavior (feeding and commuting) specific acoustic activity. The % zeroes (Z%) of the datasets, the total number of bat passe and insect counts for the datasets used in each model is also reported. For models Insect and Bats–Insects, % zeroes refer to the number of hourly detector hours for bat feeding passes and insect counts, respectively. Outputs for bat data models available in the Supporting information, insect model outputs in The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Model	Response	Zeroes (%)	Bat passes	Feeding passes	Social passes	Insect counts	Dataset
Bats total	Sum bat passes per site per night (ground level only)	13	19 206	4034	547	NA	2
SRE feeding	Sum SRE feeding passes per site per night	84	327	32	0	NA	3
SRE commuting	Sum SRE commuting passes per site per night	31	3787	0	0	NA	4
LRE feeding	Sum LRE feeding passes per site per night	62	3703	3703	0	NA	5
LRE commuting	Sum LRE commuting passes per site per night	24	10 584	0		NA	6
Insects	Sum feeding bat passes and insect count per site per night for each hour with weather data	94 and 87	372	372	NA	4546	7
Bats–Insects	Sum feeding bat passes per insect count per site per hour	94 and 87	373	373	NA	4563	8

linear fixed effect because it consistently had a positive linear effect on all bat activity. We used a tensor product interaction between temperature and wind speed for all model groups but this term either had little effect and contributed toward overdispersion in most models, so it was dropped.

To evaluate the relationship between insect counts per hour and weather throughout the season, we applied a negative binomial GAM with REML predicting the number of insect counts per hour in response to average hourly wind speeds and temperature, the night in the season, and locality as a random effect (Table 2, Insects). A thin plate regression spline was applied to wind, temperature, and a Gaussian process smooth to night in season (Julian night). There were hours when camera traps and acoustic detectors were active, but no weather data were available so seventeen insect counts and one bat feeding pass were excluded in this model. To predict the number of bat feeding passes per hour in response to insect availability, another negative binomial GAM with REML was fitted in response to a categorical binary insect count variable (0 insects counted per site per hour = 'No insects', 1 or more insects counted per site per hour = 'Insects active'), locality as a random effect and hour (hours since sunset) with thin plate regression spline smooth (Table 2, Bats–Insects).

We carried out model validation with the gam.check function to confirm that we had selected appropriate k-values and that the model fitted our data, inspecting standard graphical model validation plots. All data analysis was carried out in R (www.r-project.org).

Results

Bat pass classification

Bat acoustic data were collected over 950 detector nights across 91 nights and 16 detector site locations. A total of 19 438 passes across 56.5 h (mean bat pass length 10.8, SD 4.0 seconds) of recordings were manually verified. The LRE represented 76% of the total bat activity, of which *E. nilssonii*

Table 2. The relationship between insect activity, environmental conditions, and bat feeding activity. The Insects model expresses the relationship between the sum number of insects (per image per hour) and environmental variables throughout the season. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020. Temperature and wind speed were nightly averages (mean). The Bats–Insects model explains the relationship between insect presence (0/1) and the number of bat passes (per hour per site) where hour is the hours since sunset. Confidence intervals (95%), both the upper (UCL) and lower (LCL)) are reported for parametric terms.

Model	Variable						
Insects	*Parametric terms*	Estimate	SE	z	p	LCL	UCL
	(Intercept)	−0.372	0.668	−0.557	0.578	−1.68	0.937
	Smooth terms	Estimate	edf	X^2	p		
	Wind speed	10.823	59	89.03	0.010		
	Locality	1.722	9	4.91	0.037		
	Temperature	5.248	9	62.50	< 0.001		
	Julian night	0.955	1	21.07	< 0.001		
Deviance explained: 25%							
Bats–Insects	*Parametric terms*	Estimate	SE	z	p	LCL	UCL
	(Intercept)	4.50	0.746	−6.03	< 0.001	5.960	−3.04
	Insects active (binary)	1.61	0.393	4.09	< 0.001	0.838	2.38
	Smooth terms	Estimate	edf	X^2	p		
	Hour (since sunset)	7.821	14	65.5	< 0.001		
	Locality	0.902	1	8.67	< 0.001		
Deviance explained: 40.7%							

passes contributed 95%. Therefore, *E. nilssonii* represented 72% of total acoustic activity. SRE passes made up 21% of all bat passes, of which 86% were SR1 (*Myotis* species) passes. Only 0.5% of the passes were classified as MRE, with the remaining 2.5% classified as NoID bat passes. Therefore, MRE and NoID passes were excluded from guild specific analyses. Several species classified as threatened or near threatened on the Regional Red List for Norway were detected, including *B. barbastellus* (n = 10 passes), *Pipistrellus nathusii* (n = 9 passes), *N. noctula* (n = 182 passes) and *V. murinus* (n = 168 passes), LR2 (n = 221 passes). Passes of *B. barbastellus* and *P. nathusii* were validated by at least two external bat acoustic experts. Commuting, feeding, and social passes made up 76%, 21%, and 3% of the activity recorded, respectively (Fig. 2).

Spatial and temporal patterns in bat activity

Bat activity varied across the season and across the different detector sites. Collectively both detectors at turbine 9 contributed approximately 41% of all bat activity recorded (Fig. 2). Bat activity increased from July and peaked between August and September for nearly all sites, then steadily declined for the rest of the season (Fig. 3). Across the study period, ground level detectors recorded a mean of 20 bat passes per night while the met tower sites collected an average 12 passes per night. The met tower sites collected only 232 bat passes in total: 197 passes from Met45 and 35 passes from Met95. Of these, 223 passes belonged to bats in the LRE guild, with one MRE pass, seven SRE passes, and one NoID pass also being recorded. The behavior most often recorded at the met tower was commuting activity (n = 217 passes), however there were feeding (n = 12), and social (n = 3) passes recorded from both detectors (Fig. 3). Average nightly temperature and wind speeds had a strong influence on total bat activity at ground level sites (Supporting information). Ninety-two percent of bat activity recorded occurred when nightly average wind speeds were less than 12 m s^{-1} and when temperatures were greater 10°C. We found that temperature had a strong positive linear effect on bat activity in all models tested but the effect of wind was more varied (Supporting information). Bat activity began to decline as wind speeds increased over 10 m/s but warmer average temperatures, bats were still active at higher wind speeds (Fig. 4).

When all bat activity was aggregated by night, we found no significant difference in average bat acoustic activity between natural and turbine pad habitats during the study period, but the shapes of relationships with Julian night differed between the habitats (Supporting information). However, when the bat activity was subset by guild and behavior, it was possible to see average differences in habitat use. SRE bat activity was higher at natural sites compared to turbine sites throughout the season and feeding activity was substantially higher at natural sites than at turbine pad sites (Fig. 5a–b). LRE bat commuting and feeding activity was dominant in both natural and turbine pad habitat types, though we found some evidence that LRE bats are more active at turbine pads than natural sites later into the season but were recorded more often at natural sites in early July (Fig. 5c–d).

Relationship between bat activity and insect availability

We collected concurrent bat and insect activity data for 2041 h across 176 nights at the natural and turbine pad sites at

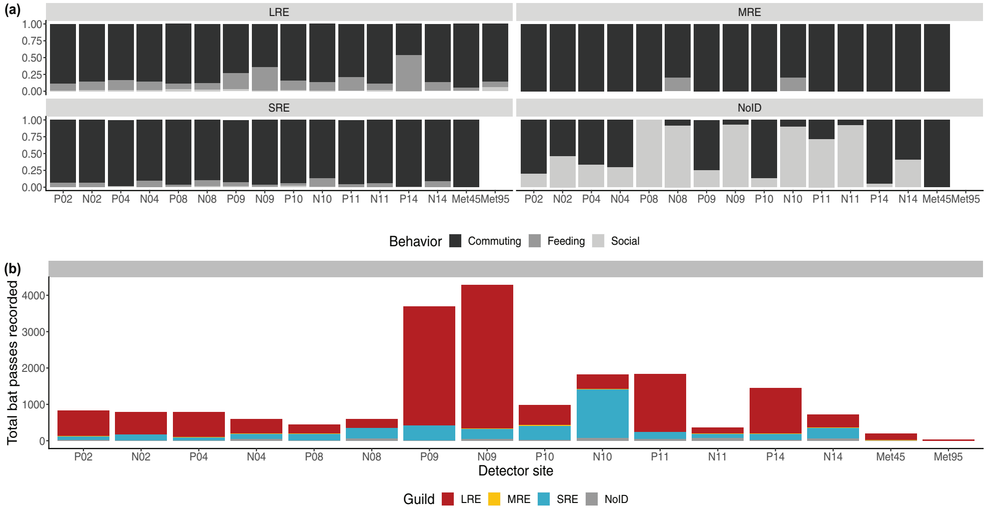

Figure 2. (a) Proportions of bat activity for behavior (dark gray = commuting, medium gray = feeding, light gray = social) for all detector sites, for the entire sampling period pooled. (b) An overview of total bat passes recorded for the entire study period by guild for each site. Foraging guilds: Short range echolocators (SRE, blue), medium range echolocators (MRE, yellow), long range echolocators (LRE, red) and unidentified bat (NoID, gray). The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020..

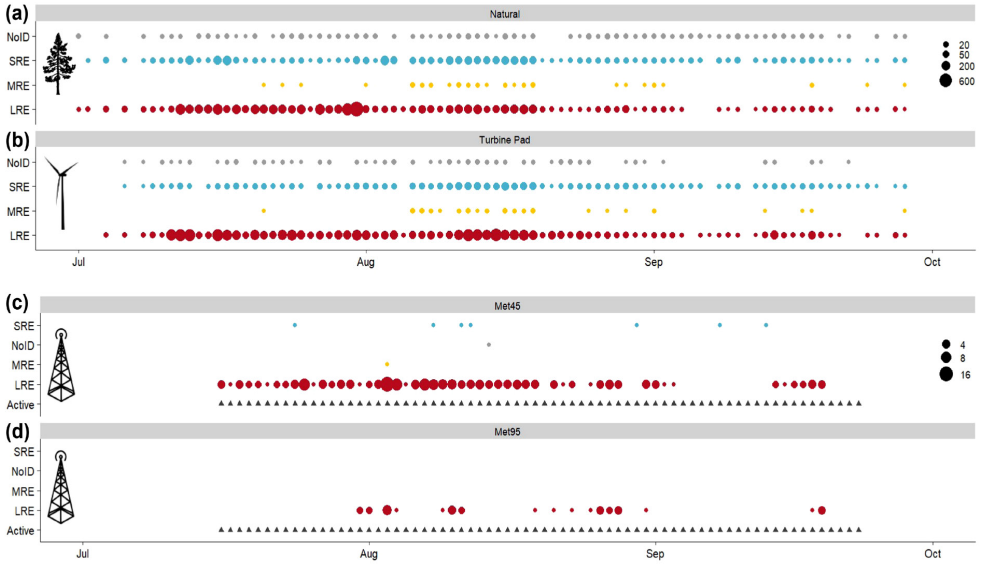

Figure 3. Seasonal activity for each foraging guild (NoID (unidentified bat) = gray, SRE (short range echolocator) = blue, MRE (medium range echolocator) = yellow, LRE (long range echolocator) = red) across the ground level sites, (a) at natural and, (b) turbine habitats and for the meteorological tower sites; microphone deployed 45m (c) and 90 m (d) heights). The size of the dots corresponds to the number of bat passes per night. Black triangles indicate nights when the met tower detectors were actively recording data. A more detailed overview of when detectors were active at each site is found in the supporting information. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

turbines 8 (N08, n = 442 h; P08, n = 454) and 11 (N11, n = 544; P11, n = 603). There were 10 642 viable photos across all sites, of which 578 photos contained at least one insect which equated to 4563 insects present overall. Bat activity was recorded in 94% of recording hours (Table 1). Of the 104 detector – camera trap hours that included bat feeding passes, there were a total of 373 bat passes counted within those hours.

We found that temperature had a strong positive influence on the number of insects counted in an image per hour, as did the night in the season. The difference in localities had a clear strong influence on insect counts. We also found strong evidence that hourly average wind speeds were associated with the number of insects, but the effect was much weaker than temperature (Table 2, Insects). The results of the Bats – Insects model suggest that if insects were observed, this increased the likelihood of observing bat feeding passes at the same site. We observed a bimodal trend in insect activity as well as in bat feeding activity, with peaks occurring at sunset and sunrise (Fig. 6).

Discussion

Nightly bat activity peaked between July and early August, with another smaller peak in late August, with mean nightly temperature explaining activity better than wind speeds. We show how assessing total bat activity without evaluating behavior can mask guild-specific responses. Species adapted to flying in and near cluttered vegetation (SRE: short range echolocators) were recorded significantly less at turbine pad sites than at paired natural sites. Feeding activity of SRE bats was almost exclusively recorded at natural sites, suggesting that the developed areas around the turbine pads remove or degrade foraging habitat for these species. Bat species adapted for flying in open spaces (LRE: long range echolocators) were most frequently observed across the study period and area, regardless of habitat or behavior type. The high activity of LRE bats across the wind park raises conservation concern for species in this foraging guild which are amongst the most at risk for direct mortality with turbines. Ground-level acoustic monitoring was more effective at sampling the bat community and seasonal activity patterns than monitoring at heights above the forest canopy and within the rotor sweep zone. However, data collected from detectors deployed at a met tower in the wind park revealed that LRE bats were active at 45 m and 95 m heights between August and September, during the same period when most turbine fatalities are observed for LRE bat species in northern Europe (Rydell et al. 2010a, Rydell et al. 2017, Apoznański et al. 2018, Gaultier et al. 2020). We found support for our hypothesis that prey availability was linked to bat feeding activity using a relatively novel insect camera trap method paired with bat acoustic detectors. There was a positive relationship between insect presence and bat feeding activity, especially during warmer night hours, regardless of habitat. The wind park hostsed a bat community of at least 8 out of 11 of Norway's known bat species, including the critically endangered *B. barbastellus*.

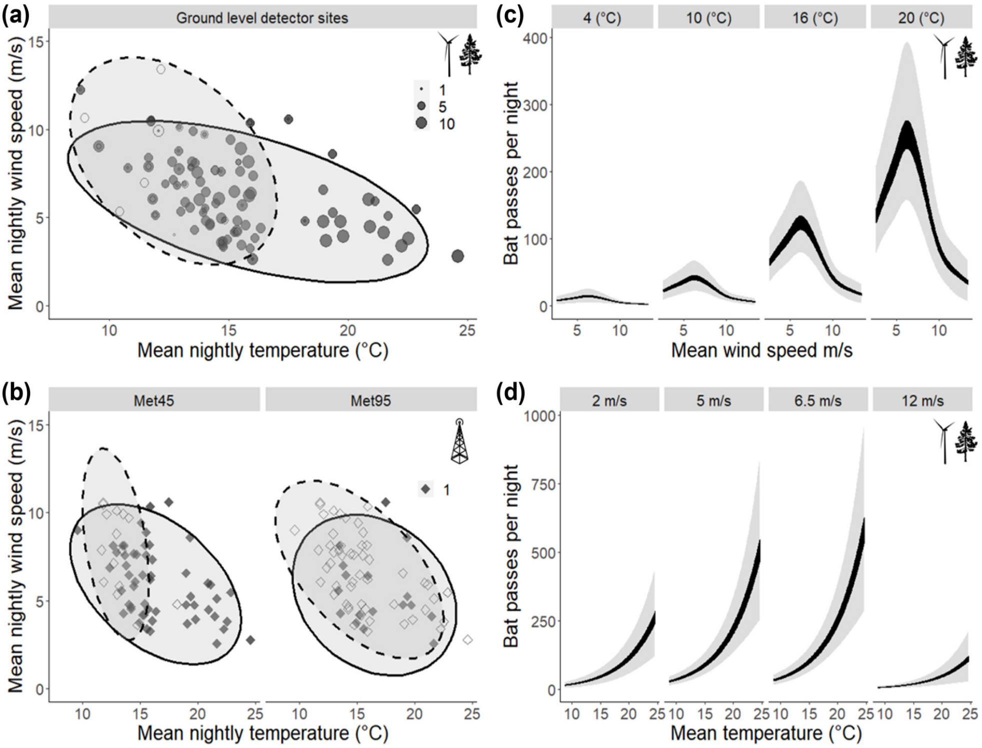

Figure 4. The relationship between average nightly temperature and wind speed and bat activity at ground-level (a, c, d) and the meteorological tower (b). For panels (a) (n = 811 detector nights) and (b) (n = 140 detector nights), filled points represent nights where bats were active and empty points represent nights with no bat activity. The size of the point is relative to the number of nights with the same temperature and wind conditions. The ellipses represent the 95% bivariate confidence interval for detector nights when bats were active (solid line) and inactive (dashed line). Panels (c) and (d) use predictions from the bats total model to show the relationship between temperature and predicted bat activity (bat passes per night) at ground level based on data from turbine 9, predicted for 31 July for both turbine pads and natural sites (black line, thickness corresponds to increased variance between habitats at different temperatures; gray shaded area = 95% confidence interval). The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Our findings provide further evidence for the critical need to enforce bat monitoring at wind parks and develop mitigation efforts towards bat-friendlier wind energy operations, especially in boreal forests.

This study is based on empirical data from only one season. Repeating the study in another year, or in several years, could disentangle weather and seasonal effects. However, we would argue that our main finding, i.e. guild-specific responses to habitat change, would likely be similar in another year, unless the study was done in a year with poor weather conditions throughout most of the season. Furthermore, the lack of between-year variation was partly compensated for by carrying out continuous monitoring throughout the season. We expect the impacts of weather and season to be similar from year to year, although effect sizes could vary with between-years variation in bat activity and environmental conditions.

Our study is one of very few studies that draw attention to the risks of bats at wind parks in this region. It can be used to draw insights on how to develop bat monitoring techniques in similar wind parks in boreal forests. Unfortunately, so long as there are no regulations that enforce pre- or post-construction monitoring of bats at wind parks on a national level, it may be challenging to gain access to wind parks to conduct studies for multiple years. Future research and bat monitoring efforts will benefit from multiple year studies that can better account for between- year variations in bat activity.

Bat activity response to weather and seasonal patterns

We found that bat activity responded to mean nightly temperature more so than wind speed. There were 43 detector nights with more than 100 total bat passes (Supporting information) when mean nightly temperatures were greater than 12°C but wind speeds were between 2.5 and 9 m s^{-1}. These high activity nights illustrate how temperature is a stronger driver than wind speeds during certain periods in the year for bats in this region. Our findings lend further support to the findings of Rydell (1989) that temperature was the main driving weather predictor of bats as well as insect abundance

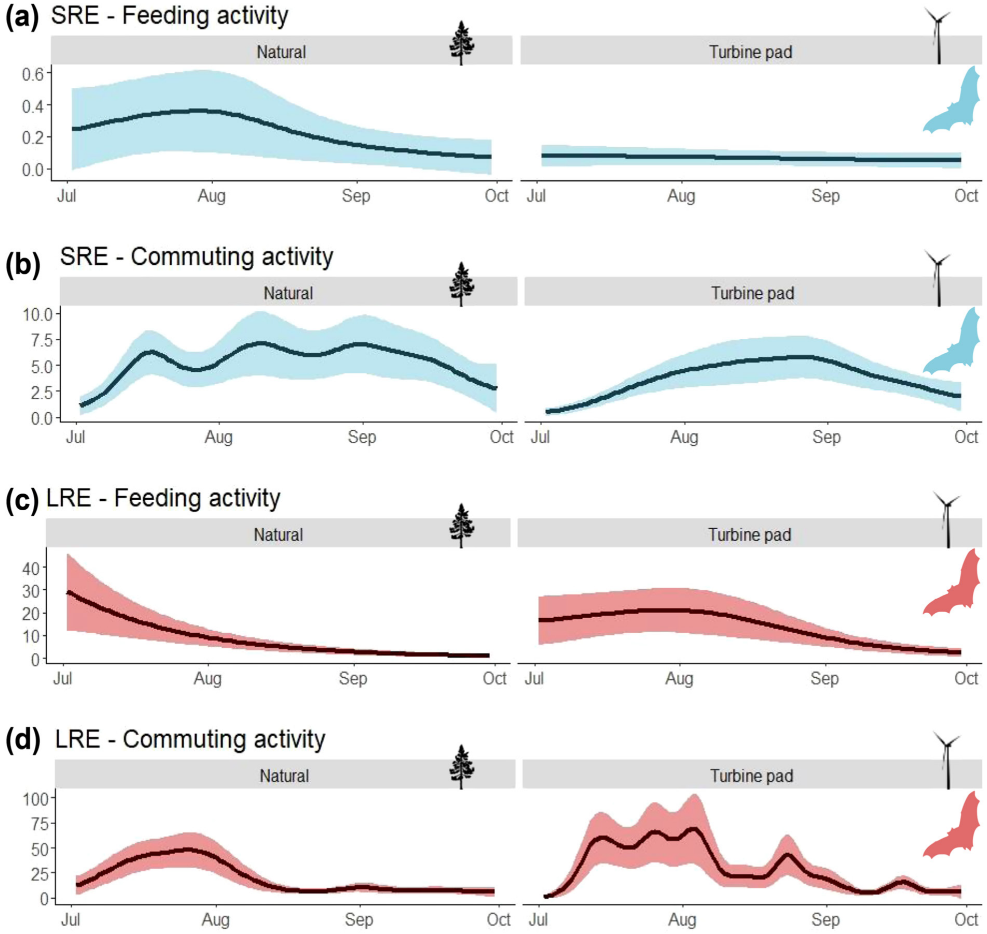

Figure 5. Predictions from models summarized in the supporting information of the guild-behavior specific GAMs of bat passes per night. These predictions are based on data for turbine 9, predicted across the season for both turbine pads and natural sites together (black line, thickness corresponds to increased variance between habitats at different temperatures, shaded area = 95% confidence interval). SRE (blue) = short range echolocators, LRE (red) = long range echolocators. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020..

in southern Sweden. The stronger influence of temperatures than of wind speeds on bat activity may be especially true in forested areas where bats as well as insects can use the vegetation as a wind break to remain active on warmer nights, as suggested by Verboom and Spoelstra (1999). Perks and Goodenough (2020) found a positive relationship between wind speeds and bat activity across most of the bat community and suggested that the effect that increased wind speeds have on bat activity is likely influenced by multiple factors.

Studies from wind parks in Europe and the US have found that bat activity dropped off after 5–6 m s-^{1} (Horn et al. 2008, Rydell et al. 2010a, Amorim et al. 2012) or 8 m s^{-1} (Cryan et al. 2014). In temperate regions, such as in the UK and in the US, bat survey guidelines do not suggest monitoring bats on nights where temperatures drop below 10°C and or wind speeds are consistently above 8 m s^{-1} (Richardson et al. 2021) or even 4 m s^{-1} (US Fish and Wildlife, 2022). Studies in boreal regions (Baerwald and Barclay 2009, Snively et al. 2021), including within Norway (Michaelsen 2017, Frafjord 2021), have reported trends in bat activity like those in temperate regions.

In our study, wind speeds of 5 or 6.5 m s^{-1} had higher predicted rates of bat activity than lower wind speeds (Fig. 3) on nights when temperatures were greater than 10°C. On 90% of the nights when bats were active at the met tower, mean nightly weather conditions were when winds were less than 10 m s^{-1} and temperatures greater than 13°C. In comparison, studies from Sweden have found similar but varied effects of how temperature and wind influence bat activity. Rydell et al. (2017) reported that 90% of bat activity recorded at turbines

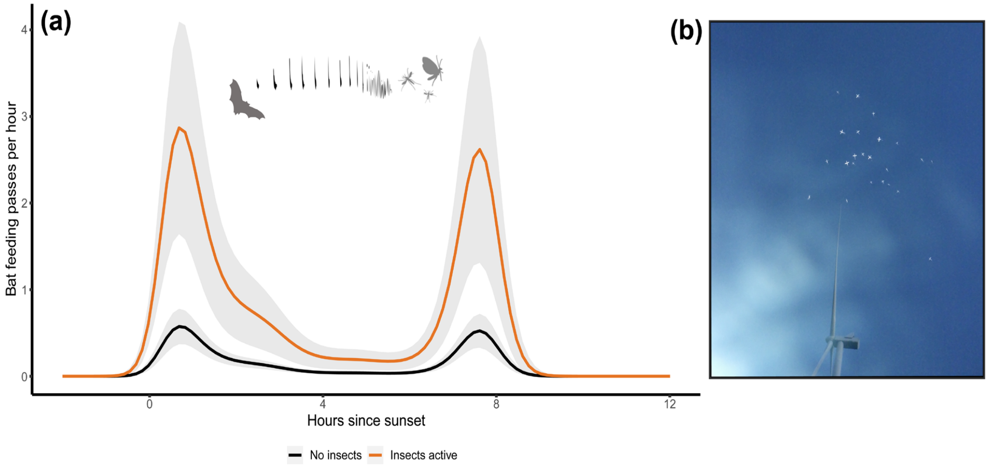

Figure 6. (a) Predictions from the GAM model “Bats – Insects” (Table 2) of bat feeding passes per hour (orange line = bat activity when insects were present, black line = bat feeding activity when insects were not recorded, shaded area = 1 SD) for the locality turbine 11 throughout the night. Time is expressed in hours since sunset. The illustration is of a bat emitting a feeding buzz at flying insects. (b) Image that contains insects collected from a camera trap during this research. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020..

(~ 100 m high, averaged over 10 min, several wind parks between 2012–2015) occurred when winds were less than 5.8 m s^{-1} and temperatures were greater than 14.6°C. de Jong et al. (2021) also measured average nightly bat activity in response to weather conditions recorded at the turbine nacelle at 3 turbines for two seasons and found that 90% of bat activity occurred when temperatures were greater than 9°C and wind speeds were less than 8.2 m s^{-1}. Even if temperature is a stronger driver of bat activity than wind speeds, wind speed in relation to turbine rotation speeds should be considered when trying to predict bat activity near active turbines as well as potential collision risks. Cryan and Barclay (2009) observed that bats will more frequently approach wind turbines at lower wind speeds (< 10 m s^{-1}) and when blades are spinning.

The weather data for this study was collected from the turbine nacelles, approximately 140 m higher than the ground level bat acoustic detector microphones. Collecting weather data from nacelle height is a method that is used in several published studies and is common in environmental assessments (Mathews et al. 2016, de Jong et al. 2021, NatureScot et al. 2021, Peterson et al. 2021) and provides – relevant weather data for determining which turbine operational wind speeds relate to bat activity. Ground-level monitoring stations may have provided a clearer indication of how bats were responding to the more local environment. However, we found average daily temperatures to be highly correlated (r2 = 0.95) with weather conditions recorded at nearby (~10 km) weather station, though temperatures collected from wind turbine nacelles were consistently slightly higher (mean average difference of 0.82°C) than measurements recorded from the weather station (2 m high). No measurements of wind speed from nearby weather stations were available. Bat acoustic activity is known to vary within an area and between years. While we do not have multiple years to compare in this study, we found rapid changes in bat activity across sites and within the season. Recently there have been several exciting studies published on the ecology of bats in the Fennoscandian region using broadscale acoustic monitoring (Vasko et al. 2020, Blomberg et al. 2021, Gaultier et al. 2023, Kotila et al. 2023) which reported similar seasonal bat activity patterns to our findings. Kotila et al. (2023) reported seasonal activity patterns of *E. nilssonii* (LRE foraging guild) and *Myotis* spp. (SRE foraging guild). from project that spanned 8 different localities stretching from latitudes approximately 60–66° North in Finland between 2015–2021. The patterns Kotila et al. (2013) reported for lower latitudes, resembled the seasonal patterns observed at Marker wind park (59° North) in 2020 with a steady increase throughout the summer leading to a peak in August followed by drop off in activity in September. While site specific considerations are important, it may be possible to apply latitudinal defined bat monitoring regions across Fennoscandia for international, broadscale monitoring programs.

Bats living in Fennoscandia are already living at some of the most far northern extents of their ranges and must operate under environmental constraints unique from conspecifics living at lower latitudes. Even in the southern extents of the Fennoscandia, summers are considerably colder and wetter than the European mainland. Night length radically shifts throughout the summer at northern latitudes. The summer nights remain light such that this period more closely resembles an extended twilight rather than true night. The nights in our study area are approx. 5 h and 20 min long at the summer solstice in late June and will nearly double in length by the start of September (Steffen Thorsen, Time and Date AS 1995–2023). The shortest nights in the year correspond with a critical period of the bat maternity season when most adult females are in the third trimester of pregnancy or lactating in southern Norway (Dietz and Kiefer 2016, Eldegard et al. 2021). The short and light nights in late June – early July exacerbates already extreme energy demands on Fennoscandian bats. This is especially true for reproductive females and for species that are not adapted to fly in open or well-lit spaces, such as SRE bats. Bats at northern latitudes have a shorter reproductive and weaning period, are inclined to rely on more ephemeral and/or energy rich prey (Boyles et al. 2016), can require smaller, more connected foraging habitats (Frafjord 2013), and may continue to forage during weather conditions that would otherwise be inclement for conspecifics at lower latitudes (Rydell 1989, 1991). Monitoring bats in Fennoscandia cannot be directly mirrored from methods used in temperate Europe. However international monitoring standards can be adapted and implemented to learn which best practices are most effective in Fennoscandian regions.

Monitoring at height

Only 1.2% of all bat passes were collected from the two met tower detectors. However, the seasonal peaks in LRE bat activity observed at 45 and 95 m high reflected similar patterns recorded from the ground level detectors (Fig. 3). Temperature and wind speeds had a similar effect on bat activity, regardless of height (Fig. 4) with slightly less activity at taller heights when temperatures were below 10°C. At height monitoring is challenging and often records less bat activity than at ground level detectors. The recording environment on turbines and similar structures tends to be poorer than typical ground-level deployments and can be expensive to deploy and maintain suggesting it may not always be an effective monitoring tool (Voigt et al. 2021). Studies which have paired ground-level and at height bat acoustic monitoring frequently find that the patterns observed between the two types of detectors are similar, even if the volume of data collected is contrasting, but make it possible to detect some high-flying species more effectively (Collins and Jones 2009) and predict fatalities at wind turbines (Roemer et al. 2019, Barré et al. 2023). de Jong et al. (2021) found that the bat activity at nacelle height was more varied than from ground-level detectors, within and between years. The low number of bat passes recorded in our study may be because bats in the study area were less drawn to the meteorological tower than an active turbine or simply reflect truly low activity at the heights measured.

Although there was little data collected from the two met tower detectors, we found it informative to have some representation of bat activity above the forest canopy and within the turbine rotor sweep zone. Many open space foraging bats i.e. LRE bats which are more vulnerable to turbine collisions are highly associated with foraging above the forest canopy and may ascend to 300 m in height (O'Mara et al. 2019) or higher for scouting, migrating or foraging insects (Gillam et al. 2009). We recorded only 7 SRE bat passes from the met tower detectors collectively. However, the boreal forest canopy is lower relative to temperate forests (Vankat 2002) and may be an important foraging area for SRE bats when navigating in densely planted plantation forests and during the short, light summer nights. We recorded 12 bat feeding passes from the met tower, both heights combined, which did not provide enough information to draw conclusions about bat foraging behavior. Given the limited knowledge of bat ecology in Fennoscandian region, we still recommend implementing some form of at height bat monitoring at wind parks to describe bat activity more likely to reflect collision risks and to explore how this may be related to insect foraging.

Avoidance effects and fatal attractions

We found that SRE bats (86% *Myotis* spp.) are less likely to hunt prey at turbine pads than in nearby natural environments, suggesting that bats in this guild are impacted by loss of foraging habitat from wind park infrastructure. SRE bats, including *Myotis* species, are mostly considered 'narrow space' foragers which are associated with interior forests (Norberg and Rayner 1987, Denzinger and Schnitzler 2013, Frey-Ehrenbold et al. 2013, Froidevaux et al. 2016). Turbine pad habitat in this study was further from vegetation and tree lines than natural sites, so it is not surprising SRE bats were less likely to commute there. However, we were surprised by how little feeding activity was observed relative to commuting activity at turbine pads. Wind turbine development can have indirect negative impacts on bats by creating an avoidance effect. The exact drivers of this avoidance effect have been debated in different regions. There is some evidence to suggest that anthropogenic noise (Finch et al. 2020, Allen et al. 2021) or lights (Bennett and Hale 2014) can be disturbing for bats at wind parks. Habitat fragmentation and degradation could also explain avoidance effects (Lesiński 2007, Barré et al. 2018), especially if turbine development causes insect declines and subsequently reduces foraging habitat (Rydell et al. 2010b, Millon et al. 2015).

Gaultier et al. (2023) and Ellerbrok et al. (2022) both monitored bats at wind parks in European forested landscapes in the same period as this study and found similar avoidance effects; *Myotis* spp. activity was more likely to be recorded further from turbines. However, these studies did not evaluate feeding behavior, so it is not possible to compare commuting vs foraging habitat use. Furthermore, both studies were more focused on studying how bats responded with increasing distance from turbines whereas all sites in our study were within 200 m of the turbine base and instead sampled developed (turbine pads) vs undeveloped (natural) habitat. Therefore, the potential avoidance effects observed for SRE bats at the wind park in this study are not likely to be linked to sound or light disturbance but rather the removal of vegetation, the ground substrate, and perhaps also subsequent reduction in prey abundance.

Without pre- and post-construction data to compare, it is not possible to quantify the impact that Marker wind park may have had in displacing SRE bats, but our findings suggest that the park infrastructure creates less desirable foraging habitat for SRE bats than natural, undisturbed habitat. All the species included in the SRE guild in this study area are highly associated with forest habitat and include the *B. barbastellus* (found in our study) and *Myotis nattereri* (not found in our study) which are critically endangered species in Norway (Eldegard et al. 2021). While *B. barbastellus* and similar SRE are rarely found as fatalities at wind parks, the removal of forest and other landscape features such as wetlands and freshwater bodies can remove roost sites, reduce feeding opportunities, or fragment habitat connectivity (Apoznański et al. 2018).

The LRE bats were found to occupy the open habitat provided by the turbine pads more often than in the natural sites, regardless of the behavior recorded. This would be expected as the species in this guild are most associated with open foraging habitats (Schnitzler et al. 2003). While LRE bats may not be at high risk of losing foraging habitat from wind energy infrastructure (Roemer et al. 2019), the risk that the turbines themselves pose to these species is a critical concern. All the species within the LRE guild for our study area are considered medium-high risk for wind turbine mortality in Europe and are representative of carcasses found at wind parks in Norway and Sweden (Follestad et al. 2007, Rydell et al. 2017, Apoznański et al. 2018). There is some evidence that high flying bat species such as LRE bats are fatally attracted toward wind turbines though the reason for this attraction is debated and is species specific. Theories include that bats approach turbines out of sheer curiosity, due to migratory activity, because tall structures can be attractive social/breeding sites, or because turbines may be hotspots for insect prey (Cryan and Barclay 2009, Voigt et al. 2018, Richardson et al. 2021). However, Gaultier et al. (2023) found some evidence to suggest that *E. nilssonii* (LRE) avoid turbines in forests in Finland.

Eptesicus nilssonii, contributed to 70% of the bat passes recorded in all habitats and throughout the survey season. *Eptesicus nilssonii* has historically been one of the most common bat species in Fennoscandia (Rydell 1993, Tidenberg et al. 2019, Suominen et al. 2022) but recently sharp population declines have been observed *(*Rydell et al. 2018, Rydell et al. 2020, Eldegard et al. 2021) resulting in its national conservation status shifting from 'Least Concern' to 'Near Threatened' and 'Vulnerable' in Sweden and Norway, respectively (Eide et al. 2020, Eldegard et al. 2021). *Eptesicus nilssonii* is a species that has been reported as fatalities at wind parks in Norway and Sweden (Follestad et al. 2007, Rydell et al. 2017) and so wind parks – such as the one in this study – where their activity is high, should be aware of the potential risk to this species which is already experiencing population declines.

Monitoring insect–insectivorous bat relationships

We found a positive relationship between insect presence and bat feeding activity by deploying bat acoustic detectors paired with insect camera traps. Bats and flying nocturnal insects are both taxa that are difficult to monitor for population declines and are often of special conservation concern (Frick et al. 2020, van Klink et al. 2022). Høye et al. (2021) identified non-invasive camera trapping such as the method used in our study, in combination with automatic identification tools, as focally important methods for revolutionizing the utility of entomological research. Scholz and Voigt (2022) as well as Voigt (2021) have drawn attention to how the phenomena of feeding bats being killed at turbines in combination with insect fatalities at turbines can be creating a biodiversity sink. Certain prey species, such as soft-bodied nocturnal Diptera and Lepidoptera species, are also dependent on forest and densely vegetated areas (Pettersson et al. 1995) such that wind parks in forests likely exacerbate the risk to foraging bats. Several studies in Sweden have found evidence to suggest insects swarming at wind turbines could be linked to bat activity (Rydell et al. 2016, Jansson et al. 2020, de Jong et al. 2021). Specifically, Rydell et al. (2016) found evidence that LRE species may be eating diurnal flies resting on the turbines themselves. It is known certain bat species will hunt for insects near turbines (Horn et al. 2008, Valdez and Cryan 2013, Roeleke et al. 2016, Foo et al. 2017) and we observed LRE feeding at turbine pads. Feeding near turbines is likely to increases the risk of collisions which creates an opportunity to identify conditions for swarming insects and feeding bats, then mitigating the risks of fatalities. However, more research is needed to test the 'feeding-attraction hypothesis' (Kunz et al. 2007, Reimer et al. 2018) and determine whether insect abundance predicts bat collisions.

Equipment failures led to gaps in the dataset such that it was not possible to account for insect abundance in this study. However, to our knowledge no existing published studies have used this camera trapping method to document the relationship between flying nocturnal arthropod availability and bat acoustic activity. The original design of the camera trapping method used in our study was prone to power source failures which led to sparse data collection of data. More information regarding the camera trap design and equipment failures are described in Johns (2021). We recommend employing similar methods during periods when weather conditions are optimal (warm nights, no rain, low winds) to make the most of the battery life and because image quality during rain or fog is extremely poor. We agree with the original developers of the method that deploying the camera trap toward an open sky produces the best quality images for identifying insects (Ruczyński et al. 2020). Another drawback of this camera trapping method is that manual analysis of images is very time consuming. Choiński et al. (2023) has developed an automated tool for identifying insects from photos collected using this method which would radically increase the efficiency of using this method. Designing a camera trap with reliable power sources, solid weatherproof housing and automated processes for insect identification would lead to more complete datasets with more exciting potential for relating insect abundance to bat acoustic data. Future studies should consider applying a combined insect camera trapping and acoustic monitoring sampling design stratified at different heights at active wind parks to study these dynamics. This camera trapping method is not designed for identifying taxa but could also be combined with genetic non-invasive methods such as eDNA for account for the insect community assemblages (Valentin et al. 2020).

Management recommendations

Our findings provide evidence that wind parks in forest remove foraging habitat for short range echolocating bats. We therefore recommend that environmental impact assessments for wind farm development in forest should assess potential loss of foraging habitat for resident bat species. We document high levels of activity throughout the summer and autumn across the wind park for bat species that are most vulnerable to fatally colliding with turbines, highlighting the need for post-construction monitoring to evaluate how bats are directly impacted by wind turbines. By manually identifying all bat passes, we were able to identify differences between commuting and feeding habitat across guilds. This demonstrates the value of evaluating behavior as well as taxa from bat acoustic monitoring data. We observed peaks in flying nocturnal insect activity as well as bat feeding activity at approx. 1 and 7 h after sunset. If further evidence arises for the feeding-attraction hypothesis, camera traps could be used to better inform wind turbine curtailment and blade feathering strategies.

There was no mention of bats in the two environmental impact assessments we are aware of which evaluated the potential costs to biodiversity for building the wind park where this study was located (Fiskevold et al. 2012, Marker Vindpark et al. 2017). If pre-construction bat monitoring surveys had implemented, it is likely that the presence of the critically endangered *B. barbastellus* would have been observed much earlier and steps could have been taken to reduce habitat loss for this rare forest specialist. This is a species for which there is only one other known location of a few individuals in Norway. Carcass searches that took place in the same season found two *V. murinus* carcasses under turbines at this wind park (unpubl.) in late August, suggesting there are direct negative impacts on high flying bats at this wind park.

Ours is one of few studies that brings attention to the risks to bats at wind parks in the Fennoscandian region, and it can be used to draw insights on how to develop bat monitoring techniques in similar forested wind parks. Building wind parks in forests is common in the Fennoscandian region (Gaultier et al. 2020, 2023) and development is predicted to increase (Enevoldsen 2016, Enevoldsen and Permien 2018). The 'green-on-green' dilemma (Straka et al. 2020) posed by expanding wind energies at the cost of biodiversity requires interdisciplinary, open science and international collaborations. This study included resident as well as migratory bat species and was also located directly on the Norwegian–Swedish border such that even residential bat populations are expected to move across international borders. Fennoscandian countries have an important role to play in developing strong bat monitoring programs at wind farms as wind energy development expands rapidly and climate change is expected to cause European bat species ranges to shift northwards.

Conclusion

We found evidence of reduced activity and a particularly strong reduction in feeding behavior in short range echolocating bats near wind turbines. Long-range echolocating bats, which are at risk of fatally colliding with wind turbines, remained highly active throughout the wind farm. By combining insect camera trapping with bat acoustic monitoring, we observed a positive correlation between bat feeding activity and insect presence. Further exploring this method may give future studies more mechanistic access to the impact of wind energy infrastructure on bats and their feeding ecology. This in turn could facilitate better-informed mitigation strategies. Our findings suggest that wind energy developments in boreal forests may produce guild-specific habitat loss.

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Author contributions

Reed April McKay: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sarah Elizabeth Johns**: Investigation (supporting); Writing – review and editing (supporting). **Richard Bischof**: Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Fiona Mathews**: Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jeroen van der Kooij**: Investigation (supporting); Writing – review and editing (supporting). **Natalie Yoh**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Katrine**

Eldegard: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01168.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x0k6djhrp (McKay et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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Supporting Information for:

Wind energy development can lead to guild-specific habitat loss in boreal forest bats

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Supporting information

Table S1. Summary of the sites, localities and habitat sampled by acoustic detector sites as well as the total number of bat passes recorded there (n) and the number of active detector nights. Distance to the closest turbine base, nearest forest edge and water body are also reported. The meteorological tower (met tower) was inside a forested area between turbines 10 and 12. *N08 was moved to from location “a” to “b”. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Site	Locality	*Habitat*	n	Detector nights	Distance to turbine base (m)	Distance to forest edge (m)	Distance to water source (m)
P02	Turbine 2	Turbine pad	836	60	90	14	194
N02		Natural	790	59	98	4	184
P04	Turbine 4	Turbine pad	783	60	105	12	695
N04		Natural	600	44	84	8	660
P08	Turbine 8	Turbine pad	441	60	90	90	756
N08*		Natural[b]	506	40	100	16	835
		Natural[a]	92	20	78	40	830
P09	Turbine 9	Turbine pad	3686	60	46	15	360
N09		Natural	4287	48	76	5	260
P10	Turbine 10	Turbine pad	976	60	107	12	227
N10		Natural	1819	60	87	4	185
P11	Turbine 11	Turbine pad	1835	60	104	12	364
N11		Natural	368	60	112	5	245
P14	Turbine 14	Turbine pad	1459	60	87	20	186
N14		Natural	728	60	84	6	235
Met45	Meteorological tower	Met tower	197	70	NA	0	356
Met95		Met tower	35	70	NA	0	356

Table S2. Review of the datasets used and description of bat guilds and taxa along with their acronyms relevant to manual acoustic analysis. Weather data is proprietary data that cannot be shared so this is excluded from all datasets. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

ID	Description	DOI
Dataset 1	All bat passes recorded for all detector sites, behavior and taxa determined by manual identification, n = 19438	
Dataset 2	Total bat activity aggregated to night (sum number of bat passes per detector per night) for all ground level detectors (meteorological tower sites excluded), n = 811 detector nights, 19206 bat passes.	
Dataset 3	Short range echolocator feeding activity aggregated to night (sum number of bat passes per detector per night) for all ground level detectors (meteorological tower sites excluded), n = 811 detector nights, 339 bat passes.	
Dataset 4	Short range echolocator commuting activity aggregated to night (sum number of bat passes per detector per night) for all ground level detectors (meteorological tower sites excluded), n = 811 detector nights, 3776 bat passes.	
Dataset 5	Long range echolocator feeding activity aggregated to night (sum number of bat passes per detector per night) for all ground level detectors (meteorological tower sites excluded), n = 811 detector nights, 3703 bat passes.	
Dataset 6	Long range echolocator commuting activity aggregated to night (sum number of bat passes per detector per night) for all ground level detectors (meteorological tower sites excluded), n = 811 detector nights, 10584 bat passes.	
Dataset 7	Total bat activity and total number of insects detected at turbines 8 and 11 when both camera traps and bat detectors were active and when weather data were available, n = 2045 detector hours, 372 bat feeding passes, 4546 insects.	
Dataset 8	Total bat activity and total number of insects detected at turbines 8 and 11 when both camera traps and bat detectors were active, n = 2041 detector hours, 373 bat feeding passes, 4563 insects.	

Table S3. Overview of all bat taxa and guilds recorded. Scientific name with abbreviated conservation status according to the 2021 Norwegian National Red List in bold parentheses: CR = Critically Endangered, EN = Endangered, NT= Near Threatened, VU = Vulnerable, LC = Least Concern. Feeding = number of feeding passes where feeding buzzes were detected. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Taxa (Conservation Status)	Foraging guild	Sub-guild	Total number of bat passes	Feeding
	SRE			
Barbastella barbastellus (CR)		NA	10	0
Myotis brandtii (LC)		SR1	NA	NA
Myotis daubentonii (LC)		SR1	NA	NA
Myotis mystacinus (LC)		SR1	NA	NA
Myotis nattereri (CR)		SR1	NA	NA
Myotis species -		SR1	3558	327
Plecotus auritus (LC)		NA	554	0
Short Range Echolocators		**SRE total**	**4141**	**327**
	MRE			
Pipistrellus nathusii (NT)		MR1	9	0
Pipistrellus pygmaeus (LC)		MR1	64	3
Pipistrellus species		MR1	22	0
Medium Range Echolocators		**MRE total**	**95**	**3**
	LRE			
Eptesicus nilssonii (VU)		LR1	14,015	3,686
Vespertilio murinus (NT)		LR1, LR2	168	11
Nyctalus noctula (EN)		LR2	182	3
Long range group 1 -		LR1	132	2
Long range group 2 -		LR2	221	12
Long range echolocators		**LRE total**	**14,718**	**327**
	NoID			
Unidentified bat – guild		**NoID total**	**484**	**0**
Total bat passes			**19,438**	**4,045**

Table S4. The relationship between total bat activity (sum number of bat passes per night per site, bats total) and guild and behavior specific bat activity (sum number of bat passes per night per site) responding to temporal and environmental variables. Guild – behavior specific models include short range echolocator feeding activity, short range echolocator commuting activity, long range echolocator feeding activity, long range echolocator commuting activity. Temperature and wind speed were nightly mean values. 95% confidence intervals, both the upper (UCL) and lower (LCL)) are reported for parametric terms. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Model	**Variable**						
Bats total	*Parametric terms*	Estimate	SE	z	*P*	LCL	UCL
	Intercept	-0.389	0.435	-0.894	0.371	-1.24	0.46
	Habitat = Turbine pad	-0.0117	0.072	-0.162	0.871	-0.15	0.13
	Temperature	0.181	0.023	7.935	<0.001	0.14	0.23
	Smooth terms	Estimate	edf	X^2	P		
	Locality	5.87	6	261.5	<0.001		
	Julian night: Turbine pad	6.99	24	103.7	<0.001		
	Julian night: Natural	11.69	24	186.0	<0.001		
	Wind speed	3.76	9	81.4	<0.001		
Deviance explained: 58.9%							
SRE feeding	*Parametric terms*	Estimate	SE	z	*P*	LCL	UCL
	Intercept	-6.138	0.8201	-7.468	<0.001	-7.75	-4.53
	Habitat = Turbine pad	-1.176	0.263	-4.47	<0.001	-1.69	-0.66
	Temperature	0.274	0.043	6.42	<0.001	0.19	0.36
	Smooth terms	Estimate	edf	X^2	P		
	Locality	5.483	6	96.475	<0.001		
	Julian night: Natural	1.986	14	8.513	0.001		
	Julian night: Turbine pad	0.571	14	0.892	0.201		
	Wind speed	2.281	9	11.777	0.002		
Deviance explained: 53.8%							
SRE commute	*Parametric terms*	Estimate	SE	z	*P*	LCL	UCL
	Intercept	-1.162	0.449	-2.60	0.009	-2.04	-0.29
	Habitat = Turbine pad	-0.421	0.081	-5.34	<0.001	-0.59	-0.27
	Temperature	0.148	0.023	6.49	<0.001	0.10	0.19
	Smooth terms	Estimate	edf	X^2	P		
	Locality	5.86	6	300.8	<0.001		
	Julian night: Natural	7.01	14	31.1	0.002		
	Julian night: Turbine pad	4.64	14	65.1	<0.001		
	Wind speed	3.69	9	63.8	<0.001		
Deviance explained: 52.0%							
LRE feeding	*Parametric terms*	Estimate	SE	z	*P*	LCL	UCL
	Intercept	-5.403	0.734	-7.36	<0.001	-6.84	-3.96
	Habitat = Turbine pad	0.819	0.163	5.01	<0.001	0.50	1.14
	Temperature	0.304	0.029	10.60	<0.001	0.25	0.36
	Smooth terms	Estimate	edf	X^2	P		
	Locality	5.883	6	297.9	<0.001		
	Julian night: Natural	0.982	4	72.6	<0.001		
	Julian night: Turbine pad	1.813	4	37.0	<0.001		
	Wind speed	2.376	4	29.7	<0.001		
Deviance explained: 59.3%							
LRE commute	*Parametric terms*	Estimate	SE	z	*P*	LCL	UCL
	Intercept	-1.898	0.488	-3.89	<0.001	-2.86	-0.94
	Habitat = Turbine pad	0.415	0.082	5.07	<0.001	0.25	0.58
	Temperature	0.213	0.026	8.29	<0.001	0.16	0.26
	Smooth terms	Estimate	edf	X^2	P		
	Locality	5.87	6	257.6	<0.001		
	Julian night: Natural	7.79	29	217.6	<0.001		
	Julian night: Turbine pad	14.53	29	221.8	<0.001		
	Wind speed	3.42	14	47.6	<0.001		
Deviance explained: 62.4%							

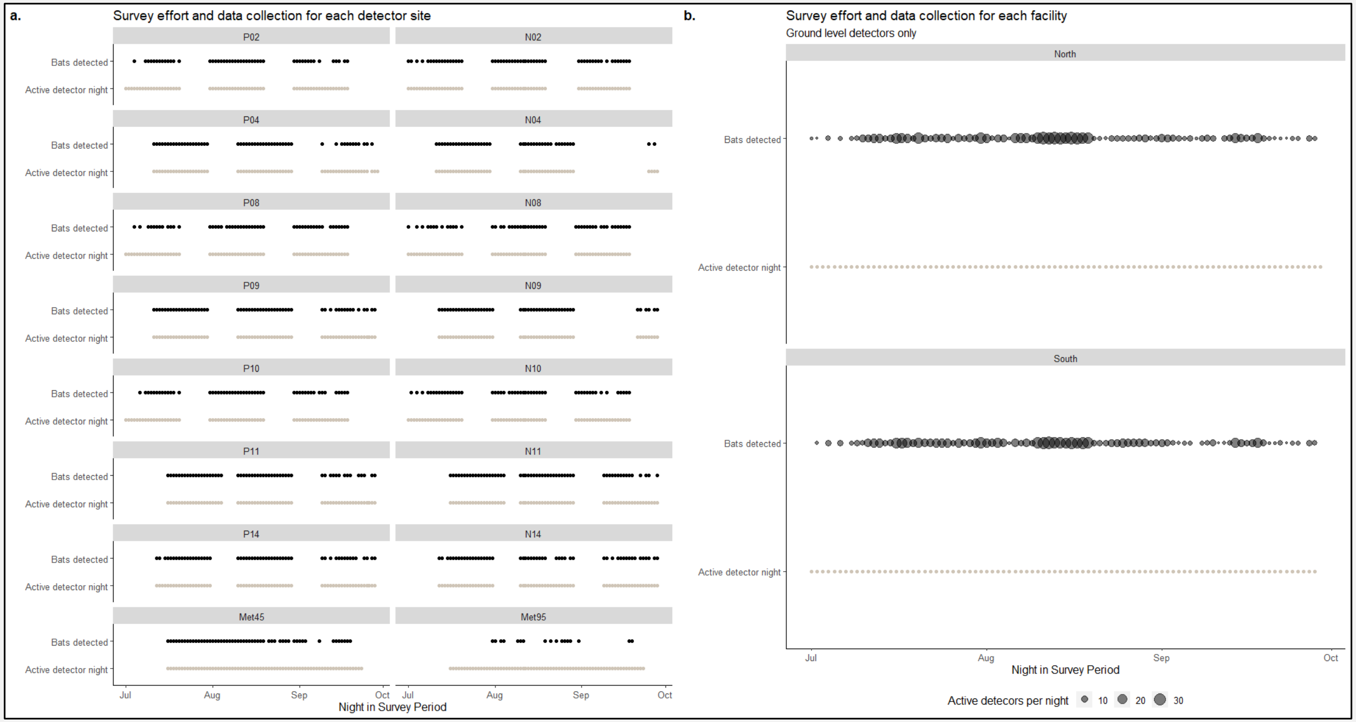


Figure S1. Overview of survey effort across all sites (a.) and between the ground level detectors at each facility (b). Sites P and N correspond to the turbine pad and natural detector sites, respectively for each turbine locality. The size of the dots in b. correspond to the number of active detector nights that occurred on a given night between the two facilities (north and south, see figure 1) at Marker Wind Park. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

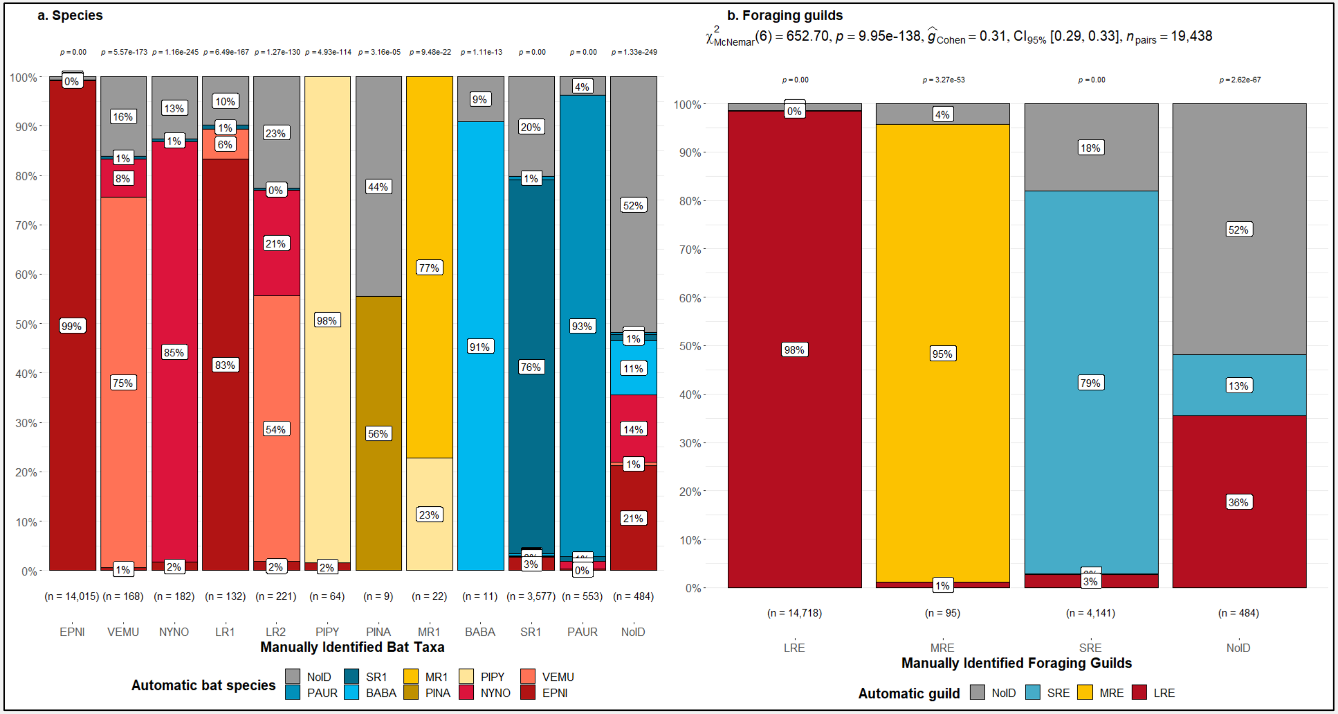


Figure S2. Proportion of agreement between the manual acoustic analysis and the automatic identification of bat passes to species, genus or sub-guild level (a.) and to foraging guild (b.). The proportion test p statistic is displayed on top of each bar comparing the acoustic analysis results to the manual analysis for both figures. Foraging guilds: Short range echolocators (SRE, light blue), medium range echolocators (MRE, yellow), long range echolocators (LRE, red) and unidentified bat (NoID, gray). EPNI = *Eptesicus nilssonii*, VEMU = *Vespertilio murinus*, NYNO = *Nyctalus noctula*, LRI = VEMU or EPNI, LR2 = VEMU or NYNO, PINA = *Pipistrellus nathusii,* PIPY = *P. pygmaeus*, MR1 = *Pipistrellus* spp., BABA = *Barbastella barbatstellus,* SR1 = *Myotis spp.,* PAUR = *Plecotus auritus.*. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

Figure S3. Overview of which nights throughout the season when both insect camera traps and bat acoustic detectors were active and hours when bats and insects were detected for each site (N08 = turbine 8, natural site; P08 = turbine 8, turbine pad site; N11 = turbine 11, natural site; P11 = turbine 11, turbine pad site). Hours when insect camera traps and bat acoustic detectors = black, hours when insects were detected at a site = orange, hours when bat feeding passes were detected at a site = grey. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.

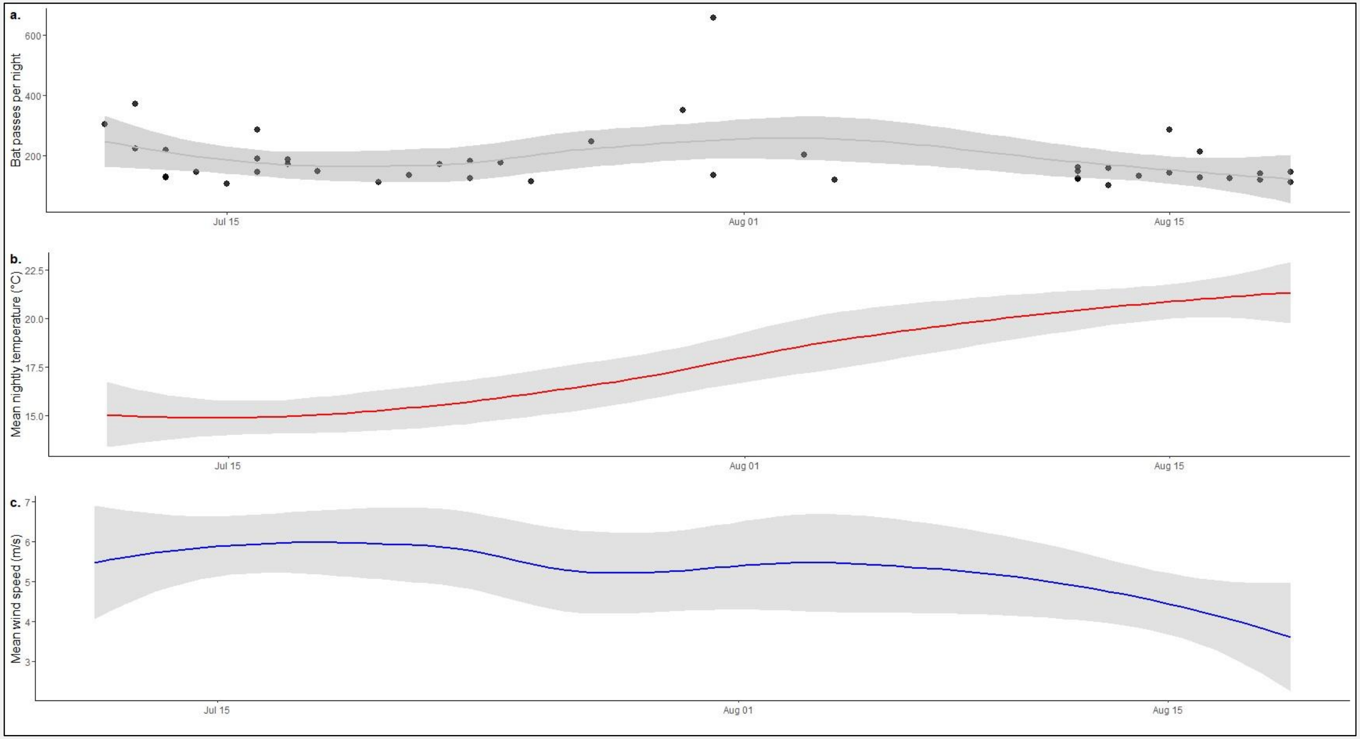
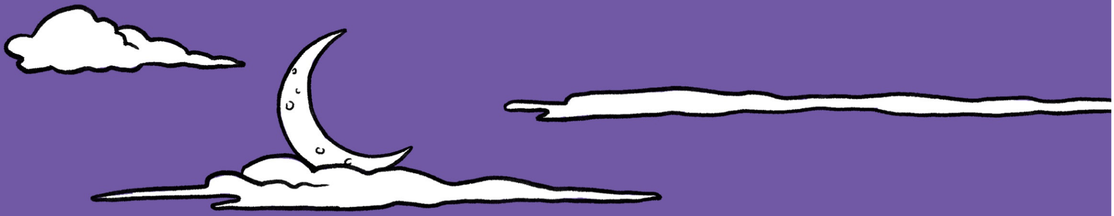
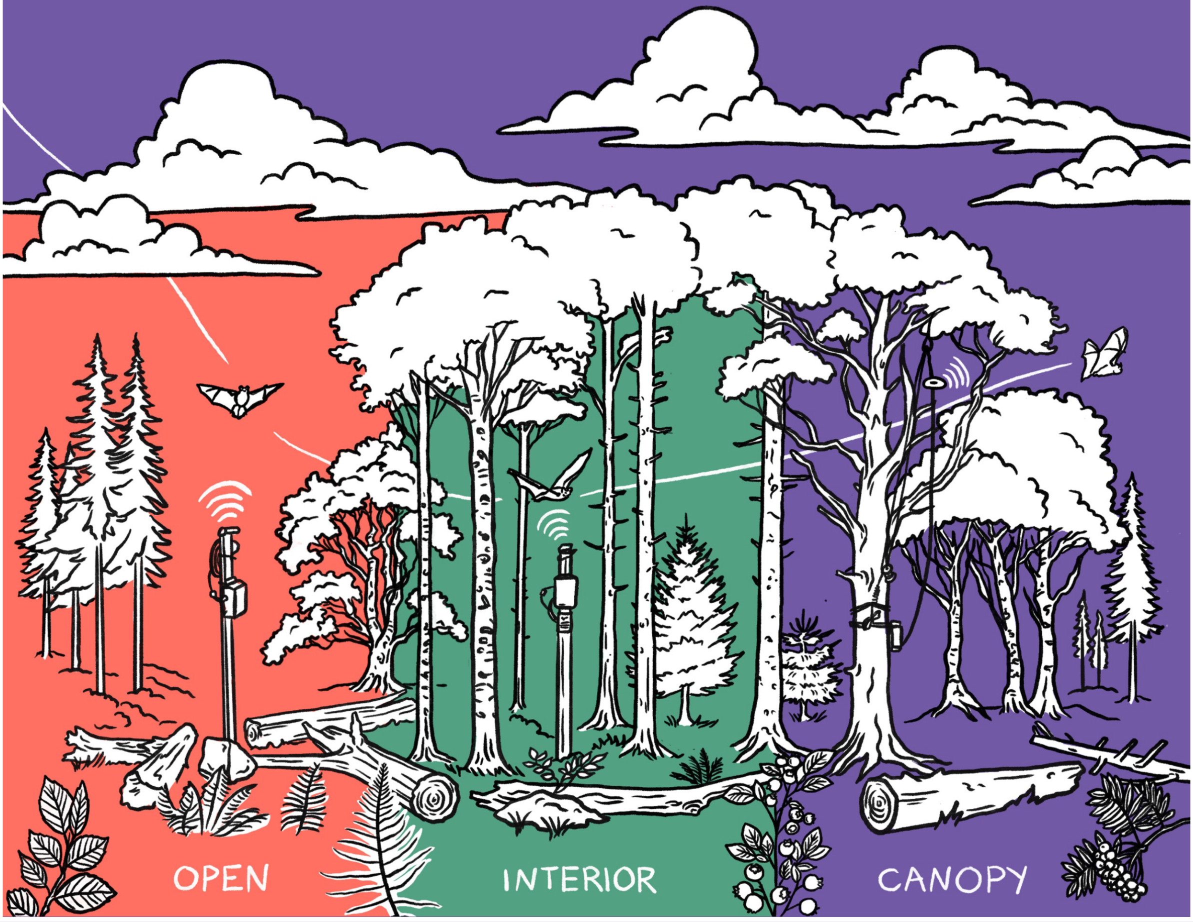


Figure S4. Detector nights (n = 43) when more than 100 bat passes were detected. (a.) Bat activity across season with black dots representing detector nights, gray line shows fitted predictions from a loess GAM. Mean nightly temperature (b., red line) and wind speed (**c.**, blue line) during the period of high activity bat detector nights fitted with a loess GAM. Gray shaded areas around the fitted lines represent the 95% confidence intervals. The data was collected at Marker wind park in southeast Norway in the summer and autumn 2020.



Paper II

Differences in sub-habitat use throughout the summer for forest specialist bats in mixed boreal forest



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Cover page

Illustration: Olina Søyland Bru

Abstract

1. Forests with high stand density are valuable for forestry but lead to structural homogeneity and dark, dense habitats that have potentially negative consequences for wildlife. All bat species in northern Europe utilize forests and short-range echolocating (SRE; *Myotis* spp., *Plecotus auritus*, *Barbastella barbastellus*) bats are highly reliant on forest habitats. There is limited information on what types of sub-habitats within forest are important for SRE bats and how this may vary in relation to forest density.

2. This research aims to provide insights into how SRE bat activity varies in relation to sub-habitat types (open, interior and canopy) and forest density within mixed boreal forest at different periods in the summer. We compare habitat use between *Myotis* spp. and *P. auritus* as well as between *Myotis* spp. commuting and feeding activity.

3. We simultaneously monitored 12 sites with three acoustic detectors sampling the forest interior, an open forest gap and the canopy. The study was carried out in Southeastern Norway throughout the summer over two years (2021-2022). Complementary mist net surveys were carried out in 2021. Forest characteristics were measured at all acoustic detector sites to quantify forest density (e.g., number of stems and basal area).

4. We collected 416,936 bat passes across 8,149 detector nights, of which a subset of 106,519 bat passes were manually identified. *P. auritus* exhibited a stronger association than *Myotis* with open sub-habitats, and *P. auritus* activity was negatively influenced by forest density regardless of sub-habitat type. *Myotis* spp. were less active in highly open habitats during the early period of the summer but otherwise activity increased at all sub-habitat types as forest density decreased. In interior sub-habitats, *Myotis* activity dropped sharply in a non-linear fashion at high forest densities. Habitat density had a more pronounced effect on *Myotis* feeding than commuting activity in all sub-habitats mid-season and for canopy sub-habitats late season.

5. *Implications for Management.* Mixed forests are assumed to be more valuable habitats for bats than forests where deciduous trees are scarce. We found that if mixed forests are too dense, SRE bat activity is reduced, and that *Myotis* require habitats of different density for foraging throughout the summer. Our findings provide further evidence for negative influence of high stand density on forest biodiversity, and the need for varying density, including gaps, in boreal forests to support wildlife.

Introduction

Identifying forestry practices compatible with thriving bat communities have repeatedly been stated as high priority research and conservation objectives (Lacki et al. 2007; Russo et al. 2016; Felton et al. 2020; Frick et al. 2020; Browning et al. 2021). Forests managed for production purposes tend to be homogenous in structure compared to forests subject to natural disturbance dynamics, which exhibit considerable variability in structure on small and large spatial scales (Angelstam 1998; Kuuluvainen 2009; Felton et al. 2020). Forests with homogenous structure provide fewer habitat features for wildlife to use (Savilaakso et al. 2021; Hekkala et al. 2023). Production forests are frequently optimized for tree growth to generate similar aged, uniform stands with few twigs and small branches by increasing forest density (Sterck et al. 2021; Thiffault et al. 2023). Standing volume at maturity in Fennoscandian production forest has increased substantially during the last decades (e.g., 30% since the 1980s in Sweden; Felton *et al.*, 2020). As the volume of timber and the extent of canopy cover increase, the amount of light reaching the forest floor diminishes (Korhonen et al. 2020) resulting in reduced cover and diversity of understory vegetation with potential trophic cascading effects (Hedwall et al. 2013).

Production forests in Fennoscandia are some of the most intensively managed forests in the world and are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Siitonen 2013; Huuskonen et al. 2021). Allowing a mixture of coniferous and broadleaved trees can support higher biodiversity (Regnery et al. 2013; Paillet et al. 2018; Hedwall et al. 2019; Felton et al. 2021; Kebrle et al. 2021). However, the biodiversity benefits of mixed forests can be masked by high stand density, as is well documented for vascular plants (Hedwall et al. 2019). High stand density can have negative effects on mammals that browse on the understory vegetation (Felton et al. 2020) and forest birds (Felton et al. 2021). Densely planted forest of similar age lack structural features valuable to wildlife e.g. uneven growth patterns, cavities, trunk rots etc. (Schall and Ammer 2013) which translates to less available habitat for arthropods as well as birds and bats (Adams et al. 2009; Basile et al. 2020; Dufour-Pelletier et al. 2020).

Many bat species rely on tree characteristics that are undesirable for forestry such as exfoliating bark and tree hollows for roost sites (Robles et al. 2011; Cockle et al. 2012; Tillon and Aulagnier 2014; Tillon et al. 2016; Kebrle et al. 2021). Additionally, forests are important foraging habitat for bats internationally (Law et al. 2016) and for nearly all European bat species (Russo et al. 2016). Furthermore, echolocating bats can be excluded from highly dense forests because of the difficulty to navigate physical obstacles compounded by an acoustic environment that produces many echoes (Brigham et al. 1997; Jones and Holderied 2007; Schmieder et al. 2012; Jacobs and Bastian 2016). However, there is limited information on how variation in forest density in the boreal forest impacts bats which are otherwise well adapted to flying near vegetation, such as SRE bats.

Knowledge and research on the relationship between bat community dynamics and forestry practices in production forests are biased toward North American or temperate forest systems (Jung et al. 1999; Kalcounis et al. 1999; Titchenell et al. 2011; Bouvet et al. 2016; Froidevaux et al. 2016, 2021, 2022; Carr et al. 2020; Tena et al. 2020). Bats are often overlooked as an important element of boreal forest fauna (Thompson 2006) and very few studies have addressed how boreal bats respond to forest characteristics in Europe (Wermundsen and Siivonen 2008; Vasko et al. 2020). Most studies and policies regarding biodiversity of European boreal forests focus on taxa such as lichens, mosses, arthropods, and birds (Kayes and Mallik 2020; Korhonen et al. 2020; Oettel and Lapin 2021; Savilaakso et al. 2021; Hekkala et al. 2023).

In recent years, several European studies have demonstrated diverse responses in the bat communities to forest structure and composition, using a range of metrics defining habitat characteristics (Müller et al. 2013; Charbonnier et al. 2016; Froidevaux et al. 2016, 2021, 2022; Kirkpatrick et al. 2017; Langridge et al. 2019; Węgiel et al. 2019; Carr et al. 2020; Tena et al. 2020; Vasko et al. 2020; Erasmy et al. 2021a; b; Suominen et al. 2023). These studies largely agree that forests with a heterogeneous structure, which encompasses a variation in sub-habitats, including the presence of gaps, support higher bat diversity and activity. However, these studies focus predominantly on temperate forests and most often rely on acoustic monitoring data that does not differentiate between bat behaviors. Therefore, it is unclear what aspects of forest structure and composition are important for bat foraging or social activity. Furthermore, the findings of studies in temperate forests are not likely to translate directly to boreal systems. Bats living at far northern latitudes are subject to more adverse weather conditions throughout the year compared to bats living in temperate regions. Additionally, bats living in far northern latitudes live through periods of extremely long photoperiods and thus shortened or "white" nights in the summer (Speakman et al. 2000), when energy demands related to reproduction are highest.

All European bat species use echolocation for navigation and hunting prey (Dietz and Kiefer 2016). Passive acoustic monitoring is an increasingly popular and effective tool for monitoring bats across broad temporal and spatial scales non-invasively (Penar et al. 2020). Echolocation calls provide the most reliable characteristics for bat species identification from acoustic recordings and so most automatic classification software are trained to identify and classify these call types (Vaughan et al. 1997; Jones et al. 2000; Rydell et al. 2017). It is also possible to identify social as well as feeding activity for some bat species from acoustic recordings (Griffin 1958; Simmons et al. 1979; Moss and Surlykke 2001). However, many studies omit this from their analyses because most automatic identification tools are unequipped to identify non-commuting bat calls. Instead, overall bat activity is often used as a proxy for foraging activity although it is not clear that there is always a high correlation between total bat activity and feeding activity (Schnitzler and Kalko 2001; Jung et al. 2012). Furthermore, there is a limited understanding of how bat feeding activity changes in relation to forest density.

In Fennoscandian forests, the bat community consists of several insectivorous echolocating species that can be separated into foraging guilds related to similarities in echolocation (i.e., sonotype), foraging habitat use and morphology (Denzinger and Schnitzler 2013). One approach to defining foraging guilds separates the bat community into short (SRE), medium (MRE) and long range (LRE) echolocators (Frey-Ehrenbold et al. 2013; Froidevaux et al. 2016; McKay et al. 2024). *Myotis* and *Plecotus* species as well as *Barbastella barbastellus* in Fennoscandia are all forest specialists which can be grouped in the SRE guild (Wermundsen and Siivonen 2008; Frey-Ehrenbold et al. 2013). SRE bats have low intensity, predominantly frequency modulated type echolocation which makes them well adapted to navigating the interior of forests, allowing them to fly through dense clutter and glean prey from vegetation. SRE bats are all considered highly intolerant to light, emerge later into the evening than other bats, and avoid flying in open spaces (Jones and Rydell 1997; Stone et al. 2015; Spoelstra et al. 2017; Apoznański et al. 2021). Studies from boreal regions in North America have found that *Myotis* species associated with forests have more energy rich diets than conspecifics at southern latitudes, most likely to compensate for the intensely ephemeral and harsh conditions experienced by bats living in cold, dark, and wet biomes (Boyles et al. 2016; Shively and Barboza 2017; Kaupas and Barclay 2018). SRE bats at northern latitudes may be even more sensitive to differences in forest vegetation and density during white nights in the summer due to their aversion to light and the subsequent energy costs associated with adapting to those challenges (Kotila et al. 2023; Slough et al. 2023).

Froidevaux *et al.*, (2014) found that the most effective means to capture acoustic activity across the bat community at forest sites in a temperate European forest was to sample forest gaps, the interior forest, and the canopy simultaneously. Froidevaux *et al.*, (2016) used the same study design and found that SRE bat activity was similarly high at all 3 sub-habitats sampled, but best sampled at interior and canopy detectors. We apply a similar approach to sampling forest sites in our study. Froidevaux *et al.*, (2014)'s bat community included nearly all the same species found in Fennoscandia, though we were curious on how well this sampling method applied SRE bats in boreal forests.

The relationships between bat activity in boreal forest habitats and the modifying influence of habitat density needs to be better understood to inform forestry management decisions. In this study, we investigate how the bat community and SRE bat activity varied between forest sub-habitats of differing densities, using a combination of acoustic monitoring and mist-net surveys. To enable assessment of the influence of forest density and avoid confounding effects of tree species composition and age, all study sites were in mature mixed boreal production forests of similar heights and site productivity, across a gradient of forest densities.

First, we describe bat community composition using the number of times sonotypes were recorded across detector locations, years, and sub-habitats. Second, we focus on forest specialist bats by quantifying bat activity for four groups: (i) total activity for *Myotis* species (*Myotis brandtii, Myotis mystacinus, Myotis daubentonii*) (ii) total activity for *Plecotus auritus,* Brown long-eared bats, specifically, (iii) *Myotis* commuting (iv) *Myotis* and feeding activity. Overall, we test the following predictions:

1. We expect that total SRE bat activity will be highest in open sub-habitats, but that *Myotis* activity may be higher in open sub-habitats relative to the interior and canopy; more so than for *P. auritus*. *Myotis* are more reliant on echolocation and therefore we expect them to be more sensitive to cluttered vegetation than *P. auritus*.
   While SRE bats are well adapted to flying in the interior forest, open sub-habitats within the forest (i.e., forest gaps) are likely to be where bats benefit the most from foraging near vegetation without struggling to navigate highly cluttered forest. Highly dense forests likely exclude any kind of bat foraging activity.
2. We expect to find a non-linear relationship between total SRE bat activity and forest density, with a steep decline in activity when the habitat gets very dense.
3. *Myotis* feeding activity will be higher at canopy and interior sub-habitats in the early and mid-periods of the summer, and this relationship will be stronger than what is seen in commuting activity. The early and mid-period of the summer are when day length is longest and when adult females are under the highest energy constraints (i.e. pregnancy and lactation) and so we expect that open sub-habitats may be too exposed and risky for feeding activities during these periods.

The results of this study are intended to inform forest management by describing how forests of varying density and different sub-habitats are utilized by SRE bats. Furthermore, our study can be used to inform future bat studies and monitoring efforts.

Methods

Study system

The study took place in Nordre Follo, Ås, Vestby and Frogn municipalities in the south-eastern part of Norway in Akershus county (approximately mean latitude and longitude: 59.71, 10.72). Daylength varies dramatically throughout the summer (12.5 – 18.8 hours, SD = 1.7 hours). Data collection occurred at eleven different localities in the summers of 2021 (May 14th – September 14th) and 2022 (May 5th – September 21st). An additional twelfth site was included in 2021 but dropped in 2022 because we did not get a permit from the landowners to deploy monitoring equipment (Figure 1).

We used SR16 (Astrup et al. 2019) and AR5 (Ahlstrøm et al. 2019) maps to identify areas of mature mixed forests within the study area with a stand age of minimum 50 years, mean canopy heights greater than five meters, and site index greater than seven were included. Productivity (site index) was defined as the dominant height in meters at 40 years of age (Eid 2001). Sites were all located within an area of 40 km^2, at least 50 meters from water bodies, and 50 meters from the forest edge to control for edge effects. We selected sites located at least one km apart (between 1 and 17 km) to avoid spatial autocorrelation. Sites were selected within a forest density gradient calculated from basal area and crown cover, with both metrics calculated based on Eid (2001). There were few forests in the area that met this criteria and which were also accessible for regular maintenance and field work. Once sites had been scouted digitally, we visited the sites to physically assess which locations matched our search criteria and could be sampled with the methods we intended to use.

All the final selected sites were in mixed forests of development class five (logging mature forest), with similar mean stand age, height, and productivity. Dominant canopy species included Norway Spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch species (*Betula pubescencs* and *B. pendula*) and variable amounts of boreal broadleaved trees; rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), and goat willow (*Salix caprea*). At some sites, there were also scattered trees of common oak (*Quercus robur*) and hazel (*Corylus avellana*).

Bat acoustic monitoring

Bats were monitored using Song Meter SM4BAT-FS stationary bat acoustic detectors (hereafter, detectors) fitted externally with SMM-U2 cardioid ultrasonic microphones and SMM-U1 omnidirectional ultrasonic microphones (Wildlife Acoustics Inc., Maynard, MA, USA).

Froidevaux *et al* (2014) found that it is important to sample bat communities in multiple sub-habitats of the forest simultaneously to account for how different bat foraging guilds utilize the forest to suit their functional abilities. Therefore, at each site, three detectors were used to record within three different sub-habitats: forest gaps (”open”), forest interior (”interior”) and forest canopy (”canopy”). Open sub-habitats represented gaps within the forest interior or where no obvious gaps were present, the most open area available (Figure 2). Interior and canopy sub-habitats were areas within the closed forest (that is, not a gap). Detectors were deployed continuously throughout the survey season and maintenance checks were performed approximately once a month to collect data and evaluate microphones for loss of sensitivity.

Detectors at open and interior sub-habitats were deployed at ground level by securing them to 1.5 m tall wooden poles at least 2 m away from vegetation clutter. To optimize each microphone recording abilities SMM-U2 microphones were deployed at the top of the wooden poles and pointing upward; SMM-U1 microphones were positioned at an approximate 45-degree vertical angle, oriented away from clutter. Canopy detectors were deployed in tall, mature trees where it was feasible to install a pulley system, sample the canopy environment within the site and limit the amount of clutter around the microphone. Detectors were attached to trees at breast height and microphones were deployed into the canopy via a rope pulley system. Extension cables (3 m or 50 m length) were used to deploy microphones in the canopy (between 4 and 8 m high). Only SMM-U2 microphones were used for canopy detectors and were facing up and positioned to avoid being in close contact with cluttered vegetation (Figure 2). Detectors between sub-habitats were at least 20 m apart from each other to reduce duplicate recordings within each site. The mean number of recording nights per detector location (detector nights) was 118 nights, SD = 19.4 nights. An overview of survey effort across all detector locations is provided in supplementary materials, Figure S1.

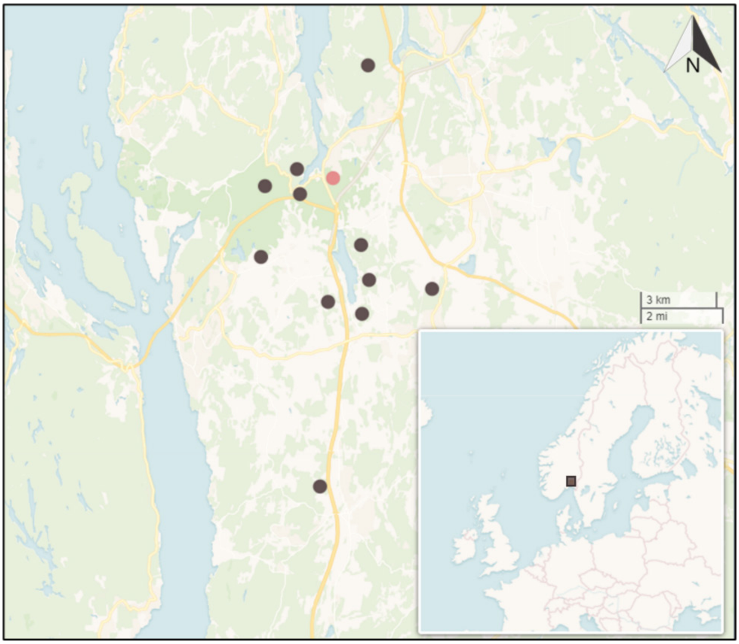

Figure 1. Map of study area located in Viken county, Norway. Inset map shows study area in relation to northern Europe. Dots represent site locations in 2021 and 2022. The light pink dot represents site 12 which was only surveyed in 2021. Light green areas are forest; blue areas are water bodies. Map layers: Leaflet, © OpenStreetMap contributors, © CARTO

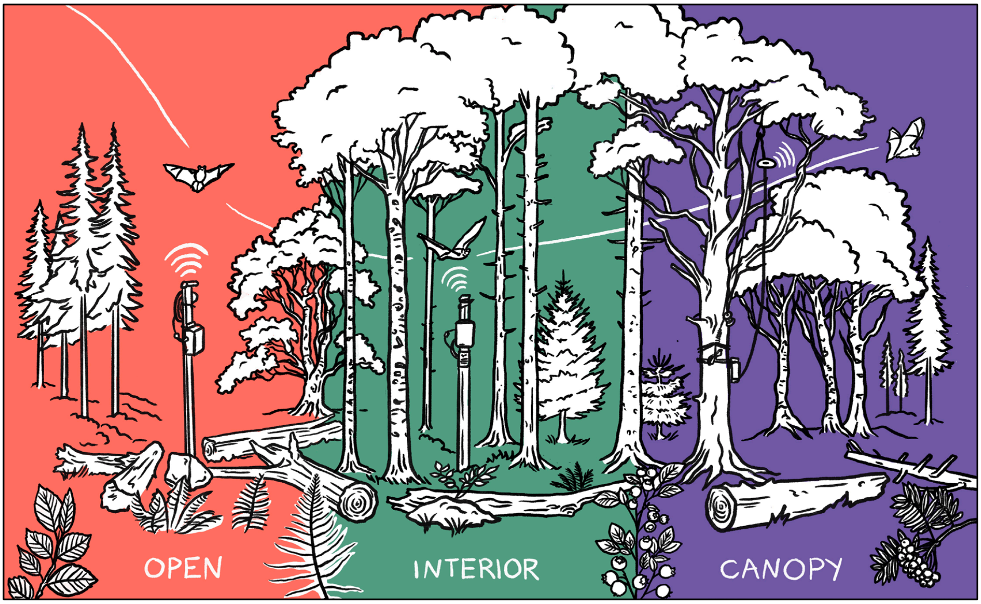

Figure 2. Illustration depicting how different sub-habitats were sampled with bat acoustic detectors within each site. Illustration: Olina Søyland Bru.

Acoustic Analysis

Acoustic data was stored as .wav files and subsequently processed using Kaleidoscope Pro 5.6.3 with Bats of Europe Classifier 5.2.1 (Wildlife Acoustics Inc., Maynard, MA, USA). In this study, a bat pass was characterized as a 5-second triggered recording which included at least two consecutive pulses (Fenton et al. 1973). Therefore,.wav files were standardized to 5-second recordings and filtered for noise using the following parameters: 8 – 120 kHz frequency range; 2 – 500 ms max length of detected pulses; 500 ms maximum inter-syllable gap, 2 pulses minimum.

Each 5-second file was then processed using the automatic identification function Bats of Europe Classifier v.5.2.1 Kaleidoscope Pro, Wildlife Acoustics to identify bat passes to species and filter additional noise files. The classifier settings were adjusted to only consider species found in Norway and Sweden (Table S1). We sampled 8,149 detector nights (3,802 and 4,347 in 2021 and 2022 respectively) generating 978,571 5-second recordings. Recordings identified as noise during automatic processing (n=271,747 in 2021, n=299,853 in 2022) were removed from further analysis.

We used the following sonotype-defined foraging guilds in our automatic and manual acoustic analyses. short range echolocators (SRE: *Myotis species, Plecotus* spp., *Barbastella barbastellus*), medium range echolocators (MRE; *Pipistrellus* spp.), and long range echolocators (LRE, *Nyctalus* spp., *Vespertilio murinus,* and *Eptesicus* spp.).

All files that were classified as an SRE species (n = 84,666 passes), including *Myotis* species, *Plecotus* species or *Barbastella barbastellus,* were manually vetted by one analyst (RAM). A subset of the remaining files was included in manual acoustic analysis to account for the inaccuracy of the automatic classifier and to be able to describe the bat community present at sites. One randomly selected recording per night per detector (n = 69 across both years) per species detected by the classifier (Table S1.) included in the manual acoustic analysis (MRE = 5,944 recordings, LRE = 10,464). For the recordings classified as unknown bat species (NoID), 2500 randomly selected per sub-habitat across both years (7,500 total NoID recordings) were included in the manual acoustic analysis. Only passes from complete detector nights were included in manual acoustic analysis. In total, 106,519 recordings were manually identified.

Bat passes were manually identified to the lowest taxonomic rank or functional group (hereafter, sonotype) for which a confident identification could be made. Any file that did not include bat acoustic activity that met the criteria for a bat pass was treated as noise and removed (n = 2,464). Only bat species included in the Norwegian National Red List for Species (Eldegard et al. 2021) were considered during the manual acoustic analysis. *Myotis* species were grouped into one sonotype due to their similar echolocation call types. The common pipistrelle, *Pipistrellus pipistrellus*, is not currently recorded in Norway so any bat pass which diagnostically met the conditions for *P. pipistrellus* more so than *P. nathusii* or *P. pygmaeus* was categorized as *Pipistrellus* spp. To account for overlap in similar echolocation of LRE bats, especially in clutter, two further sonotypes were included in manual acoustic analysis for when it was not obvious if a pass belonged to *E. nilssonii* or *V. murinus* (LR1) or passes that could belong to either *V. murinus* or *N. noctula* (LR2).

Bats produce a distinct series of calls when they have detected their prey, during the approach, and when they intercept their prey, known collectively as a feeding buzz. Similarly, bats produce different calls specifically for communication (e.g., mating, or territorial calls) known as social calls. Behavior was also assigned for each bat pass (commuting, social and feeding passes) following Middleton, Froud and French, (2014), Middleton, (2020), and Russ, (2021). Bat passes that included both feeding and social activity were categorized as feeding activity. Comparisons between the results of the manual and acoustic analysis are provided in the Supplementary Materials (Table S1, Figure S2).

Bat captures

Mist net surveys were carried out over 3 nights (2 consecutive nights between June 1st and August 5th, and a third night between August 10th and September 13th) at all 12 sites (36 total nights of surveying) in the summer of 2021. The purpose of the survey was to record species that would be difficult to identify from acoustic monitoring alone (e.g., species with overlapping calls) and provides detailed information about individual bats that can only be observed in hand. AVINET TB mist nets with varying widths (4, 6, 9, 12 m) were deployed as single high (~2.6 m) or double high (~5.2 m high) nets set in flyways or over water and checked at least once every 15 minutes. A minimum of two mist net locations, located at least 30 m apart, were used per survey night. The combined net effort represented a minimum of 10 net hours and up to 22.5 net hours where there was minimal activity. Surveys were not conducted during the threat of lightning, persistent rain, or high winds (>10 km/s) and began one hour before sunset, continuing for five hours or until sunrise. An Apodemus bat acoustic lure (Apodemus Field Equipment, Mheer, Netherlands) was deployed on trees or on a short metal pole (between 1 – 1.5 m high) near mist net sites, playing the manufacturer's default call library. We recorded time of capture, species, age (juvenile/adult), sex (M/F), reproductive status (F: non-reproductive, pregnant, lactating, postlactating. M: 0 (testes not visible), 1 (testes visible), 2 (testes swollen)), right forearm length (mm), weight (g), pathologies or unique identifying features, and the presence of parasites for all captured bats (Y/N). Bat species were identified following Dietz and Kiefer (2016). All mist net surveys were carried out with permits provided by the Norwegian Environment Agency and following IUCN guidelines for reducing the risk of disease transmission from bat workers to bats.

We captured two lactating bats (*M. brandtii* and *M. mystacinus*) and one pregnant female *(M. Mystacinus)* between June 11th and 17th, at which point we paused mist netting for approximately 2 weeks to avoid capturing females during the peak of the maternity season.

Forest density

To quantify forest density, we sampled different forest attributes within a 100 m^2 radius (plot) of each detector. We measured the diameter at breast height (DBH, that is 1.35 m above the tree's base) of all trees with a DBH greater than 5 cm as well as the number of all (i) living and (ii) dead trees >5 cm), (iii) snags (tree > 5 cm DBH with top broken off), (iv) the number of bushes >1m, and (v) small dead and living trees (DBH<5 cm), (vi) the relascope sum, (vii) ground vegetation cover, and (viii) vegetation type. The relascope sum (proxy for stand level basal area) was sampled from the center of each 100 m^2 plot, using a chain relascope (Bitterlich 1952). Main vegetation type within each 100m^2 plot was determined using the categories in the Norwegian National Forest Inventory guidelines (Viken 2021). Basal area was calculated by measuring the diameter at breast height of all tree species with a DBH of > 5 cm (living and dead) to establish the area of each 100m^2 plot occupied by stems. These metrics were sampled separately for each detector location for each year.

The forest attribute metrics were highly correlated. To create a single measure of forest density for each detector location (hereafter, habitat openness), we used the first principal component (PC1) of a principal component analysis (PCA), calculated with the "vegan" R package (Oksanen et al. 2007), combining the forest metrics (FigureS3). All metrics were standardized and scaled to be centered at zero before calculating the PCA. The proportion of variance that PC1 explained was 40%. We explored the relationship between PC1 and the individual forest attributes using simple linear regressions to evaluate how PC1 described forest density.

Abiotic variables

Weather data included daily precipitation (mm) and temperature (°C) data for each site throughout the acoustic monitoring period that was extracted from the public database SeNorge.no. To account for seasonal effects in the statistical models, we separated the survey season into three periods: early (May 4th – June 19th), mid-season (June 20th – August 5th) and late (August 6th – September 20th). We also interpreted our data in relation to photoperiod. Photoperiod was calculated using the R package "suncalc" (Thieurmel and Elmarhraoui 2022) for a single location, approximately in the center of the study area (59°45'29.2"N, 10°45'36.0"E). The shortest day of the season is Sep 20th (12.5 hours of day length), and the longest day is June 21st (18.8 hours) with a standard deviation of 1.7 hours throughout the study period.

Statistical analyses

We investigated differences in bat community composition between site locations using Non-metric Multi-dimensional Scaling (NMDS) ordination (Clarke 1993) calculated using Bray-Curtis dissimilarities. We used the R package "vegan" with the function 'metaMDS' to generate the NMDS (Oksanen et al. 2007). We then used the function 'envfit' to fit linear trend surfaces (vector fitting) for site, year, and habitat type, for each detector location. The bat community for each detector location was defined by adding the total number of bat passes detected for each sonotype per detector location within each year.

To assess how *Myotis* and *P. auritus* responded to forest density and between sub-habitats, we made 4 data subsets for further analysis: (i) all *Myotis* species passes, regardless of behavior (74,633 bat passes, 33% zero observations); (ii) all *P. auritus* passes, regardless of behavior (2,340 bat passes, 85.7% zero observations); and to further investigate *Myotis* habitat use in response to forest density, (iii) *Myotis* commuting activity (61,006 bat passes, 34.5% zero observations); (iv) *Myotis* feeding activity (13,775 bat passes, 65.2% zero observations). Each of the four data subsets were aggregated to the sum of bat passes per detector per night.

We fitted a series of generalized linear mixed effect models (GLMMs) using the R package "glmmTMB" package (Brooks *et al.*, 2023). For each of the four response variables, that is: (i) total *Myotis* activity, (ii) total *P. auritus* activity, (iii) *Myotis* commuting activity, and (iv) *Myotis* feeding activity, six candidate models were fit with a Poisson, generalized Poisson, and a negative binominal distribution, as both a zero-inflated and non-zero-inflated model to handle overdispersion) (Table S3). For each of the models we included habitat openness, sub-habitat type, and period in season (early, mid-season and late) as fixed effects, as well as all possible interactions between these three terms as fixed effect terms, along with main effects temperature, precipitation, and year. Site location and Julian night were specified as random intercepts (Table S4, Table S5). The continuous variables habitat openness, temperature and precipitation were scaled to be centered at zero using the function "scale" in R.

For each of the four response variables, we selected the model with the smallest Akaike Information Criterion (AIC) value (Table S3). We then conducted model validation using the R package "DHARMa" (Hartig and Lohse 2022) as well as using diagnostic plots to ensure that the models provided an adequate fit to the data. Model predictions were based on the full model for each response variable, to so that the explanatory terms were the same when comparing *Myotis vs. P. auritus* activity *Myotis* feeding *vs.* commuting activity.

Results

Bat acoustic activity

The manual acoustic analysis resulted in 77,377 SRE, 12,466 MRE, 15,812 LRE and 864 NoID bat passes. Nine different sonotypes were detected within the three bat foraging guilds (Table S1) including *Myotis spp., P. auritus, Pipistrellus pygmaeus, Pipistrellus nathusii,* MR1 (*Pipistrellus spp.), E. nilssonii, Nyctalus noctula,* LR1 (*E. nilssonii* or *V. murinus*), and LR2 (*V. murinus* or *N. noctula*). Commuting activity made up 78% of all bat passes, while 15% of bat passes included feeding activity and only 7% were passes with social activity independent of feeding activity. For all bat activity combined, 98% of bat passes were recorded on nights when the mean temperature and precipitation for the day had been above 8 °C and below 20 mm, respectively.

The proportion of sonotypes detected across sub-habitats and between years was relatively consistent (Figure S3). Open habitats had the highest number of bat passes (46.9%), followed by the canopy (29.7%) and interior (23.4 %). There was a peak in SRE bat activity in the mid-season period, near the summer solstice (June 21st) and then another higher peak in the late period of the season (Figure 3). The amount of bat activity recorded varied substantially between sites (Figure 4).

Bat community

The NMDS revealed that bat community composition across detector locations was similar between sub-habitats sampled (p = 0.42, R^2 = 0.03) and between years (p = 0.15, R^2 = 0.03). Differences in the bat community across detectors was most strongly linked to site location (p = 0.04, R^2 = 0.25). The number of bat passes recorded at each site and sub-habitat varied substantially in both years (Figure 4).

Our dataset only included a subset of non-SRE bat recordings, so it was not within the scope of this study to further explore changes in the entire bat community across time and space. However, the similarities in sonotype richness detected across all detector locations for both years provide further evidence that our sites were in similar quality forest which supported diverse bat communities.

Bat captures

In total, 34 bats were captured across 9 of the 12 sites sampled during mist net surveys in the summer of 2021. Species captured included *Myotis brandtii* (n = 13), *M. mystacinus* (n = 11), *M. daubentonii* (n=1), *P. auritus* (n = 5) and *P. pygmaeus* (n = 3). The number of bats captured per site was highly variable (mean = 2.8, SD = 2.6) and was not directly related to survey effort (Table S2, Figure S4).

There were nine juveniles of four different species (*M. brandtii;* n = 5, *M. mystacinus;* n = 1, *P. pygmaeus* (n = 2), *P. auritus* (n = 1) captured in total. The first *Myotis* juvenile captured was of *M. brandtii* on August 3rd and for *P. auritus* on August 25th. We captured five post-lactating female *M. brandtii* between August 5th and September 2nd. The remaining nine females captured were non-reproductive, including 5 juveniles. We captured 7 males with visible testes of *M. brandtii* (n = 1), *M. daubentonii* (n = 1), *M. mystacinus* (n = 3), *P. auritus* (n = 2) between June 6th and the 13th of September. On September 1st we captured 4 males with visibly swollen testes, indicating that they were ready or soon ready to breed, for one of each of the following species: *M. brandtii, M. mystacinus*, *P. pygmaeus*, *P. auritus*.

Forest density

We found that the PC1 axis scores from the PCA analysis of forest attribute variables had a consistent negative relationship with each of the individual forest attribute variables that were used as proxies for forest density. PC1 had the strongest negative relationship with the number of stems in each 100 m^2 plot around a detector location (R^2 = 0.76, Figure S4), and was positively related to vegetation cover (R^2 = 0.44, Figure S4) so we treated PC1 as a proxy for forest or habitat openness i.e., the opposite of density.

Short range echolocators: activity across sub-habitats and response to forest density

Comparing total activity of *P. auritus* and *Myotis* (Figure 5 a and b) we found that *P. auritus* was more strongly associated with open sub-habitats (gaps) across all seasons. *P. auritus* activity across all habitat types was very low during the early period of the season and increased as the season progressed. *P. auritus* activity increased with increasing habitat openness in all sub-habitats, but the positive influence of habitat openness was most pronounced late in the season. The most apparent difference between *Myotis* and *P. auritus* was that in the early period of the season, there was a negative relationship between *Myotis* activity and habitat openness in the open habitats. In contrast to *P. auritus*, *Myotis* bats did not have an overall higher activity in open habitats. We found no effect of year sampled for explaining *Myotis* and *P. auritus* activity. Precipitation and temperature had a negative influence on both *Myotis* and *P. auritus* activity.

Although the overall trend in how *Myotis* activity changed in relation to habitat openness and sub-habitat type throughout the summer was similar for both commuting and feeding activity, the magnitude of change differed between behaviors (Figure 5 c and d). Early in the season, the negative relationship with habitat openness was stronger for commuting than feeding activity. For all other sub-habitats and periods, there was a positive influence of habitat openness on *Myotis* commuting and feeding activity. The positive influence of habitat openness was consistently stronger in interior sub-habitats. A stronger positive response to habitat openness for feeding than for commuting activity was found mid-season in all sub-habitats and late season for canopy sub-habitat. Commuting activity was somewhat higher in 2022 than in 2021, whereas the opposite was the case for feeding activity (Table S1).

The relationship between bat activity and density was non-linear, as expected, but was most obvious for interior sub-habitats in the mid and late period of the season. SRE bat activity at interior sub-habitats, for both species groups, behaviors, and all seasons, dropped steeply when habitat openness fell below the median (0.23, Figure 5). *Myotis* activity also steeply decreased with increasing openness at open sub-habitats in the early period of the season. (Figure 4).

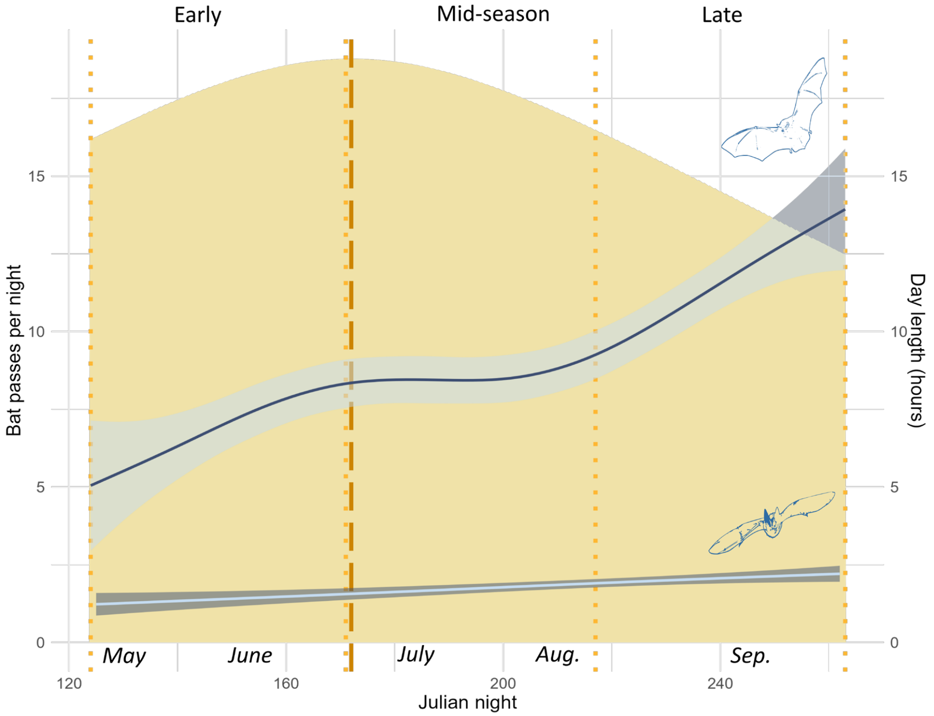

Figure 3. The seasonal activity of *Myotis* species (light blue line) and *P. auritus* (dark blue line) bats throughout the summer in relation to changes in photoperiod and different seasons. The yellow area on the figure represents the number of hours (left y axis) of daylight per day between May 4th and Sep 20th with the date represented as Julian night. The dark orange dashed line shows the summer solstice (June 21st). Light yellow dotted lines delineate the different seasons within the summer were defined (Early = May 4th – June 19th; Mid-season = June 20th – August 5th, Late = August 6th – September 20th). Bat activity represents the average number of bat passes for SRE bat activity given night in season (Julian night) fitted using a generalized additive model with a shrinkage version of a cubic regression spline (lines) with 95% confidence intervals (shaded area surrounding the line).

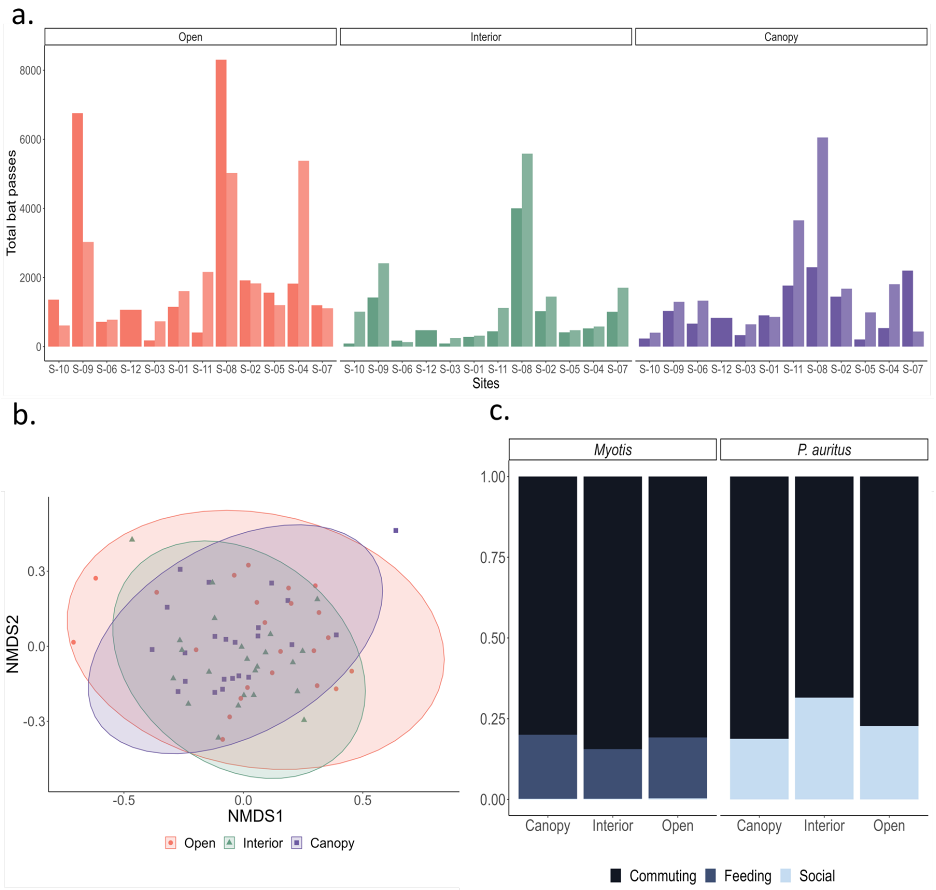

Figure 4. (a.) The total number of bat passes recorded for each detector location (Sites; n = 12, S-01 – S-12) in 2021 (light shaded bars) and 2022 (dark shaded bars). (b.) The normalized ordination of the non-metric multidimensional scaling (NMDS) analysis of bat sonotype defined taxa abundance across all detector locations for both years combined, comparing sub-habitat types. (c.) The proportion of different behaviors recorded for *Myotis* and *P. auritus* activity. The number of total bat passes recorded are found in Table S1.

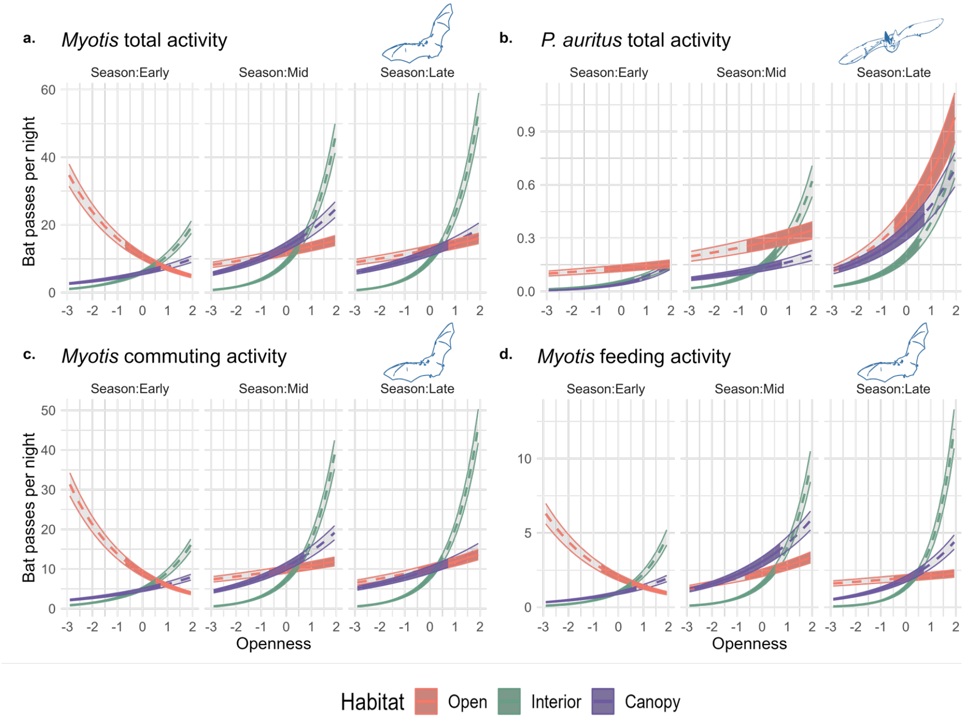

Figure 5. Predicted number of bat passes per night for (a.) total *Myotis* and (b.) total *Plecotus auritus* activity (Table 1), as well as (c.) *Myotis* commuting and (d.) feeding activity (Table 2) in response to increasing habitat openness for each sub-habitat sampled and between seasons. Predictions were averaged (mean) over a subset of three nights from within each season and across all site locations within a sub-habitat type and season. Predictions for ranges of habitat openness that fall outside of the input dataset for each sub-habitat are made see through with dotted lines. Habitat openness is the PC1 axis scores from the PCA analysis of forest attribute variables (Figure S4).

Discussion

We found that SRE bats utilized the 3 sub-habitats sampled differently and that how SRE bats utilized the 3 sub-habitats depended on forest density as well as the period in the season. Contrary to our predictions, we found that *Myotis* activity increased with increasing forest density at open sub-habitats in the early period of the season whereas *P. auritus* activity consistently increased with increasing openness at all sub-habitats throughout the season. We did find non-linear trends in how SRE bats responded to forest density in all models tested, lending support to the prediction that there are certain thresholds of forest density that drive bat activity. *Myotis* feeding activity shifted toward canopy and interior habitats more so than commuting in the mid period of the summer, but not in the early period as we had expected (Figure 5). Our study sheds light on the value of varying forest density and access to multiple sub-habitats for SRE bats in mixed boreal forests. These findings can inform bat monitoring in similar systems. Our findings also demonstrate the importance of considering bats when defining forests that foster biodiversity.

Bat community

It is not always possible to reliably differentiate bat species from acoustics alone. In our study area, *Myotis* use structurally similar echolocation as well as low intensity call types which make them difficult to detect and differentiate. *P. auritus* also uses low intensity echolocation and is known to forego echolocation while foraging to stealthily hunt prey (Russ 2021). SRE bats are more easily sampled with bat capture surveys than MRE and LRE bat species because SRE bats tend to fly low, near vegetation in the interior forest or along edges where it is easiest to deploy harp traps and mist nets (Lintott et al. 2014). Our bat capture surveys complemented our acoustic monitoring by allowing us to identify changes in the reproduction status of bats throughout the season and confirm the presence of species within our study area. Therefore, we recommend combining bat acoustic monitoring with mist net surveys, where species-specific information or life-history information is required.

We recognize that this study is limited by our grouping all *Myotis* species together acoustically such that we cannot address the species-specific differences in habitat use amongst *M. daubentonii, M. brandtii* and *M. mystacinus*. *M. daubentonii* is more associated with foraging on or near waterways than *M. brandtii* and *M. mystacinus* (Dietz and Kiefer 2016). We deployed our acoustic detectors away from aquatic habitats and our bat capture surveys were dominated by *M. brandtii* and *M. mystacinus*. Therefore, it is likely that most of the *Myotis* activity recorded from acoustic detectors is from *M. brandtii* and *M. mystacinus,* which are both highly associated with forest systems in Fennoscandia (Wermundsen and Siivonen 2008; Vasko et al. 2020; Kotila et al. 2023). However, we caution that these two species can have unique foraging needs even within the same area (**Paper IV**).

Only a subset of the MRE, LRE and NoID activity was selected for manual acoustic analysis, so we are limited in the level of detail we can describe bat activity and behavior for the entire bat community. However, by selecting one random bat pass per bat species per detector location per night that a species was detected by the automatic classifier, we expect that proportional relationships should closely represent what a manual acoustic analysis of the entire sample would have resembled.

Myotis & brown long-eared bats

We were surprised to find that *P. auritus* were consistently best sampled in open sub-habitats whereas total *Myotis* activity in open sub-habitats shifted relative to forest density and changes in the period of the season (Figure 5). We had predicted that open sub-habitats would be where *Myotis* activity was highest throughout the season because we expected them to be more sensitive to cluttered vegetation than *P. auritus*. Notably, *Myotis* activity decreased at the less dense open sub-habitats in the early period of the season.

P. auritus were rarely detected in the early period of the season, but when they were detected, they were most often in open sub-habitats. Given the low detectability of *P. auritus* due to their very quiet and infrequent echolocation (Dietz and Kiefer 2016), this trend may be reflective of how these bats forage differently from *Myotis.* Studies on the diet of *P. auritus* in Sweden and Finland show that beetles are an import food resource for this species (Rydell 1989; Vesterinen et al. 2018; Wood and Cousins 2023). Perhaps during the early period of the season when day length is long and the vegetation is less developed, *P. auritus* adjusts its hunting strategy to target larger, ground dwelling prey such as beetles and therefore benefit from foraging in open sub-habitats the most. During the mid and late period of the summer, both *Myotis* species and *P. auritus* increase their activity in less dense forest locations across the three sub-habitats sampled, which is generally in line with our expectations and the findings of previous studies (Entwistle et al. 1997; Froidevaux et al. 2016; Müller et al. 2018; Ancillotto et al. 2022; Hendel et al. 2023)

The late period of the season is when juvenile bats become volant in our study area. The increased use of more open habitats as the summer progresses may in part be explained by young bats preferentially flying in more open habitats while they are learning to navigate clutter (Wund 2005). However, other factors such as changes in available prey, interactions between conspecific and heterospecific bats could also be playing a role.

Both *Myotis* and *P. auritus* are typically associated with flying near ground vegetation in forest (de Jong 1995; Denzinger and Schnitzler 2013; Müller et al. 2018). However, we found that *Myotis* total activity steeply increased at canopy detectors deployed in less dense forests during the mid-season. We also saw that *P. auritus* activity was increased in canopy and open sub-habitats in the late period of the season. Our findings share similarities with Froidevaux *et al.*, (2016)'s that open and canopy are both important sub-habitats for sampling SRE bats. Plank, Fiedler and Reiter, (2012) also found that several *Myotis* species at deciduous forests in Vienna shifted to be more active at habitats sampled using canopy detectors more so than ground level detectors in the periods of the season after most bats have been pregnant. Within our system, there are many potential explanations for why we found high levels of SRE bat activity near canopy detectors. Boreal forests in Fennoscandia are relatively low in height compared to temperate forests, in part because of the climate which promotes slow growing trees but also because the intensive management of forests which has removed most old, tall trees (Vankat 2002). Bat monitoring efforts in boreal forests should make efforts to sample sub-habitats stratified horizontally and vertically. We suggest that monitoring efforts in the early period of the summer consider that even gaps within the forest may be too exposed for SRE bats.

Myotis feeding vs. commuting activity

We found differences in the magnitude of effect that density, sub-habitat, and period in season had on *Myotis* feeding compared to commuting activity in this study. *Myotis* feeding activity increased with decreasing forest density at interior and canopy habitats more so than was expressed in commuting activity during the mid and late periods of the summer. There are many possible explanations for this trend such as shifts in prey resource, competition for foraging habitat in open habitats or aspects related to phenological events during the later periods of the summer. Possibly this trend can be attributed to *Myotis* spending more time foraging in canopy and interior habitats as the daylength shortens and foliage becomes lusher. At which point, denser sub-habitats, insect associated with the understory vegetation would also become more abundant and consequently create more foraging opportunities for bats. For example, Aihartza *et al.*, (2023) provides a detailed example of how insectivorous bats must adjust their prey consumption in relation to prey as well as habitat availability throughout the season.

We found similar trends in habitat use throughout the season between commuting and feeding activity for *Myotis* in this study. In a study carried out in parallel to this one, we found that *Myotis* feeding activity 75% correlated with total activity in open sub-habitats, which was far less than the 99% correlation between *Myotis* commuting and total activity (**Paper III**). While this is a relatively high correlation between feeding and total *Myotis* activity, we find that there are important nuances in habitat use between *Myotis* commuting and feeding activity that are mediated by environmental conditions. Previous studies have also found that *Myotis* species have higher feeding activity in less exposed habitats (Ellerbrok 2023; McKay et al. 2024). Therefore, we maintain that identifying feeding activity within bat acoustic recordings is valuable when it is important to identify foraging habitat use.

Bat responses to forest density

We expected to find a non-linear relationship between total SRE bat activity and forest density, with overly dense forest sites and sub-habitats being too challenging to navigate for these bats (Adams et al. 2009; Müller et al. 2013; Froidevaux et al. 2016). This trend was observed for *P. auritus* more so than *Myotis* in our study. Though, *Myotis* total, commuting and feeding activity all sharply declined at interior sub-habitats below median levels of density (Figure 5).

There are numerous approaches to describing habitat in relation to bats and bat communities in the forest. Previous studies have used coarse categorical descriptions at the landscape scale (Berge 2007; Aihartza et al. 2023), in field measurements of forest structure (Bender et al. 2015; Cruz et al. 2019), as well as remote sensing techniques (Froidevaux et al. 2016; Carr et al. 2018; Müller et al. 2018) with a large amount of variety in how these tools were implemented. In this study we used a composite of forest structure measurements collected in field from 100 m^2 plots around detectors. Furthermore, by using a PCA we account for the collinearity across forest structure variables that bats respond to in similar ways. We recognize that multiple spatial scales can be valuable to explore in relation to bat foraging activity. However, we feel confident that the measures of habitat openness we use in this study effectively describes the area sampled by acoustic detectors for SRE bats which have a relatively short detection range of approximately less than twenty meters.

We found that more densely forested habitats can be valuable for *Myotis* in the early period of the summer. This period is also when bats in our study area may be experiencing pregnancy and lactation as well as when daylength is longest. Early in the season, vegetation in mixed boreal forests is less developed due to the brief and intense growing season. Therefore, open habitats are even more exposed in the early period of the summer due to lack of ground and canopy cover. Likewise, dense sub-habitats are easier to navigate when the understory and foliage is less dense. Between May and early June, we observed pregnant and lactating SRE bats in the study area. Kotila *et al.*, (2023) found that *Myotis* species were more closely associated with mature forests as latitude increased when sampling bats across on a vertical gradient across Finland. The authors of this study suggested that *Myotis* species would avoid open habitats more so at far northern latitudes due to the additional exposure posed by "white nights" in the summer. It is possible that SRE bats are more averse to open forest habitats during the early period to avoid additional risks caused by flying in exposed, well-lit areas during a time when their energy demands are very high. Horever, Vasko *et al.*, (2020) found little evidence that *Myotis* living at latitudes similar to our own study area selected for habitat with high canopy cover during the lightest nights of the year. The authors of this study suggest that *Myotis* are more averse to artificial light than the natural light found in the forest interior. Even so, Vasko *et al.*, (2020) also find that *Myotis* are highly associated with mature forests in summer and autumn.

Our habitat sampling methods closely followed Froidevaux *et al.*, (2016) which took place in Switzerland in forests dominated by beech and Norway spruce. Froidevaux *et al.*, (2016) found that SRE bats were most associated with the interior and canopy detectors though they found a negative relationship between foliage height density and the density of trees and SRE activity, suggesting a preference for more open sub-habitats within the forest. We also found that SRE bats were highly active at interior and canopy sub-habitats but that interactions with forest density and time in season were important factors determining sub-habitat use (Table S4, Table S5). Froidevaux *et al.*, (2016) also found that there is a certain threshold of density for which forests become inefficient to navigate, even for SRE bats that are adapted to flying near clutter, as has been reported in other studies (Arlettaz et al. 2001; Schnitzler and Kalko 2001; Rainho et al. 2010). However, these studies have not explored the influence of seasonal effects using continuous sampling throughout the summer as we have and did not account for the potential differences between feeding and commuting activity in *Myotis*.

Myotis activity as well as *P. auritus* activity increased substantially at interior forest habitats during the mid- and late periods of the season, suggesting that these are important habitats for SRE bats, but more so between mid-June and mid-September in our study area. This was somewhat surprising as we had expected that SRE bats would be highest in interior sites when day length was longest, during the early and mid-season periods (Figure 3). The increase in understory and foliage density throughout the growing season is likely to play a role in the shift observed. These trends may also be explained by prey availability which will be subject to seasonal shifts.

Open habitat detector locations more closely resemble the “ideal” forest bat acoustic sampling location. In more dense sites, vegetation and clutter reduce the range of detectability for detectors compared to less dense sites (Browning et al. 2021). Open sub-habitats had the highest proportion of SRE bat passes recorded overall but our results revealed that SRE bat activity at the different sub-habitats changed considerably relative to period in season (Figure 4). These findings indicate that the sampling the interior forest using acoustic detectors to monitor SRE bats in similar systems may be most effective after the summer solstice.

Recordings bats in the canopy and in interior forest habitats poses inherent technical challenges, especially for SRE bats which already produce very quiet and low intensity call types (Adams et al. 2009; Plank et al. 2012; Müller et al. 2018). These are challenging recording environments where proximity to cluttered vegetation can result in noisier, poor-quality recordings which are more challenging to analyze (O’Keefe et al. 2014). However, previous studies have found that the detection of bats in forests is not likely to be highly influenced by vegetation structure, whereas whether or not certain species choose to use more cluttered habitat may be influenced (Yates and Muzika 2006; Obrist et al. 2011; Bender et al. 2015). When deploying acoustic detectors in the field, we took care to avoid vegetation while also sampling varying level of density intended. Even so, it is possible that detection rates at interior and canopy detector sites were negatively affected by vegetation density.

Management Implications

Our findings are in line with previous studies that have documented a negative influence of high stand density on forest biodiversity; providing further evidence for the value of varying density, including gaps, in boreal forests to support wildlife. Boreal forests in the Fennoscandian region are primarily managed for timber production (Blattert et al. 2023). Production forests are typically denser and darker than forests dominated by natural dynamics, with a lower diversity of understory vascular plants (Hedwall et al. 2019) and saproxylic insects (Lindhe et al. 2005). Research on the potential cascading negative effects on insectivorous vertebrates resulting from forestry-induced alterations in habitat structure has primarily concentrated on avian species (Mäntylä et al. 2011; Schulze et al. 2019; Przepióra et al. 2020). However, our finding that increased habitat openness can improve the quality of the forest as foraging habitat for SRE bats, concurs with recommendations to improve habitat quality for boreal forest birds by Felton et al. (2021), to "*limit the density of trees per ha in production forest to promote a more diverse and productive understory vegetation*". Heterogeneous forest structure is clearly important to maintain even in production forests so that these landscapes can maintain their ecological function as habitat for wildlife.

Mixed forests can provide high quality habitat for a broad range of species, including bats. However, if these forests are intensively managed in a way that homogenizes the age, size, and features of trees over a large area, then these simplified forests lack the complexity necessary for diverse communities to meet their needs. This study provides a lens into how forest density influences SRE bat habitat across seasons and within sub-habitats of the forest interior. The findings and methodologies defined in this research can inform other studies within the region and emphasizes the importance of considering bats in boreal forest management. Our study provides an additional voice to the chorus of previous studies that urge managers to incorporate gaps and changes in density within production forests to provide suitable habitat for bats as well as other wildlife.

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Author contributions

Reed April McKay: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Natalie Yoh:** Investigation (supporting); Formal analysis (supporting); Writing – review and editing (supporting). **Richard Bischof:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Fiona Mathews:** Conceptualization (equal); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Katrine Eldegard:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (supporting).

Ethics statement

Handling and capturing of wildlife in this study was conducted by trained personnel in accordance with the appropriate permits provided by the Norwegian Environment Agency. Landowners granted permission to install passive acoustic detectors and insect camera traps.

Data availability statement

The workflows for analyses are available on GitHub: https://github.com/airmckay/BatsInsectsBorealForest_FolloRegion. The data will be stored in a repository such as Dryad when this manuscript is accepted for publication in a scientific journal. Inquiries about the data and how it was analyzed or managed are welcome and can be addressed to Reed April McKay (reed.april.mckay@nmbu.no).

Supplementary materials

Table S1. Overview of the number of bat passes and noise recordings across different bat taxa and foraging guilds detected using automatic classification software Kaleidoscope Pro, Bats of Europe Classifier v.5.2.1 (Wildlife Acoustics Inc, USA) with all species recorded in Norway and Sweden included (left) and the results of the manual acoustic analysis (right). The number of feeding and social passes found for each taxa is reported for the manual acoustic analysis (right). MR1 = *Pipistrellus spp.*, LR1 = *E. nilssonii* or *V. murinus*, LR2 = *V. murinus* or *N. noctula*. The difference in total recordings between Auto ID and Manual ID is on account of multiple bat species detected in bat passes originally defined using the automatic classification software, which were then parsed into separate bat passes after manual acoustic analysis. Bat species that are listed on the Norwegian Red List for Species (Eldegard et al. 2021) included in the automatic acoustic analysis are bolded in blue text. See Acoustic Analysis in the methods section and Figure S2 for information on the amount of agreement between the automatic classifier and the results from the manual acoustic analysis. Data was collected using Wildlife Acoustics SM4-BATFS acoustic detectors in Akershus county, Norway in the summer and autumn 2021 and 2022.

Auto ID	**n**	**Manual ID**	**n**	**Feeding**	**Social**
Myotis alcathoe	240	*Myotis* spp.	74979	13698	198
Myotis bechsteinii	379	*P. auritus*	2398	0	558
Myotis brandtii	20195	*B. barbastellus*	0	0	0
Myotis dasycneme	6622				
Myotis daubentonii	25764				
Myotis myotis	291				
Myotis mystacinus	16713				
Myotis nattereri	627				
Plecotus auritus	5448				
Plecotus austriacus	1928				
Barbastella barbastellus	2337				
Short range echolocators	***80544***		***77377***	***13698***	***756***
Pipistrellus pygmaeus	4450	*P. pygmaeus*	11725	388	6845
Pipistrellus nathusii	197	*P. nathusii*	22	0	0
Pipistrellus pipistrellus	1030	MR1	719	24	3
Medium range echolocators	***5677***		***12466***	***412***	***6848***
Eptesicus nilssonii	5302	*E. nilssonii*	14191	1202	195
Eptesicus serotinus	1809	LR1	263	2	3
Vespertilio murinus	239	LR2	1130	11	1
Nyctalus leisleri	992	*V. murinus*	0	0	0
Nyctalus noctula	1810	*N. noctula*	233	2	0
Long range echolocators	***10152***		***15817***	***1217***	***199***
Unknown bat (NoID)	***7500***	NoID	**864**	**15**	**81**
		Noise	2464		
Total recordings	***103873***		***108989***	***15342***	***7884***

Table S2. Overview of the different bat species captured and total number of bat captures (total) during mist net surveys in the summer of 2021. The number of net hours (n hours) and number of distinct net set ups (n nets) used across three nights of surveys is reported. MBRA = *M. brandtii*, MMYS = *M. mystacinus,* MDAU = *M.* daubentonii, PAUR = *P. auritus,* PPYG = *P. pygmaeus*.

Site	**MBRA**	**MMYS**	**MDAU**	**PAUR**	**PPYG**	**Total**	**n hours**	**n nets**
1	2	0	0	0	0	2	53	4
2	0	1	0	0	0	1	43	6
3	2	2	0	0	1	5	47.7	4
4	0	1	0	1	0	2	46.2	9
5	1	0	0	0	0	1	48.6	7
6	0	3	0	0	0	3	44.6	3
7	0	2	0	0	1	3	55.5	5
8	8	1	1	2	1	13	46.5	4
9	0	0	0	0	0	0	52.3	7
10	0	0	0	0	0	0	43.4	3
11	0	0	0	0	0	0	49.3	9
12	0	1	0	3	0	4	43.3	5

Table S3. Overview for alternative statistical models explaining the relationship between nightly bat activity for (i. *Myotis* total activity, ii. *P. auritus* total activity, iii. *Myotis* commuting activity, iv. *Myotis* feeding activity) and the follow explanatory variables: habitat openness, sub-habitat type, and period in season (early, mid-season and late) as fixed effects, as well as all possible interactions between these three terms, temperature, precipitation, and year as main effects. Site location and Julian night were specified as random intercepts. Bold models are those with the lowest AIC weights which were identified as the best models.

Model	Dataset	Error distribution	df	AIC
MY1	*Myotis* total	Poisson	23	132301.39
MY2	*Myotis* total	Zero-inflated Poisson	24	112325.01
MY3	*Myotis* total	Generalized Poisson	24	43702.74
MY3b	***Myotis* total**	Zero-inflated generalized Poisson	25	**43668.78**
MY4	*Myotis* total	Negative binomial	24	43998.66
MY4b	*Myotis* total	Zero-inflated negative binomial	16	44536.75
PL1	*P. auritus* total	Poisson	23	9387.13
PL2	*P. auritus* total	Zero-inflated Poisson	24	8688.30
PL3	*P. auritus* total	Generalized Poisson	24	8411.06
PL3b	*P. auritus* total	Zero-inflated generalized Poisson	25	8399.78
PL4	***P. auritus* total**	Negative binomial	24	**8249.35**
PL4b	*P. auritus* total	Zero-inflated negative binomial	25	8251.35
MY1c	*Myotis* commuting	Poisson	23	107272.51
MY2c	*Myotis* commuting	Zero-inflated Poisson	24	91188.46
MY3c	*Myotis* commuting	Generalized Poisson	24	41677.00
MY3cb	***Myotis* commuting**	Zero-inflated generalized Poisson	25	**41645.00**
MY4c	*Myotis* commuting	Negative binomial	24	41895.11
MY4cb	*Myotis* commuting	Zero-inflated negative binomial	25	41897.11
MY1f	*Myotis* feeding	Poisson	23	41918.20
MY2f	*Myotis* feeding	Zero-inflated Poisson	24	33362.75
MY3f	***Myotis* feeding**	Generalized Poisson	24	**21190.08**
MY3fb	*Myotis* feeding	Zero-inflated generalized Poisson	25	21192.08
MY4f	*Myotis* feeding	Negative binomial	24	21409.27
MY4fb	*Myotis* feeding	Zero-inflated negative binomial	25	21411.27

Table S4. Model summary outputs for (a.) the zero-inflated generalized Poisson mixed-effect model explaining total *Myotis* activity and (b.) the negative binomial mixed-effect model explaining total *Plecotus auritus* activity.

			a. Total *Myotis* activity					**b. Total *Plecotus auritus* activity**		
Explanatory terms	*Est.*	*std. Error*	*CI*	*z*	*p*	*Est.*	*std. Error*	*CI*	*z*	*p*
Count Model										
Intercept	2.03	0.19	1.66 – 2.39	10.85	**<0.001**	-2.30	0.34	-2.96 – -1.65	-6.86	**<0.001**
Habitat:Interior	-0.57	0.08	-0.73 – -0.42	-7.27	**<0.001**	-0.88	0.27	-1.41 – -0.35	-3.26	**0.001**
Habitat:Canopy	-0.61	0.07	-0.76 – -0.46	-8.16	**<0.001**	-1.14	0.26	-1.66 – -0.63	-4.34	**<0.001**
Openness	-0.41	0.07	-0.54 – -0.28	-6.04	**<0.001**	0.09	0.20	-0.30 – 0.47	0.45	0.654
Season:Mid	0.11	0.15	-0.19 – 0.40	0.71	0.478	0.75	0.28	0.19 – 1.31	2.63	**0.009**
Season:Late	0.16	0.15	-0.14 – 0.46	1.06	0.290	1.21	0.29	0.63 – 1.78	4.09	**<0.001**
Temperature	-0.13	0.02	-0.18 – -0.08	-5.34	**<0.001**	-0.11	0.06	-0.22 – 0.00	-1.94	0.052
Precipitation	-0.15	0.02	-0.19 – -0.11	-7.70	**<0.001**	-0.17	0.05	-0.27 – -0.07	-3.48	**0.001**
Year:2022	0.05	0.03	-0.01 – 0.11	1.62	0.104	-0.07	0.08	-0.22 – 0.08	-0.89	0.375
Habitat:Interior × Openness	1.01	0.10	0.80 – 1.21	9.72	**<0.001**	0.43	0.35	-0.26 – 1.12	1.23	0.220
Habitat:Canopy × Openness	0.68	0.08	0.52 – 0.84	8.49	**<0.001**	0.54	0.32	-0.08 – 1.17	1.71	0.088
Habitat:Interior × Season:Mid	0.28	0.10	0.08 – 0.49	2.71	**0.007**	0.28	0.32	-0.35 – 0.91	0.86	0.388
Habitat:Canopy × Season:Mid	0.74	0.10	0.54 – 0.93	7.42	**<0.001**	0.42	0.31	-0.20 – 1.04	1.33	0.184
Habitat:Interior × Season:Late	0.29	0.11	0.07 – 0.52	2.57	**0.010**	0.09	0.34	-0.57 – 0.75	0.26	0.792
Habitat:Canopy × Season:Late	0.56	0.11	0.34 – 0.77	5.11	**<0.001**	0.89	0.33	0.25 – 1.52	2.72	**0.007**
Openness × Season:Mid	0.54	0.09	0.37 – 0.71	6.30	**<0.001**	0.03	0.24	-0.44 – 0.49	0.11	0.915
Openness × Season:Late	0.54	0.09	0.35 – 0.72	5.65	**<0.001**	0.33	0.25	-0.16 – 0.82	1.31	0.190
(Interior × Openness) × Medium	-0.30	0.14	-0.57 – -0.03	-2.20	**0.028**	0.18	0.43	-0.66 – 1.02	0.42	0.673
(Canopy × Openness) × Medium	-0.51	0.10	-0.71 – -0.32	-5.12	**<0.001**	-0.44	0.36	-1.15 – 0.27	-1.22	0.222
(Interior × Openness) × Late	-0.24	0.14	-0.52 – 0.04	-1.71	0.087	-0.17	0.43	-1.01 – 0.67	-0.40	0.692
(Canopy × Openness) × Late	-0.58	0.11	-0.80 – -0.36	-5.27	**<0.001**	-0.59	0.37	-1.31 – 0.13	-1.62	0.106
(Intercept)	29.74		27.36 – 32.32							
Zero-Inflated Model										
Intercept	-4.14	0.31	-4.75 – -3.54	-13.44	**<0.001**					
Random Effects						**Random Effects**				
σ^2	1.92					σ^2		2.42		
τ_{00} Site	0.28					τ_{00} Site		0.76		
τ_{00} jnight.f	0.32					τ_{00} jnight.f		0.32		
ICC	0.24					ICC		0.31		
N_{Site}	12					N_{Site}		12		
$N_{jnight.f}$	140					$N_{jnight.f}$		140		
Observations	8149					Observations		8149		
Marginal R^2 / Conditional R^2	0.119 / 0.328					Marginal R2 / Conditional R2		0.203 / 0.449		

Table S5. Model summary outputs for (a.) the zero-inflated generalized Poisson mixed-effect model explaining *Myotis* commuting activity and (b.) the generalized Poisson mixed-effect model explaining *Myotis* feeding activity.

	a.	***Myotis* commuting activity**				b.	***Myotis* feeding activity**			
Explanatory terms	*Estimate*	*std. Error*	*CI*	*z*	*p*	*Estimate*	*std. Error*	*CI*	*z*	*p*
Count Model										
Intercept	1.86	0.19	1.49 – 2.22	10.01	**<0.001**	0.40	0.22	-0.03 – 0.82	1.83	0.067
Habitat:Interior	-0.59	0.08	-0.74 – -0.43	-7.42	**<0.001**	-0.68	0.11	-0.90 – -0.46	-5.99	<0.001
Habitat:Canopy	-0.64	0.08	-0.79 – -0.49	-8.41	**<0.001**	-0.74	0.11	-0.95 – -0.52	-6.66	<0.001
Openness	-0.43	0.07	-0.57 – -0.30	-6.29	**<0.001**	-0.39	0.10	-0.58 – -0.20	-4.07	<0.001
Season:Mid	0.09	0.15	-0.19 – 0.38	0.64	0.521	0.14	0.17	-0.20 – 0.48	0.79	0.430
Season:Late	0.13	0.15	-0.16 – 0.42	0.86	0.389	-0.02	0.18	-0.38 – 0.34	-0.12	0.904
Temperature	-0.12	0.02	-0.17 – -0.08	-5.09	**<0.001**	-0.13	0.03	-0.20 – -0.07	-3.87	<0.001
Precipitation	-0.15	0.02	-0.19 – -0.11	-7.55	**<0.001**	-0.14	0.03	-0.20 – -0.09	-5.14	<0.001
Year:2022	0.06	0.03	-0.00 – 0.12	1.95	0.051	-0.11	0.04	-0.19 – -0.02	-2.53	0.011
Habitat:Interior × Openness	1.04	0.10	0.83 – 1.24	9.89	**<0.001**	1.18	0.16	0.86 – 1.50	7.17	<0.001
Habitat:Canopy × Openness	0.70	0.08	0.54 – 0.86	8.61	**<0.001**	0.75	0.12	0.51 – 0.98	6.26	<0.001
Habitat:Interior × Season:Mid	0.29	0.10	0.08 – 0.49	2.73	**0.006**	0.29	0.15	-0.01 – 0.59	1.91	0.056
Habitat:Canopy × Season:Mid	0.71	0.10	0.52 – 0.91	7.12	**<0.001**	1.01	0.14	0.73 – 1.29	7.10	<0.001
Habitat:Interior × Season:Late	0.35	0.11	0.12 – 0.57	3.05	**0.002**	0.30	0.17	-0.04 – 0.63	1.75	0.080
Habitat:Canopy × Season:Late	0.60	0.11	0.38 – 0.81	5.43	**<0.001**	0.69	0.16	0.37 – 1.02	4.25	<0.001
Openness × Season:Mid	0.53	0.09	0.36 – 0.70	6.12	**<0.001**	0.58	0.12	0.35 – 0.82	4.83	<0.001
Openness × Season:Late	0.58	0.09	0.39 – 0.77	6.12	**<0.001**	0.46	0.14	0.19 – 0.74	3.30	0.001
(Interior × Openness) × Medium	-0.27	0.14	-0.54 – 0.00	-1.94	0.052	-0.44	0.22	-0.86 – -0.02	-2.04	0.042
(Canopy × Openness) × Medium	-0.49	0.10	-0.69 – -0.29	-4.84	**<0.001**	-0.61	0.14	-0.89 – -0.32	-4.17	<0.001
(Interior × Openness) × Late	-0.28	0.14	-0.56 – -0.00	-1.96	**0.050**	-0.12	0.23	-0.58 – 0.34	-0.51	0.607
(Canopy × Openness) × Late	-0.62	0.11	-0.84 – -0.41	-5.67	**<0.001**	-0.39	0.17	-0.72 – -0.06	-2.29	0.022
(Intercept)	21.71		20.07 – 23.49							
Zero-Inflated Model										
Intercept	-4.09	0.31	-4.70 – -3.49	-13.23	**<0.001**					
Random Effects						**Random Effects**				
σ^2	1.80					σ^2		2.35		
$\tau_{00\ Site}$	0.28					$\tau_{00\ Site}$		0.38		
$\tau_{00\ jnight.f}$	0.30					$\tau_{00\ jnight.f}$		0.31		
ICC	0.24					ICC		0.23		
N_{Site}	12					N_{Site}		12		
$N_{jnight.f}$	140					$N_{jnight.f}$		140		
Observations	8149					Observations		8149		
Marginal R^2 / Conditional R^2	0.126 / 0.339					Marginal R2 / Conditional R2		0.134 / 0.331		

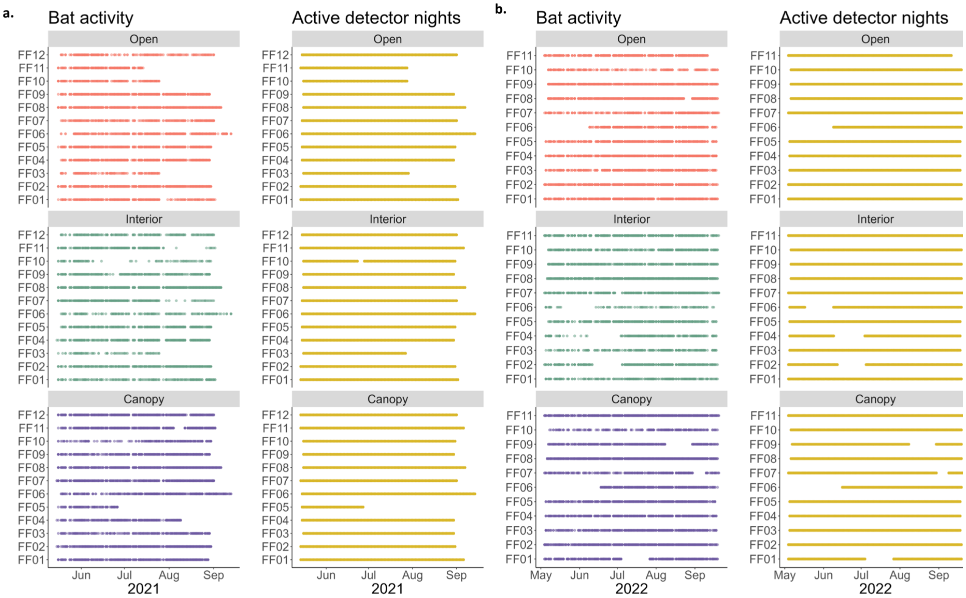

Figure S1. Overview of data collection and survey effort across the entire survey period spanning the summer and autumn of 2021 and 2022. In the "Bat activity" figures, dots represent nights when at least on bat pass was detected at a detector location, with colors corresponding sub-habitat types. In the "Active detector night" figures, yellow dots represent a night when a detector was deployed in the field and no equipment failure was detected i.e., active detector nights. Gaps or the absence of yellow dots in active detector nights are nights when a detector was not deployed in the field or when there were equipment failures.

Detectors were programmed to record from one hour before sunset until 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 (gain = 12 dB, sample rate = 256 kHz, minimum duration = 1.5 ms, minimum trigger frequency = 12 kHz, maximum length = 15 seconds).

Two detector nights were incomplete due to detectors being collected shortly after sunset, which produced six bat passes. Passes from incomplete detector nights were removed from further analysis. Two detectors were moved after initial deployment between 2021 and 2022 to avoid highly cluttered areas of understory vegetation regrowth which could affect the microphone performance, but the site locality remained the same. In 2022, several sub-habitat detectors were deployed a short distance away from the location the previous seasons because we determined the original location had become too overgrown to sample effectively. Site 10 was thinned between the 2021 and 2022 field seasons.

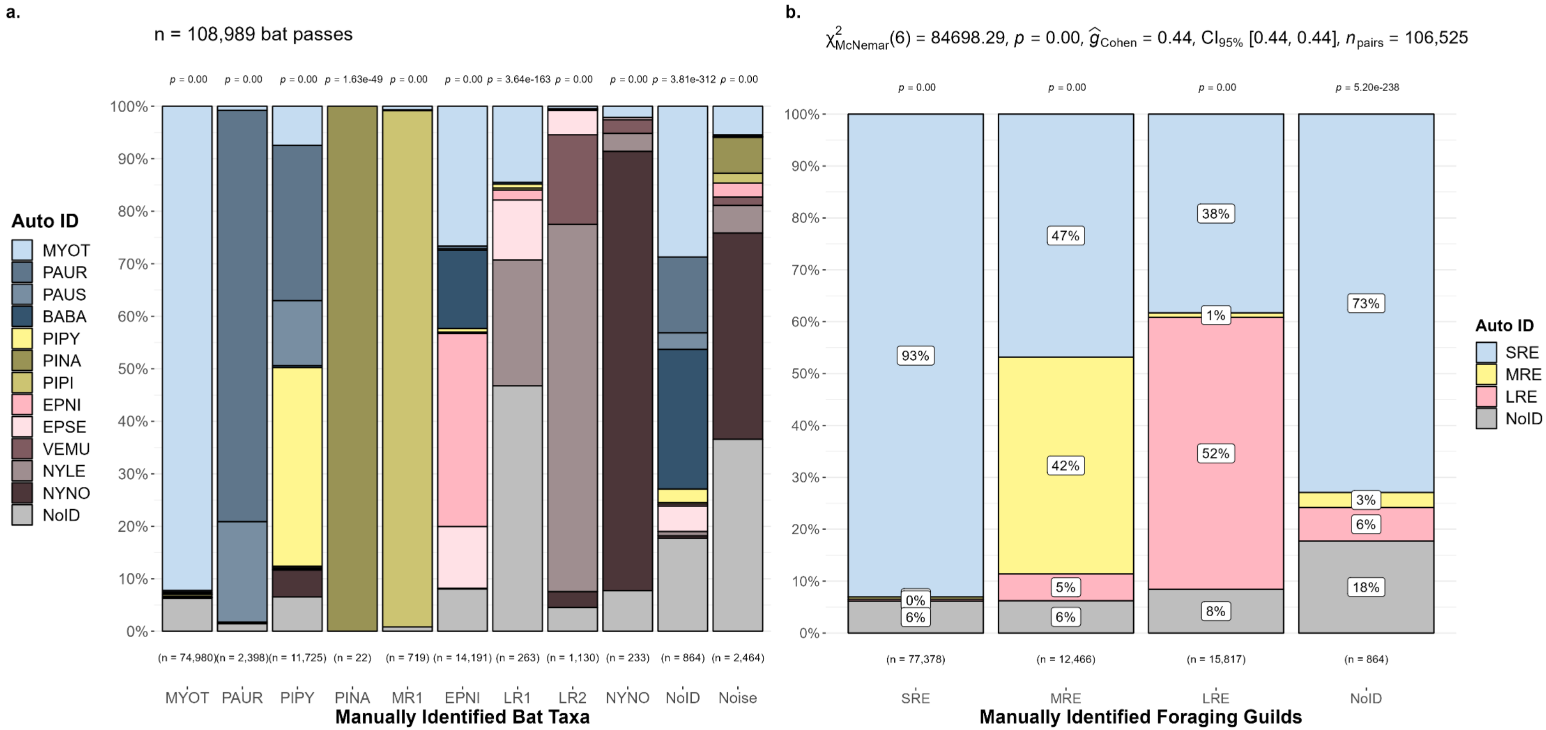

Figure S2. Proportion of agreement between the manual acoustic analysis and the automatic analysis results (Wildlife Acoustics, Kaleidoscope Pro, Bats of Europe Classifier v.5.2.1) of (a.) bat passes to species, genus, or sub-guild level and (b.). to foraging guild, with percents printed inside the bar chart. The proportion (goodness of fit) test p-value is displayed on top of each bar comparing the automatic identification (Auto ID) to the manual analysis results for both figures. For the guild-level analysis (b.), recordings that the automatic classifier identified as a bat but were revealed to be noise (n = 2464) were removed from the dataset visualized. The results of the non-parametric McNemar's test are provided above the bar charts for the guild-level analysis (b.). Bat taxa: NYNO = *Nyctalus noctula,* NYLE = *Nyctalus leisleri*, VEMU = *Vespertilio murinus,* EPNI =

Eptesicus nilssonii, EPSE = *Eptesicus serotinus*, LRI = VEMU or EPNI, LR2 = VEMU or NYNO, PIPI= *Pipistrellus pipistrellus,* PINA = *Pipistrellus nathusii*, PIPY = *Pipistrellus pygmaeus*, MR1 = *Pipistrellus* spp., BABA = *Barbastella barbastellus*, PAUR = *Plecotus auritus,* PAUS= *Plecotus austriacus,* MYOT = *Myotis* spp. All *Myotis* spp. included in the automatic identification process are grouped here but a list of the species included is provided in Table S1.TableS1. Foraging guilds: Short range echolocators (SRE, light blue), medium range echolocators (MRE, yellow), long range echolocators (LRE, pink) and unidentified bat (NoID, gray). More information about the analysis is found in the methods section Acoustic analysis and Table S1 in supplementary materials. The data was collected in Akershus county, Norway during the summer and early autumn of 2021 and 2022. Plots created with the R package ‘ggstatsplot’ (Patil 2021)

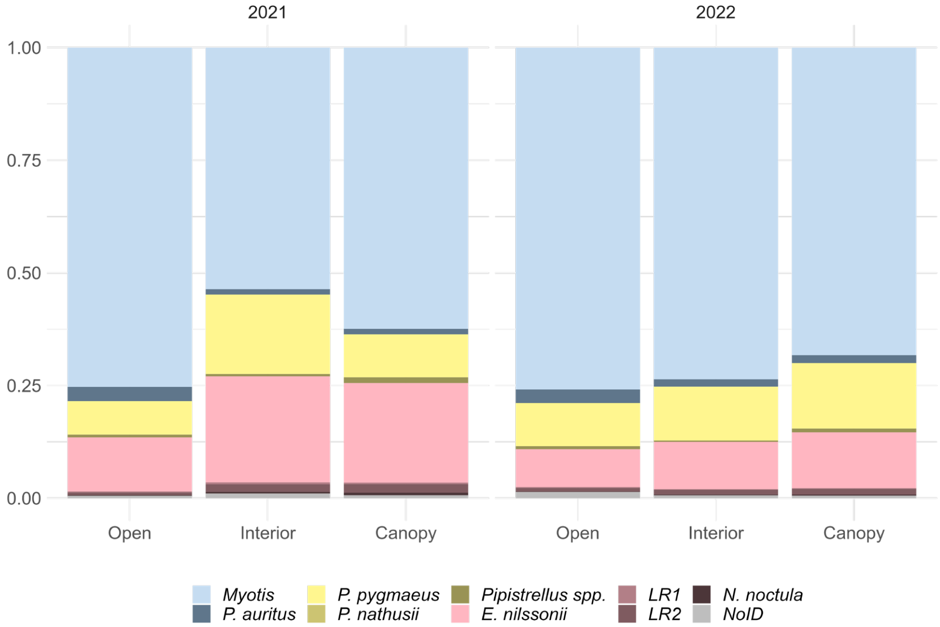

Figure S3. Proportion bar charts of (a.). the number of total bat passes recorded in each sub-habitat type (Open, Interior, Canopy) across sonotypes for each year, and (b.) across foraging guild and behavior. Foraging guilds: SRE = short range echolocating bats (blue), MRE = medium range echolocating bats (yellow), LRE = long range echolocating bats (pink/red), NoID = Unidentified bats (gray). LR1 (*E. nilssonii* or *Vespertilio murinus*), LR2 (*V. murinus* or *N. noctula*).

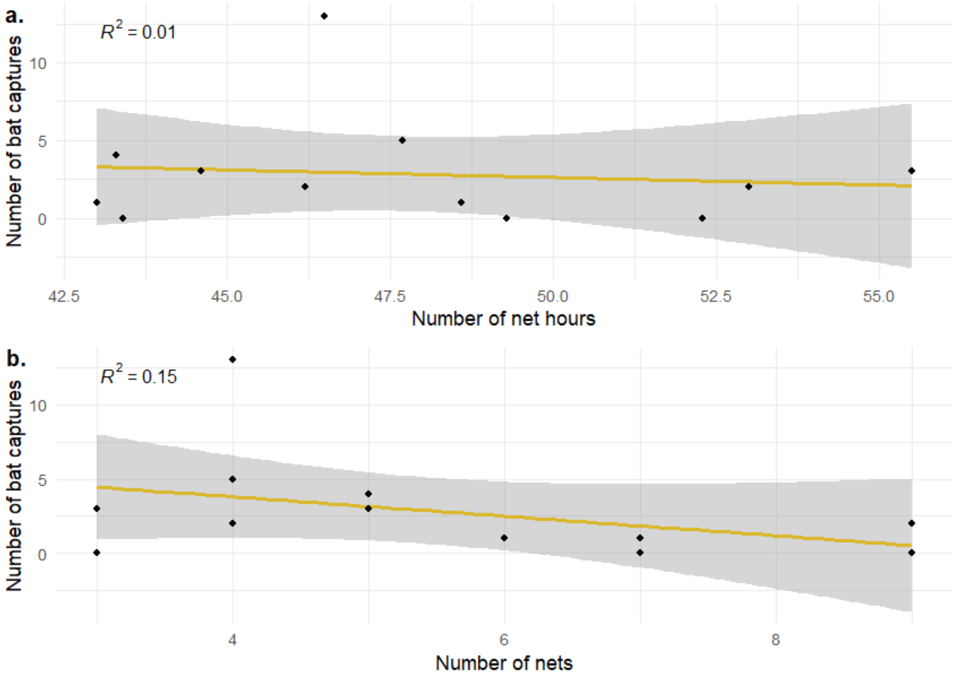

Figure S4. Relationship between the number of bats captured and (a.) the for the number of net hours and (b.) number of different nets deployed at mist net sites. The lines and shaded polygons are the estimated means and associated 95% confidence interval from simple linear regression models.

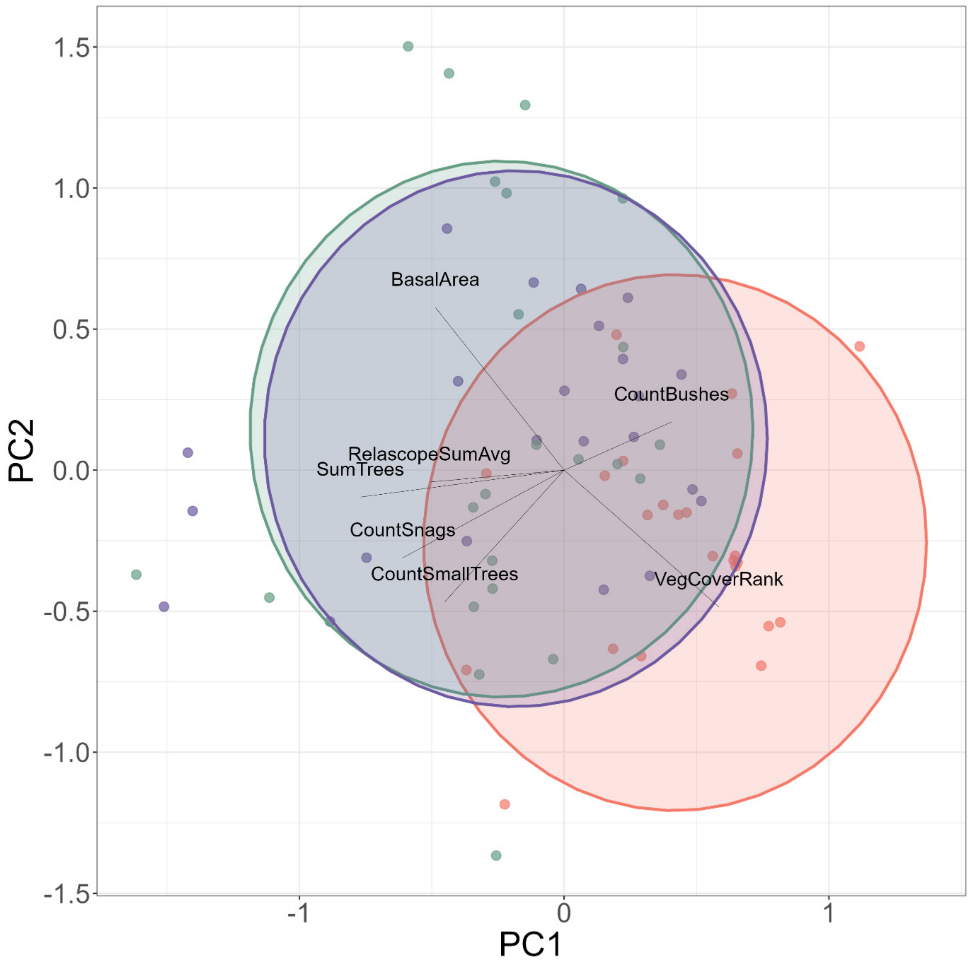

Figure S3. Principal Component Analysis showing the first two components of the Euclidean distance between points which represent detector locations in relation to forest density measurements. Colors represent sub-habitat types: orange (open), green (interior), purple (canopy).

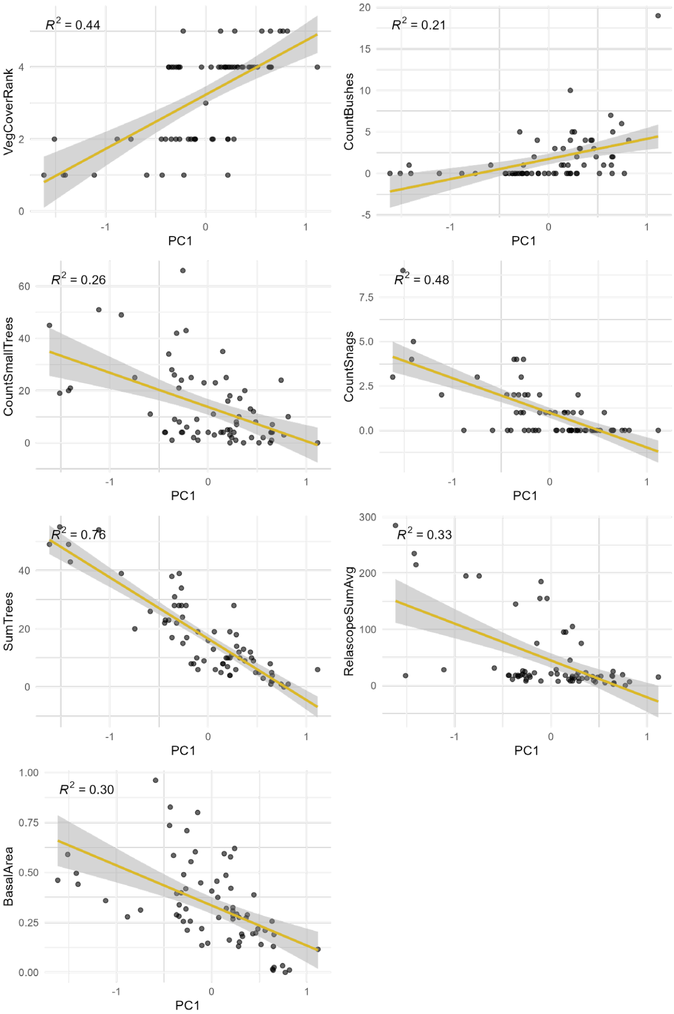

Figure S4. The relationship between each forest structure inventory measurement and the first principal component axis from the PCA in Figure S2. The yellow line represents the simple linear regression line and the gray area behind the line is the 95% confidence interval. The R^2 value for each regression is printed in the upper lefthand corner of each plot. VegCoverRank is an ordinal variable that is a combination of the variables ground cover and vegetation type, where 1 = none/very sparse, 2 = sparse, 3= intermediate, 4 = full, low field layer vegetation (*Vaccinium* shrubs and small ferns) and 5 = full, tall field layer vegetation (tall ferns, grasses, and forbs). Ground cover was estimated through visual inspection of the field layer vegetation in the 100m^2 plot surrounding each acoustic detector and assigned to one of the following categories: none/very sparse (0-20% cover), sparse (>20-50%), intermediate (>50 to 80%) and full (>80%). Basal area (BA) was calculated by measuring the diameter at breast height of all tree species with a DBH of > 5 cm (living and dead) to establish the area of each 100m^2 plot occupied by stems.

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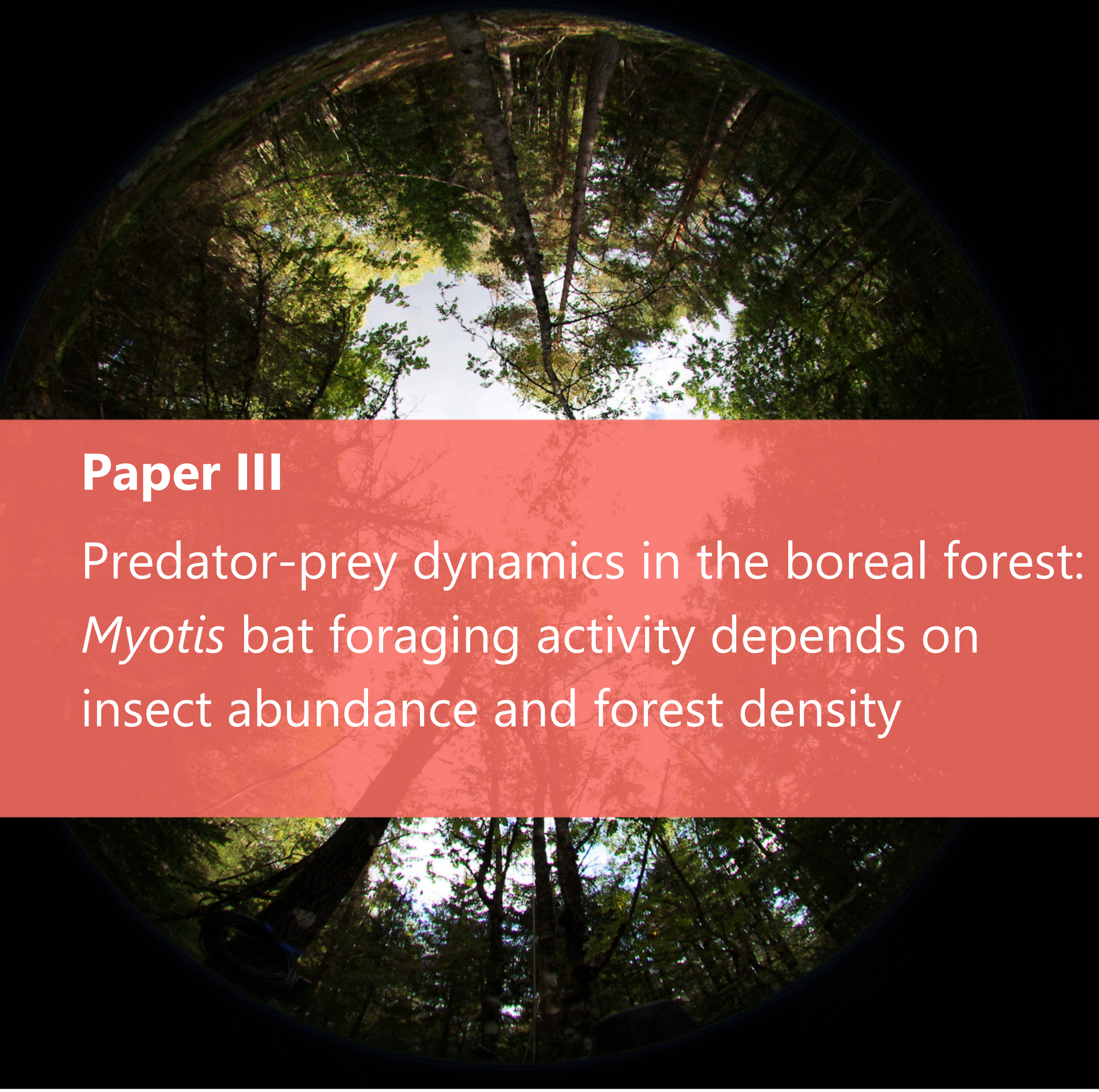

Paper III

Predator-prey dynamics in the boreal forest: *Myotis* bat foraging activity depends on insect abundance and forest density

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Abstract

1. All bat species found living at high latitudes rely on insects as a primary food source. *Myotis* species in the Nordic region tend to hunt for insects in forest habitats and use similar echolocation and have similar foraging strategies. Primary foraging habitats for bats hunting inside the forest should have abundant and accessible prey. If the habitat is too cluttered, bats may not be able to maneuver and forage effectively, even if prey is abundant. However, the relationship between bat foraging activity, structural density, and insect abundance is poorly understood in boreal forest systems.

2. This study aims to elucidate the nature of the relationship between feeding (recordings that include feeding buzzes) *versus* commuting activity of *Myotis* bats and the abundance of insects. We also investigate how forest density can alter these relationships.

3. Bat acoustic detectors were combined with insect camera traps at forest gaps in mixed boreal forest in southeast Norway for two consecutive summers in 2021 (12 sites) and 2022 (11 sites). We used canopy openness, quantified from hemispherical images of the canopy, as a measure of forest density. We successfully conducted concurrent monitoring of bat acoustic activity and insect abundance during 401 observation nights.

4. All 35,845 *Myotis* bat passes were manually identified and classified as feeding, commuting, or social behavior. The relationship between *Myotis* feeding activity and insect abundance exhibited an initial increase followed by a subsequent plateau, whereas commuting activity initially surged but quickly reverted to the same level observed at low insect abundances. Both feeding and commuting activity generally peaked at intermediate canopy openness, albeit with the peak in commuting activity occurring at a lower canopy openness.

5. When assessing the quality of bat foraging habitat based on bat acoustic activity, neglecting to differentiate between feeding and commuting behavior can lead to the loss of crucial information regarding how bats respond to their environment. Our findings suggest that mixed production forests with large areas of extremely high or low canopy openness may be poor quality foraging habitats for *Myotis* bats.

Introduction

In high-latitude regions of Europe, all bat species rely on insects as their primary food source (Dietz and Kiefer 2016). In the brief summer periods, bats at these latitudes must exploit their ephemeral prey and optimize foraging and accumulate the necessary fat reserves for reproduction and survival throughout the long winter months (Fjelldal et al. 2023; Vesterinen et al. 2016). The bats inhabiting northern latitudes face heightened vulnerability due to the shortened "white" nights during summer, limiting their hunting opportunities compared to their conspecifics at lower latitudes (Speakman et al. 2000; Jones and Rydell 1997; Boyles et al. 2016). Moreover, these northern populations contend with more challenging weather conditions, characterized by colder, wetter, and windier climates. Forests are crucial habitats for insectivorous bats in Fennoscandia, offering not only roosting sites and protection from predators, but also essential foraging opportunities (Dietz and Kiefer 2016; Kirkpatrick et al. 2017; Law, Park, and Lacki 2016).

Large-scale declines in insect numbers, which have been documented across taxonomic lineages, ecosystems, and geographic regions (Hallmann et al. 2017; Vogel 2017; Wagner 2020), also take place in forest ecosystems (Staab et al. 2023). This decline in insect numbers has led to concerns about ramifications for higher trophic levels, i.e., impacts on vertebrate insectivores as well as consequences for ecosystem function and services (Dirzo et al. 2014; Kehoe, Frago, and Sanders 2021). Recent field experiments have provided solid evidence that insectivorous bats suppress forest-defoliating insects through top-down trophic cascades (Beilke and O'Keefe 2023). However, bat-insect relationships are also influenced by bottom-up processes, such as forest management practices, which can lead to changes in the biomass of insect prey, as well as bat population density, bat species richness and activity (Carr, Weatherall, and Jones 2020; I. Hanski, Walls, and Vuorisalo 2000; Hanski 2008; Bouvet et al. 2016; Dodd et al. 2012; Froidevaux et al. 2021; 2022). Jones et al. (2009) provided compelling arguments for the notion that insectivorous bats can serve as indicators for ecosystem change. However, while bats primarily live in forests, and numerous studies suggest species-specific responses to forest management, there has been limited effort to explicitly utilize insectivorous bats as indicators to assess forest ecosystems (Russo et al. 2021).

Regardless of whether we adopt a top-down or bottom-up perspective, or opt for using bats as bioindicators, understanding bat-insect relationships requires synchronous measurements of bats and insects across pertinent biological, spatial, and temporal scales. For insectivorous bats that depend on echolocation for navigation and prey detection (Schnitzler and Kalko 2001), it is common to use passive acoustic monitoring to sample bat responses (Browning et al. 2017). Passive acoustic monitoring typically provides larger volumes of data that can be more easily standardized and can lead to more effective spatial and temporal coverage than other sampling methods (Sugai et al.

2019). As a non-invasive approach, this methods also avoid the observer effect, i.e., changes in bat behavior in response to the human presence (Vaughan, Jones, and Harris 1997). Recordings of bat echolocation can be identified to species level in many cases, but more often it is possible to group activity using sonotype-defined foraging guilds (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013; Frey-Ehrenbold et al. 2013). There are several approaches to qualifying and quantifying bat activity from acoustic recordings; measuring the number of bat recordings per unit of time is often used as a surrogate for abundance (Gibb et al. 2019). Some bat species exhibit a distinct terminal feeding buzz when capturing prey (Griffin, Webster, and Michael 1960), making it possible to distinguish feeding behavior from commuting and social behavior in acoustic recordings (Schnitzler and Kalko 2001).

While bat acoustic data are noninvasively sampled with high temporal resolution, insects are usually physically trapped and collected cumulatively with an array of methods (Leather and Watt 2005). These methods are useful to understand changes in insect communities and diversity, but the time-consuming and costly identification process limits the temporal and spatial scale of studies. Physical trapping also kills many insects (van Klink et al. 2022). Quantifying the abundance of insects can be valuable for assessing spatiotemporal variation in habitat quality, at least for generalist bat species that forage opportunistically on flying insects.

For habitat to be suitable for insectivorous bat foraging, the space should have high prey abundance as well as prey availability. Although bat species hunting in the interior of forests are adapted to capturing insects off and near vegetation (Schnitzler and Kalko 2001; Elizabeth Anderson and Racey 1991; Denzinger and Schnitzler 2013), overly cluttered spaces can exclude bats by making it difficult to maneuver (Müller et al. 2012; Brigham et al. 1997; Carr, Weatherall, and Jones 2020; Bender et al. 2021). Prior research has found that bat activity in forest ecosystems is more closely associated with habitat structure than with abundance of prey (Müller et al. 2012; Carr, Weatherall, and Jones 2020; Bender et al. 2021). However, studies on the combined influence of prey abundance and habitat structure on bat activity are scarce. In a notable exception, Froidevaux et al. (2021) discovered that the positive influence of moth abundance on *Barbastella barbastellus* was altered by vegetation clutter. However, the links between bat foraging activity, forest density, and insect abundance are still poorly understood and requires further exploration.

Within the Fennoscandian region, *Myotis* bat species demonstrate a distinct affiliation with forest habitats (Ekman and de Jong 1996; Vasko et al. 2020; Wermundsen and Siivonen 2008; Kotila et al. 2023); **Paper IV**), prey on a range of nocturnal flying insects (Vesterinen et al. 2018; **Paper IV**), and produce a terminal feeding buzz when they capture, or nearly capture, insects (Ratcliffe et al. 2013; Russ 2021). These terminal feeding buzzes can be identified from acoustic recordings. The echolocation of *Myotis* species tend to have short detection distances, under approximately 15 m (Dietz and Kiefer 2016). This makes *Myotis* in the Fennoscandian forests uniquely suitable taxa for research combined with insect monitoring sampling forest habitats at small spatial scales.

The 3 *Myotis* species associated with our study include the Daubenton's bat, *M. daubentonii,* whiskered bat, *M. mystacinus*, and the Brandt's bat, *M. brandtii.* These species are challenging to differentiate from acoustics alone, and are therefore often grouped within a single sonotype (Russ 2021; Froidevaux et al. 2016). *M. daubentonii* are specialized to trawl for prey over freshwater but are also associated with a broad range of habitats, including forests (Dietz and Kiefer 2016). *M. brandtii* and *M. mystacinus* are both considered forest specialists in Fennoscandia (Wermundsen and Siivonen 2008; Vasko et al. 2020; Kotila et al. 2023). However, there is limited knowledge on what kinds of species-specific and range specific differences in habitat use there may be for *M. brandtii* and *M. mystacinus* because they are part of a cryptic group of species (Budinski and López-Baucells 2023). *M. brandtii* and *M. mystacinus* can have differences in foraging ecology (Berge 2007; **Paper IV**), but as they are both closely associated with forest habitats, they likely make up the majority of the *Myotis* activity recorded at forest habitats sampled in this study. All *Myotis* species found in our study area can be defined in the short range echolocators (SRE) foraging guild, which includes bat species that are well adapted to aerial hawking and gleaning prey near vegetation (Froidevaux et al. 2016; Frey-Ehrenbold et al. 2013)

This study aims to understand whether and how the feeding and commuting activity of *Myotis* bats in forest gaps correlates with insect abundance, as quantified by camera trapping (Ruczyński et al. 2020; Choiński et al. 2023) Additionally, we investigate how forest density may modulate this relationship. Our study addressed the following questions:

1. Is the feeding activity of *Myotis* bats in forest gaps related to insect abundance?
2. If such a correlation exists:
    a. What characterizes the nature of the relationship between bat feeding activity and insect abundance?
    b. Does the relationship between bat feeding activity and insect abundance depend on forest density?
    c. What characterizes the nature of the relationship between insect abundance and forest density?
    d. Is there a difference between the feeding and commuting activity of *Myotis* bats with respect to how these behaviors relate to the abundance of insects and forest density?

Methods

Study area and study sites

The study sites were distributed within the municipalities of Nordre Follo, Ås, Vestby, and Frogn in the Southeastern geographical region of Norway, within Akershus county (Figure 1). This area is located within the hemiboreal zone with a relatively mild climate.

The 12 study sites (11 in 2022; Figure 1) included were situated in mixed boreal forests of similar age, productivity, and height. The dominating tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.), but also a mix of mainly boreal deciduous tree species (https://kilden.nibio.no/). All sites were in forest managed for timber production; 10 sites on privately owned land and 2 sites on land owned by the Norwegian University of Life Sciences. One of the sites was not monitored in 2022 because the landowners did not grant permission to deploy equipment that year.

The study sites were selected to be representative of the mixed production forests in the region that are approaching harvest age. To extract information about the forests in the study area, SR16 and SR16beta Norwegian forest maps (Astrup et al. 2019) and national area resource maps (AR5) of Norway (Ahlstrøm, Bjørkelo, and Fadnes 2019) were processed in the mapping software QGIS (QGIS.org 2021). Sites were then selected along a forest density gradient calculated from basal area and crown cover, based on (Eid 2001). All sites were located within an area of 40 km^2, at least 50 meters from the coastline or water bodies, and at least 50 meters from the nearest external forest edge. Each site was positioned at a distance ranging from 1 to 17 kilometers from its nearest neighboring site. Further information about site selection is described in **Paper II**.

Bat acoustic monitoring

Bat acoustic monitoring took place from May 14th – September 14th in 2021 at 12 sites, and from May 5th – September 20th at 11 of the sites monitored in 2021 (141 nights sampled across both seasons). Wildlife Acoustics Song-Meter4-BATFS detectors (hereafter detectors) combined with either SMM-U2 or SMM-U1 microphones (hereafter U2 or U1 microphones) were deployed in forest gaps at each site (Figure 2a). Detectors were affixed to wooden poles approximately 1.5 m high, with the microphones positioned at the top of the wooden pole, away from vegetation clutter. The mean number of detector nights per detector location for 2021 was 102.4 nights (SD = 17.1, min = 74, max = 123 nights) and 124 nights in 2022 (SD = 10.5, min = 103, max = 140 nights).

Bat acoustic data included in this paper are a subset of data collected and analyzed from "open sub-habitats" in **Paper II**. A detailed description of acoustic detector settings and a description of the deployment is provided in the methods of **Paper II**.

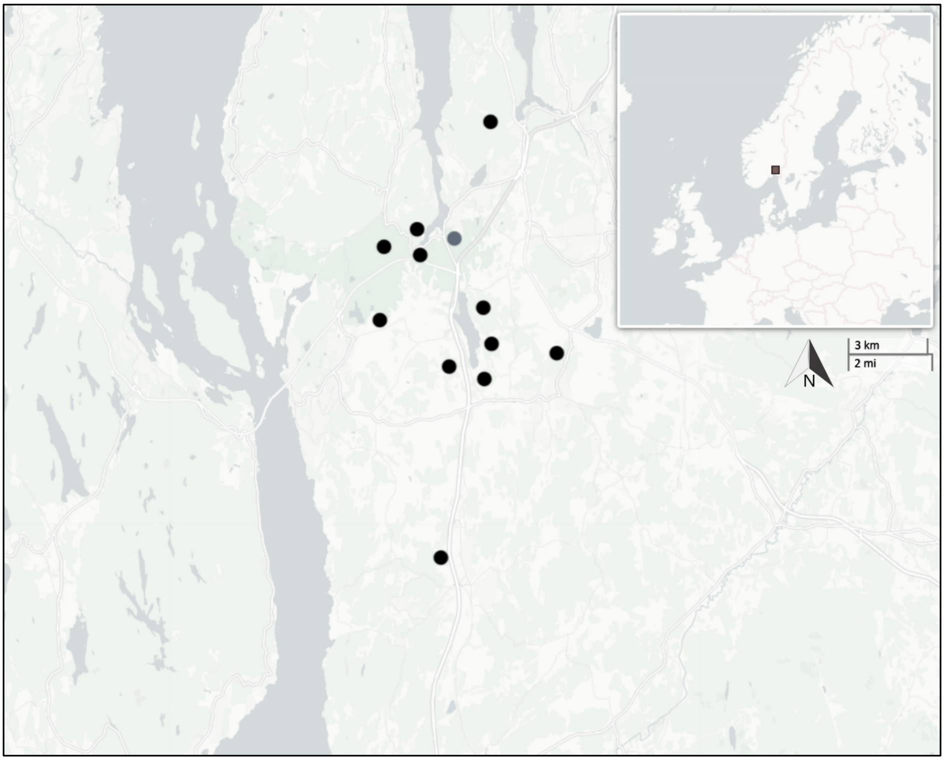

Figure 1. Map of the study area in southeast Norway and the 12 study sites for acoustic sampling of bat foraging activity and monitoring of insect abundance with camera traps. Internal map of the study area, where the large water body to the west is the Oslo fjord. The site marked with a light grey symbol was only sampled in 2021, the other sites were sampled in 2021 and 2022. The map in the upper right corner shows where the study area was in relation to northern Europe. Light green areas are forest; water is represented by gray areas. Map layers: Leaflet| ©OpenStreetMap contributors ©CARTO

Insect camera trapping

To assess site-specific insect abundance, we deployed insect camera traps (Figure 2b) at each site, placed near (3-15 m) bat acoustic detectors. In 2021, the camera traps were deployed between 23rd - 25th June and retrieved between August 30th and September 9th. In 2022, the camera traps were deployed in between June 7th – 9th and retrieved between July 26th – 27th. There were two weeks in late June 2022 without recordings.

Following the method outlined in (Ruczyński et al. 2020), we utilized Ricoh WG-6 Digital cameras (Model R02050 2019) placed in specially designed waterproof boxes with a transparent glass plate in front of the lens, facing the sky atop tripods at approximately 80 cm from the ground. Connected to external motorcycle gel batteries (12V, 15Ah-21Ah) housed in plastic car battery boxes, the cameras were set to flash every 10 minutes, 24 hours a day. Weekly maintenance involved battery checks, verifying camera settings, lens and lid cleaning, memory card retrieval, and ensuring secure equipment placement.

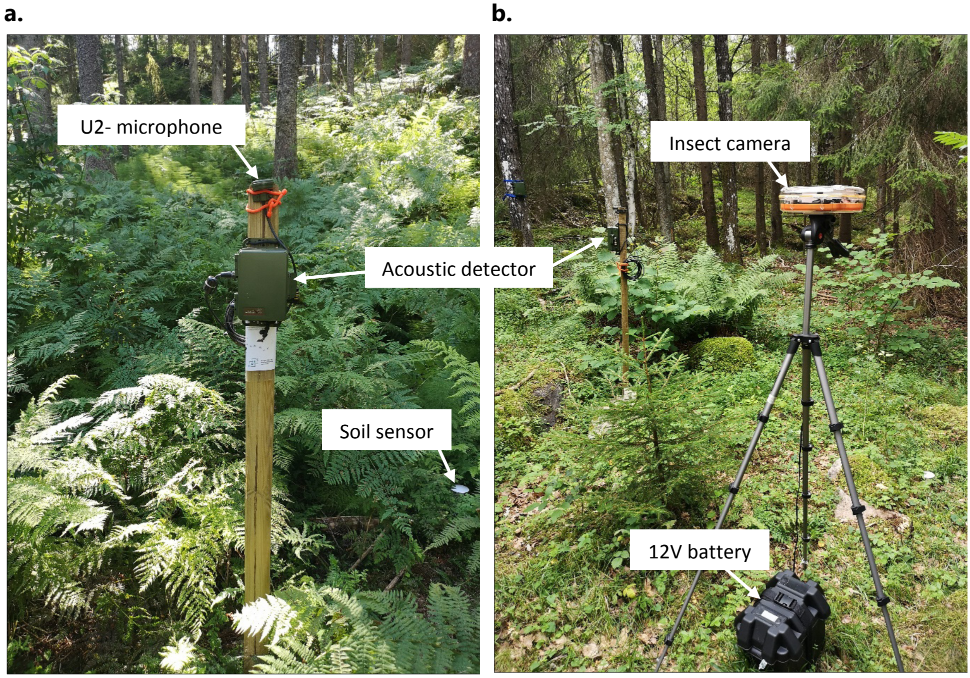

Figure 2. Setup of monitoring equipment at each site: **(a.)** An acoustic detector that recorded bat acoustic activity, a soil sensor that logged above and below-ground temperature and soil moisture, and **(b.)** a camera trap directed towards the sky to take images of flying insects. All sites were situated in a gap in the forest. Photos: Mathilde Klokkersveen Thomle.

Hemisphere images

At each site, we collected hemisphere images (Figure 3) after full foliage development to quantify canopy openness, serving as a measure of forest openness. In 2021, images were taken using a Nikon COOLPIX 4500 camera during the period 23rd – 25th June. In 2022, hemisphere images were obtained in early September using a PENTAX K-5II DSLR camera with a 4.5 mm f/2.8 EX DC HSM circular fisheye lens. Due to equipment availability, the photos were taken later in the season (September 1st – 9th) in 2022, but before autumn yellowing. The camera was mounted on a 130 cm high leveled tripod, positioned skyward, and photos were taken in proximity to bat acoustic detectors and insect camera traps at each site under consistent weather conditions. We prioritized overcast weather for higher photo quality, refrained from photography during rain, and minimized exposure to bright sunlight.

Environmental conditions

One soil sensor TMS-4 TOMST® datalogger (Wild et al. 2019; Figure 2a) was deployed at each site to monitor soil moisture and air temperature 15 cm above the soil surface. The loggers were deployed within 10 meters from the bat detector and programmed to record temperature and soil moisture every 10 min throughout the study period.

Figure 3. Hemisphere images of forest canopy to quantify forest openness. *Left:* a site with high canopy openness (value = 0.42). *Right:* a site with low canopy openness (value = 0.17).

Acoustic analysis

Raw acoustic data was recorded in 8 bit .wav files and then processed using Kaleidoscope Pro 5.6.3 with Bats of Europe Classifier 5.2.1 (Wildlife Acoustics Inc., Maynard, MA, USA). We define a bat pass as a 5-second triggered recording which included at least two consecutive pulses (Fenton, Jacobson, and Stone 1973). We standardized .wav files to 5-second recordings and filtered for noise using the following parameters: 8 – 120 kHz frequency range; 2 – 500 ms max length of detected pulses; 500 ms maximum inter-syllable gap, 2 pulses minimum. Each 5-second file was then processed using the automatic identification function Bats of Europe Classifier v.5.2.1 Kaleidoscope Pro, Wildlife Acoustics to identify bat passes to species and filter noise files.

We recorded 20,750 and 18,510 bat passes in detectors deployed in open forest habitats, hereafter "gaps"; in 2021 and 2022, respectively. Recordings that were identified as noise by the automatic classifier were removed (n = 37 files). Initially, we were interested in all bat species that are associated with flying in the interior forests: *Myotis* species, *Plecotus* species, or *Barbastella barbabstellus.* All recordings that the automatic classifier identified as belonging to these taxa were manually identified by one analyst (RAM, n = 39,982 files). A subset of non-target taxa was also manually identified: one bat pass per taxa detected per detector location per night, and 2500 NoID's (recordings the classifier identified as an unknown bat) for all open detectors combined, to account for uncertainties in the automatic classifier (n = 7,942 files). All *Myotis* activity was grouped into a single sonotype because of similarities in echolocation across species within this genus (Russ 2021; Middleton 2020).

Behavior (commuting, feeding and social) activity was also defined during the manual acoustic analysis (Middleton, Froud, and French 2014). Commuting passes only included typical echolocation calls. Feeding passes included at least one terminal feeding buzz which was preceded by commuting and approach phases. Social passes were those that included any social activity, but this primarily included social activity alongside normal echolocation. Recordings that included activity of multiple bat taxa were treated as separate bat passes.

Further information on the methods of the manual acoustic analysis is provided in the methods and supplementary materials in **Paper II**.

Insect camera image annotation and preparation

We collected 1,162,627 images captured by insect camera traps (2021: n = 941,434; 2022: n = 221,193). Subsequently, each image file received a unique identifier and was further organized according to date, time, and location using R Studio. Images taken between one hour before sunset ("nocturnal images") and one hour after sunrise were selected for annotation.

Two analysts in 2021 (RAM and VS) and one analyst in 2022 (MKT) manually annotated all nocturnal images (2021: n=17,046, 2022: n = 4755) using the VGG Image Annotator (Dutta and Zisserman 2019). In the annotation process, potential insects were circled (Figure 4) and categorized based on the certainty of being an insect. Objects with 40-60% certainty were labeled 'Uncertain,' while those with >60% certainty were labeled 'Certain'. Objects with <40% certainty were disregarded. The quality of the image was also annotated; images for which water droplets, condensation or glare obstructed more than 30% of the frame were considered "bad quality" and not included in further analyses.

Figure 4. Example of an image including flying nocturnal insects (circled in pink) captured by a camera trap.

Calculating canopy openness

Preparations of hemisphere images (Figure 3) for analysis were executed by analyst Jenna Fairchild. This process involved the meticulous removal of disruptive elements, as well as the adjustment of lighting to address areas where reflections created a misleading impression of open sky. Subsequently, the refined images were subjected to analysis in RStudio, employing the R package "Hemiphot" (ter Steege 2018). This analytical approach aimed to derive a comprehensive measure of canopy openness, thus a measure of forest openness.

Environmental data

Soil moisture and above ground (+15 cm) temperature data were obtained from TOMST®-TSM4 loggers at each site. We used the Lolly software v1.25 to download the data from the loggers. We extracted a subset of the soil moisture and temperature data that included only measures from 18:00 in the evening to 6:00 in the morning and calculated mean soil moisture and temperature per site and night. Average daily precipitation (mm per day) was collected for each site for the entire insect monitoring period for both years from the public database SeNorge.no. Photoperiod was calculated using the R package "suncalc" (Thieurmel and Elmarhraoui 2022) for a single location, approximately in the center of the study area (59°45'29.2"N, 10°45'36.0"E).

Statistical analyses

All exploratory and statistical analyses were carried out in the R software v.4.3.2 (R Core Team 2023). Our analyses included 401 nights (293 in 2021 and 108 in 2022) when camera traps and detectors were operating in parallel at the same site locations. Data on insect abundance were aggregated per night for each site and year. Bat acoustic data was aggregated to sonotype and behavior per site per night (day centered at midnight). There were only 459 *P. auritus* bat passes (6% of bat passes recorded in this period) and so we chose to only focus on *Myotis* activity (7,347 bat passes). There were only 33 social *Myotis* passes included in this dataset, so we excluded these observations as well.

Due to the loss of power supply, cameras sometimes failed before a full observation night was completed. To account for unequal sampling, we created an index of insect abundance: number of insects per night/number of photos. Original insect index values ranged from 0 to 4.53, but only four values exceeded 2. These four outliers were replaced with the value 2 to avoid statistical problems. To avoid statistical problems, we excluded sites with less than 10 observation nights/year (2 sites in 2021 and 4 sites in 2022). The remaining 364 observation nights were used for further analyses.

To define the nature of the relationship between *Myotis* feeding activity and insect abundance, we fitted Generalized Additive Mixed Models (GAMM; Wood 2017). GAMMs allow any shape of relationship between the response variable and explanatory variables. The response variable was feeding activity, i.e., number of bat passes with at least one complete feeding buzz. Explanatory smooth terms in the full (most complex model) were insect abundance, canopy openness, air temperature, rainfall, soil moisture, Julian night, daylength, as well as the interaction between insect abundance and each of the other explanatory variables, to assess if canopy openness or any of the other environmental variables modified the bat-insect relationship. Numerical explanatory variables were standardized before fitting statistical models. A Gaussian process smooth was applied to Julian night and daylength to account for temporal autocorrelation. Year and site were included as random effects. Because the response variable was zero-inflated (59% zeros), we fitted two candidate full models; a negative binomial GAMM and a zero-inflated Poisson GAMM. Model validation revealed that the negative binomial GAMM could handle the zero-inflation, provided the best fit to the data, and had the lowest AIC value. Thus, we proceeded with the negative binomial GAMM. Model reduction was carried out by backwards elimination using p-values; that is by sequentially dropping the single fixed effects term with the highest non-significant p-value ($p>0.05$) from the model and re-fitting, until all terms were significant. When comparing candidate models, smoothing parameters were estimated with maximum likelihood (ML) estimation. After arriving at a model for which all terms were significant ($p<0.05$), we refitted this final model with restricted maximum likelihood (REML) estimation. Model validation was carried out by checking k-index values and inspecting diagnostic plots: QQ plots, residuals versus fitted values, frequency distribution of residuals and response variable versus fitted values.

To assess if *Myotis* feeding and commuting activity responded differently to insect abundance (and canopy openness), we used an input dataset containing bat passes of both *Myotis* feeding and commuting passes and expanded the GAMM model for explaining feeding activity (Table 1). We used the model described in Table 1 and added behavior (with two levels: commuting and feeding) as explanatory variable, as well as allowing the relationship between bat pass and each of the explanatory terms to differ between commuting and feeding behavior (adding a by = behavior term) (Table 2).

Results

We found evidence of a positive influence of insect abundance on bat feeding activity in forest gaps, but the shape of the relationship depended on canopy openness (Figure 5a, Figure 5b, Figure S1, Table 1). At intermediate canopy openness, there was a marked increase in *Myotis* feeding activity up to insect abundance (index value) of 0.30-0.50, and then the relationship levelled out or decreased slightly before plateauing (Figure 5c, Figure 7a, Figure S1). At high canopy openness there was a similar relationship between feeding activity and insect abundance, but the magnitude of feeding activity was generally much lower at high canopy openness (Figure 5a, Figure S1). The initial increase in feeding activity with increasing insect abundance was also apparent when including only insect abundance as explanatory variable (Figure S2a, Table S2a).

Canopy openness influenced *Myotis* feeding activity in a non-linear fashion. Feeding activity increased with canopy openness to peak at intermediate openness, followed by a subsequent decline as canopy openness continued to increase (Figure 5b, Figure 7b, Figure S2b, Table S2b). There was much higher feeding activity at intermediate canopy openness than at high openness, whereas at low openness, there was hardly any feeding activity at all (Figure 5a,Figure 7b, Figure S1).

Myotis feeding activity was highest at low soil moisture, markedly reduced at intermediate soil moisture, and negligible at high soil moisture (Figure 5c). Notably, site-level soil moisture was highly influenced by rainfall. We noticed that there were marked peaks in soil moisture on data outputs from TMS4-loggers in connection with rainfall (Katrine Eldegard, *pers. obs.*) but we did not collect site-level data on rainfall to test this. However, there was a weak positive correlation between soil moisture and rainfall (mm precipitation) extracted from senorge.no (Pearson's product-moment correlation: r = 0.15, df = 352, p=0.0042).

Myotis feeding activity was higher at longer daylengths, which in our study was in late June (around mid-summer), and was lower at intermediate daylengths (i.e., late July) and lowest at short daylengths (i.e., early August) (Figure 5b). Julian night was excluded from the model in Table 1 in the backward elimination but is inherently related to daylength. There was a strong relationship between Julian night and insect abundance; insect abundance increased from early June to peak around mid-summer and subsequently declined steeply until early August before levelling out (Figure S3, Table S3). Temperature was also dropped from the model, but there was a positive relationship between temperature and insect abundance (Figure S3, Table S3).

We found that there was a positive correlation between total *Myotis* activity (i.e., the sum of feeding, commuting, and social bat passes) and feeding activity (r = 0.75), but the correlation between total and commuting activity was stronger (r = 0.99, Figure S4). By expanding the model in Table 1 to also include behavior (Table 2), we were able to assess whether there was a difference in feeding versus commuting activity with respect to response to insect abundance and canopy openness. Both feeding and commuting activity increased with insect abundance up to insect abundance values approximately 0.25 (Figure 6, Figure 7). Thereafter, feeding activity remained at this level or even continued to increase, while commuting activity dropped back to the same level for low insect abundance (Figure 6, Figure 7a). Feeding activity peaked at intermediate canopy openness, declined at high openness, and was negligible at low openness (Figure 7b). Commuting activity also peaked at intermediate canopy openness, but at somewhat lower openness than the peak in feeding activity (Figure 7b).

Table 1. Estimated smooth terms and test statistics for the final negative binomial GAMM explaining the relationship between *Myotis* bat feeding activity and insect abundance. The response variable was the number of bat passes per night that contained at least one feeding buzz. Explanatory variables in the full model were insect abundance, canopy openness, daylength, soil moisture, Julian night, temperature, and rainfall as well as the interaction between insect abundance and each of the other explanatory variables. Site and year were included as random effects in the full model, but year was dropped (p = 0.21) after all the other non-significant (p>0.05) terms had been dropped in a stepwise backward elimination. Deviance explained = 64.4%, n = 354. See Figure 5a-c and Figure S1 for visualizations.

	Estimate	**SE**	**z**	**p**
intercept	-0.3798	0.6678	-0.569	0.72
	edf	**Ref.df**	**χ^2**	**p**
s(insect abundance)	1.00	1.00	1.61	0.205
s(canopy openness)	2.54	2.84	6.41	0.046
s(daylength)	1.00	1.00	4.24	0.040
s(soil moisture)	6.98	8.05	64.58	<0.001
s(insect abundance, canopy openness)	4.26	27.00	11.32	0.018
s(Site)	8.95	10.00	127.75	<0.001

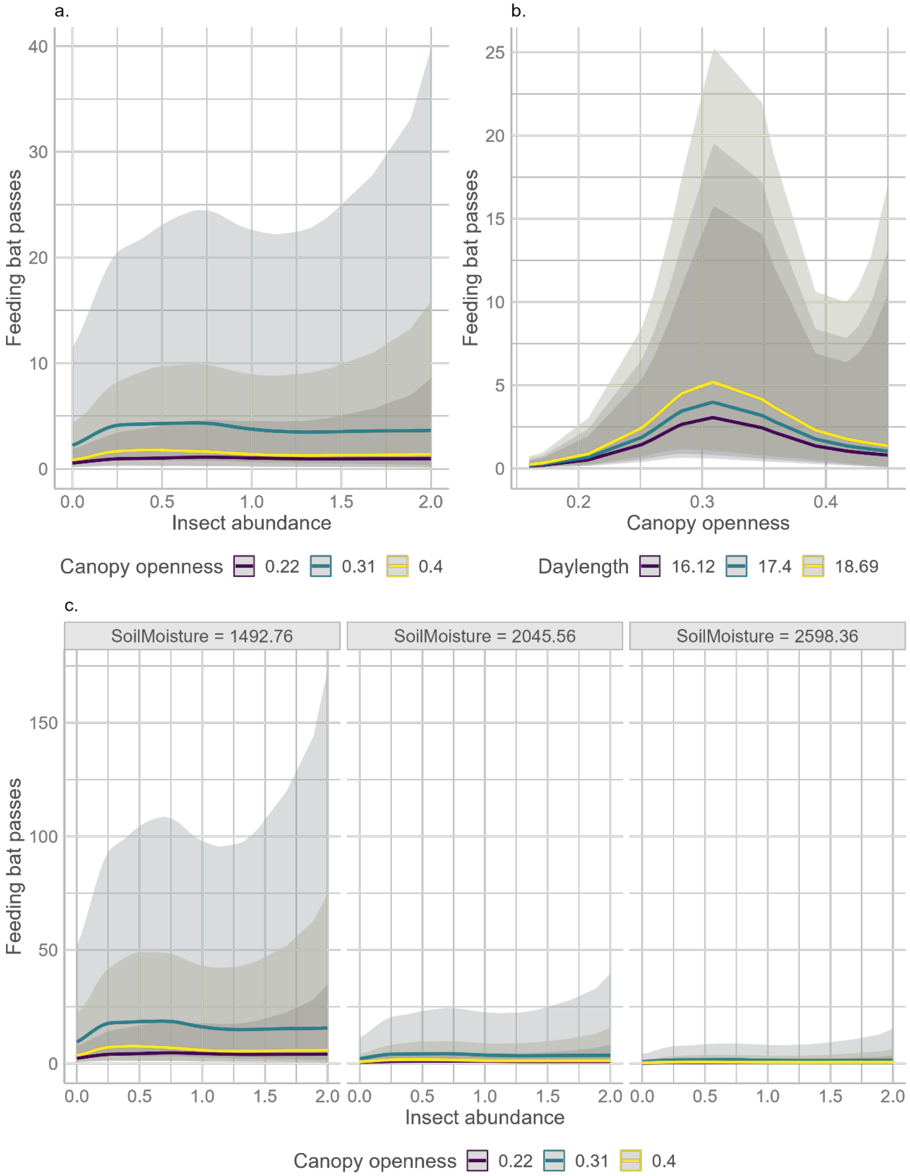

Figure 5. (a.) Estimated feeding activity of *Myotis* bats, in response to insect abundance for three different levels of canopy openness (low: 0.22, medium: 0.31, high: 0.4). (b.) Estimated feeding activity of *Myotis* bats, in response to canopy openness for three different values of daylength (hours). In our study area daylengt 16.1 is around midsummer, 17.4 is late July and 18.7 is early August. (c.) Estimated feeding activity of *Myotis* bats, in response to insect abundance and canopy openness for three different levels of soil moisture (from left to right: low, medium, high). Estimated lines and associated 95% confidence limits from the GAMM in Table 1. See Figure S1 for a 3D-graph based on the same model. Note that insect abundance was <0.50 for most (85%) of the nights when *Myotis* feeding activity as recorded.

Table 2. Estimated parameters, smooth terms and test statistics for a GAMM explaining the relationship between *Myotis* bat feeding and commuting activity, insect abundance, and modifying environmental variables. The response variable 'bat pass' was the number of bat passes per night containing at least one feeding buzz or commuting activity. We used the model described in Table 1 as starting point and added behavior (with two levels: commuting, feeding) as explanatory variable, as well as allowing the relationship between bat pass and each of the explanatory terms to differ between each behavior. Site was included as random effect. Deviance explained = 6.2%, n = 708. See Figure 6 and Figure 7 for visualizations.

	Estimate	**SE**	**z**	**p**
intercept	1.6423	0.643	2.554	0.0106
Behavior:Feeding	-1.9494	0.1191	-16.369	<0.001
	edf	**Ref.df**	**χ^2**	**p**
s(insect abundance):behaviorCommuting	1.004	1.005	3.57	0.05956
s(insect abundance):behaviorFeeding	1.00	1.00	2.432	0.11896
s(canopy openness):behaviorCommuting	3.221	3.776	11.547	0.01739
s(canopy openness):behaviorFeeding	3.009	3.53	11.337	0.01589
s(daylength):behaviorCommuting	2.079	2.637	2.996	0.3564
s(day_ daylength):behaviorFeeding	1.00	1.00	5.11	0.0238
s(soil moisture):behaviorCommuting	5.172	6.293	53.71	<0.001
s(soil moisture):behaviorFeeding	7.157	8.182	88.549	<0.001
s(insect abundance, canopy open):behaviorC	7.099	27	22.829	0.00117
s(insect abundance, canopy open):behaviorF	5.981	27	16.406	0.00264
s(Site)	9.548	10	338.928	<0.001

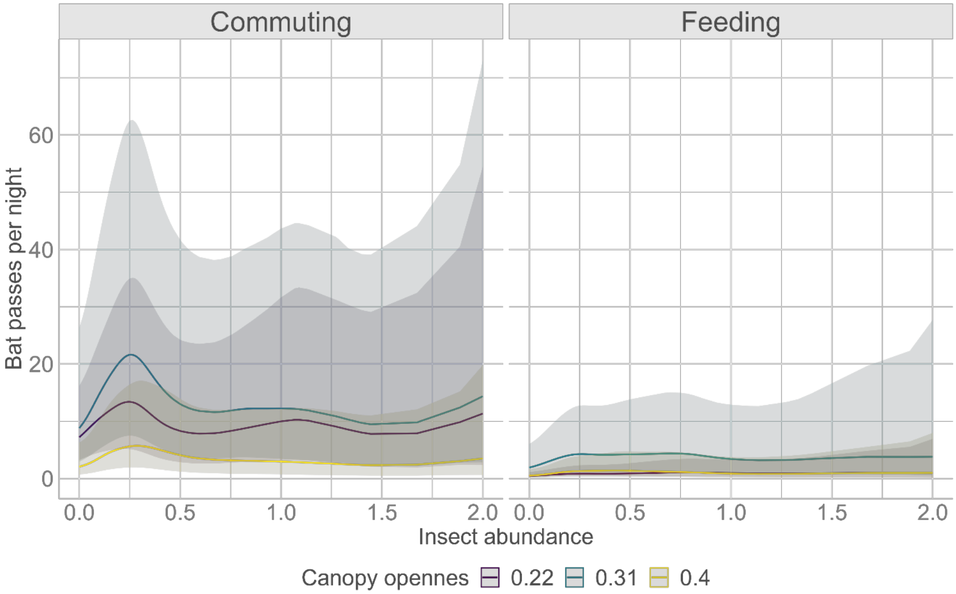

Figure 6. Estimated number of commuting and feeding bat passes of *Myotis* activity in forest gaps, in response to insect abundance at different levels of canopy openness. Estimated lines and associated 95% confidence limits are based on the GAMM in Table 2.

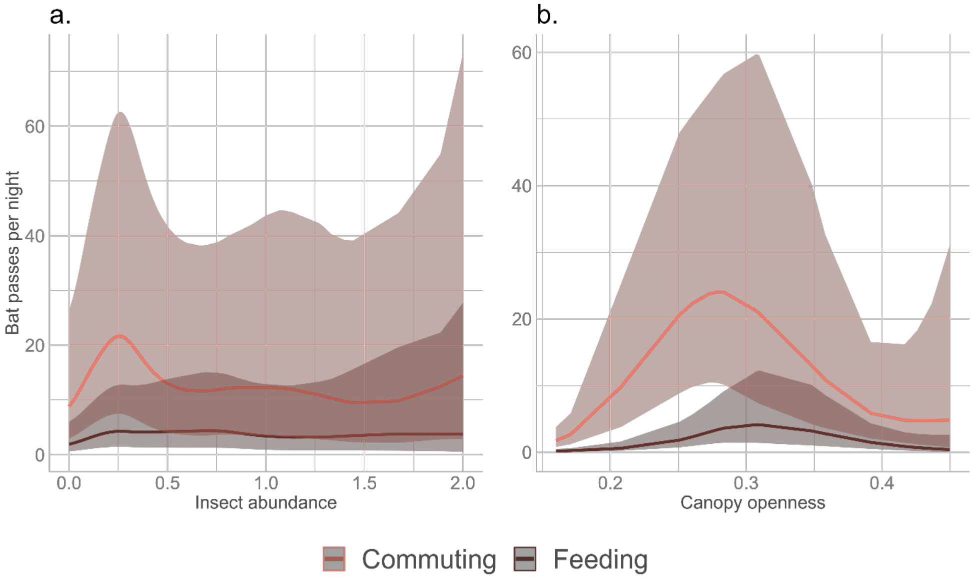

Figure 7. Estimated number of commuting and feeding bat passes of *Myotis* activity in forest gaps, in response to (a) insect abundance and (b) canopy openness. Estimated lines and associated 95% confidence limits are based on the GAMM in Table 2.

Discussion

We have identified trends in the interactive influences of insect abundance and forest openness on *Myotis* bat feeding activity in forest gaps, demonstrated by combining passive acoustic monitoring of bats with non-lethal insect camera trapping and hemispherical images of canopy openness. We discovered that the relationship between *Myotis* feeding activity and insect abundance exhibited an initial increase followed by a subsequent plateau. In contrast, commuting activity initially surged but quickly reverted to the same level observed at low insect abundances. Feeding activity reached its peak at intermediate canopy openness, while remaining nearly negligible at low canopy openness. Commuting activity also reached its peak at intermediate canopy openness. However, in contrast to feeding activity, the peak of commuting activity was observed at a lower level of canopy openness. Insects were present across the range of observed canopy openness but was highest at intermediate openness. By focusing on bats that have a short detectability distance and manually identifying their feeding activity, we provide a fine scale lens into interactions between *Myotis* bats as insectivore predators in the boreal forest ecosystem.

Feeding activity of *Myotis* bats was positively related to insect abundance but depended on canopy openness. The highest feeding activity was recorded for the combination of high insect abundance and intermediate canopy openness. At low openness, feeding activity was negligible. Previous studies have found a positive relationship between insect abundance and bat foraging activity, with forest habitat structure improving the explanatory power of models (Brigham et al. 1997; Carr, Weatherall, and Jones 2020; Bender et al. 2021; Froidevaux et al. 2021; Dodd et al. 2012). It is well understood that denser understory likely results in decreased prey availability because highly cluttered vegetation produces more complex echoes and poses challenges for echolocating bats while hunting. Brigham et al. (1997) experimentally increased clutter in the forest without reducing insect abundance and found that *Myotis* bats were restricted by the presence of artificial clutter, regardless of prey abundance. Kusch et al. (2004) reported a strong positive correlation between European *Myotis* activity with more open canopy cover in forests, similar to our own findings, though they found no important differences in the proportion of feeding activity across habitats sampled. Froidevaux et al. (2021) discovered a positive influence of moth abundance on *Barbastella barbastellus* activity that was altered by vegetation clutter. Bender et al. (2021) found that "*bat site-occupancy was better explained by a combination of vegetation characteristics and insect abundance than either separately*" but found no indication of an interaction between insect abundance and vegetation structure. To our knowledge, except from Froidevaux et al. (2021), other previous studies have only explored additive effects of forest vegetation structure's influence on bat foraging and insect abundance. Additionally, because we used a relatively novel combination of methods to study these interactions, it is challenging to directly compare our findings to previous studies. Furthermore, studies that explicitly focus on foraging activity of *Myotis* species in the Fennoscandian boreal forest system are rare (Ekman and de Jong 1996; J. de Jong 1995; Kotila et al. 2023; Vasko et al. 2020; **Paper IV**). In **Paper IV**, we found that adult female *Myotis brandtii* selected foraging habitat in forests of low canopy density, while we found the opposite effect in *M. mystacinus*. There are likely species-specific differences in the effect of canopy openness that are not possible to explore in the context of this study. However, our finding that *Myotis* feeding and community activity declined at high values canopy openness is in line with Wood et al. (2017) who found that forest specialist bat species activity decreased severely with decreasing wood pastures tree density in southern Sweden.

Using bat activity as a surrogate for bat abundance is challenging because there is no straightforward metrics to use as a connection between the number of recordings from passive acoustic monitoring and animal density (Gibb et al. 2019). Some studies choose to use bat occupancy rather than abundance to quantify bat acoustic activity, to account for these issues (Bender et al. 2021; Yates and Muzika 2006; Amelon 2007; Gorresen et al. 2008; Burns, Loeb, and Bridges 2019). Heightened activity indices could represent increased effort from one or a small number of individuals, reflecting suboptimal foraging conditions, or many individuals utilizing the foraging habitat, signifying favorable foraging conditions. This precludes a deeper understanding of the predator-prey relationship, for example by adopting the functional response framework (Holling 1959) to assess if the bats' response to increased insect abundance follows a type 1 (linear), type 2 (saturating), or type 3 (sigmoidal) response. However, the pattern in the relationship between feeding activity and insect abundance found in our study bore the closest resemblance to a type 2 functional response (Figure 7). Noisy/uncertain estimates of both bat abundance and insect abundance probably explains why bat-insect relationships *per se* have generally been found to be rather weak (Brigham et al. 1997; Carr, Weatherall, and Jones 2020; Bender et al. 2021; Froidevaux et al. 2016; 2021; Johnny de Jong et al. 2021) (Bringham et al. 1997, Carr et al. 2020, Bender et al. 2021, Froidevaux et al. 2021, de Jong et al. 2021).

The relationship between commuting activity and insect abundance, as well as canopy openness, differed from the association observed with feeding activity. Commuting activity initially surged in response to increasing insect abundance but quickly reverted to the same level observed at low insect abundances. Conversely, feeding activity remained at a high level as insect abundance increased. Commuting activity also peaked at intermediate canopy openness, albeit with the peak in commuting activity occurring at a lower canopy openness than feeding activity. It is common practice in research studying bat foraging activity from acoustic data to not quantify bat passes with feeding buzzes, but rather use total activity as a surrogate for feeding activity, based on an assumption or formal test showing that total and feeding activity are highly correlated (Jung et al. 2012; Vaughan, Jones, and Harris 1997; Plank, Fiedler, and Reiter 2012; Froidevaux et al. 2014). However, studies that do explore bat acoustic activity by treating bat passes with feeding buzzes separately often find differences in bat feeding and commuting activity (Kusch et al. 2004; Scott et al. 2010; Boonchuay and Bumrungsri 2022; Russo and Jones 2003; McKay et al. 2024). Although we found a strong positive relationship between total activity and feeding activity, if we had used total activity (r = 0.99 with commuting activity in this study) as a substitute for feeding activity, we would have overlooked crucial information about how bats respond to canopy openness when hunting. We suggest identifying feeding activity by detecting feeding buzzes, manually or using automatic tools, to account for differences in behavior when the objective is to study differences in bat foraging habitat use, at least for *Myotis* bats in similar systems.

In our study we have grouped all *Myotis* activity under a single sonotype instead of studying species specific acoustic activity. The *Myotis* species documented in our study area include *M. daubentonii*, *M. mystacinus* and *M. mystacinus* (Artsdatabanken.no). The foraging behavior of these species within the forest are relatively similar, including aerial hawking and gleaning insect prey from vegetation (Norberg, Rayner, and Lighthill 1997). However, *M. daubentonii* is more specialized toward trawling insects from near water surfaces. Mist net surveys that took place in the summer of 2021 in our study area as part of parallel research objectives (**Paper II**) found a high proportion of *M. brandtii* and *M. mystacinus* at sites where bat capture surveys were successful. Based on the foraging behavior of the *Myotis* species in our study area and the results of the mist net surveys, we are confident that the *Myotis* activity recorded is predominantly from *M. brandtii* and *M. mystacinus*. Although these two species are similar in morphology and their populations often overlap, there are likely species-specific differences in habitat use and diet (Berge 2007; Budinski and López-Baucells 2023; **Paper IV**) that we cannot account for in the scope of this study.

Insects are of enormous ecological importance, however, tools for quantifying insect abundance often depend on killing or disturbing the study taxa. There is a wide array of methods used for describing differences in insect abundance and many options for which spatiotemporal scales relate insects to their environment (Montgomery et al. 2021; van Klink et al. 2022). Montgomery et al. (2021) highlights multiple recent studies that have used camera trapping methods to measure insect abundance and highlights the potential such techniques have for being further developed and implemented as a non-invasive alternative to trapping insects. A few studies have shown that the method we have used can effectively measure nocturnal flying insects' occurrence and/or abundance (Ruczyński et al. 2020; Choiński et al. 2023; McKay et al. 2024). However, sampling nocturnal insects with the camera trapping method used in these studies is dependent on a stable power supply as well as weather conditions with limited humidity or precipitation that would obstruct the camera lens. A further limitation of this method is that it does not easily lend itself to measuring biomass or the taxonomy of insects. A solar panel power supply may alleviate some of the challenges of deploying and maintaining these camera traps. However, the traps remain dependent on consistent, clear, weather conditions. Furthermore, if too much of the background is obstructed by vegetation or other kinds of clutter, it may be more difficult to identify insects from the images. We used manual identification and annotation to measure insect abundance from images which is time consuming. It is now possible to carry out automatic counting for these types of images, streamline data processing by use of deep learning (Choiński et al. 2023). However, the automatic counting tool should be carefully tested in interior forest habitats where the view of the sky may be obstructed by vegetation, complicating the ability of the tool to identify insects thereby influencing insect detectability.

Other studies have measured bat activity in relation to forest structure with a wide range of tools including 3-dimensional approaches such as ALS and LiDAR (**Paper IV,** Froidevaux et al. 2016; Erasmy et al. 2021; Rauchenstein et al. 2022; Carr et al. 2018; Müller et al. 2018) and more coarse categorical descriptions of habitat using satellite-derived forest characteristics or in-field measurements (Gorresen, Willig, and Strauss 2005). The only previous study to our knowledge to use hemisphere images to measure canopy openness in relation to bat activity was in a subtropical system (Cruz et al. 2019). The benefit of measuring canopy openness using hemisphere images is that it is relatively easy to collect data once a suitable camera and mount is acquired (Chianucci and Cutini 2012; Fournier and Hall 2017; Beeles, Tourville, and Dovciak 2022). The analysis of images can be done quickly with open-source methods (Rueden et al. 2017; ter Steege 2018). Additionally, measuring canopy openness with hemisphere photos provides an elegant and easy-to-communicate link between flying bats and the vegetation in the immediate vicinity of a detector location. However, this method also requires rain-free weather conditions and is best used on overcast days when the risk of over-exposed images is limited.

When comparing bat activity recordings from different sites, one should consider that acoustic data might exhibit systematic bias due to variations in the ability to detect echolocation calls, which can be influenced by vegetation structure and clutter (Patriquin and Barclay 2003; Darras et al. 2016; O'Keefe et al. 2014). In this study we took great care when deploying microphones to avoid sampling bias by controlling for variation in forest age, height composition, productivity, and the distance to edges or water bodies.

Conclusion

Our results highlight the value of mature mixed boreal forests that are neither too dense nor too open as foraging habitats for *Myotis* bats. In forest gap sub-habitats characterized by higher vegetation density, the bats' ability to forage effectively is reduced. Our study also suggests that distinguishing between feeding, and commuting activity provides a more comprehensive insight into the factors affecting the quality of bat habitats in northern forest environments.

Acknowledgments

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Author contributions

Katrine Eldegard: Conceptualization (lead); Formal analysis (lead); Investigation (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review & editing (equal). **Reed April McKay**: Conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Investigation (lead); Methodology (equal); Writing – original draft (equal); Writing – review & editing (equal). **Mathilde Klokkersveen Thomle:** Investigation (supporting); Methodology (supporting); Visualization (supporting). Writing – original draft (supporting); Writing – review & editing (supporting). **Vilde Sætre:** Investigation (supporting); Methodology (supporting). Writing – original draft (supporting). **Jenna Katrina Fairchild:** Investigation (supporting); Methodology (supporting). Writing – original draft (supporting); Writing – review & editing (supporting). **Fiona Mathews:** Methodology (supporting); Supervision (supporting); Writing – review & editing (supporting). **Richard Bischof:** Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review & editing (supporting).

Ethics statement

All data collection in this study was done using noninvasive techniques and no wildlife were handled. Landowners granted permission to install passive acoustic detectors and insect camera traps. The camera traps were properly marked with information about purpose and owner and placed facing the sky so high above the ground that there was no chance of accidentally taking pictures of passing humans.

Data availability statement

The workflows for analyses are available on GitHub:https://github.com/airmckay/BatsInsectsBorealForest_FolloRegion. The data will be stored in a repository such as Dryad when this manuscript is accepted for publication in a scientific journal. Inquiries about the data and how it was analyzed or managed are welcome and can be addressed to Reed April McKay (reed.april.mckay@nmbu.no).

Supplementary information

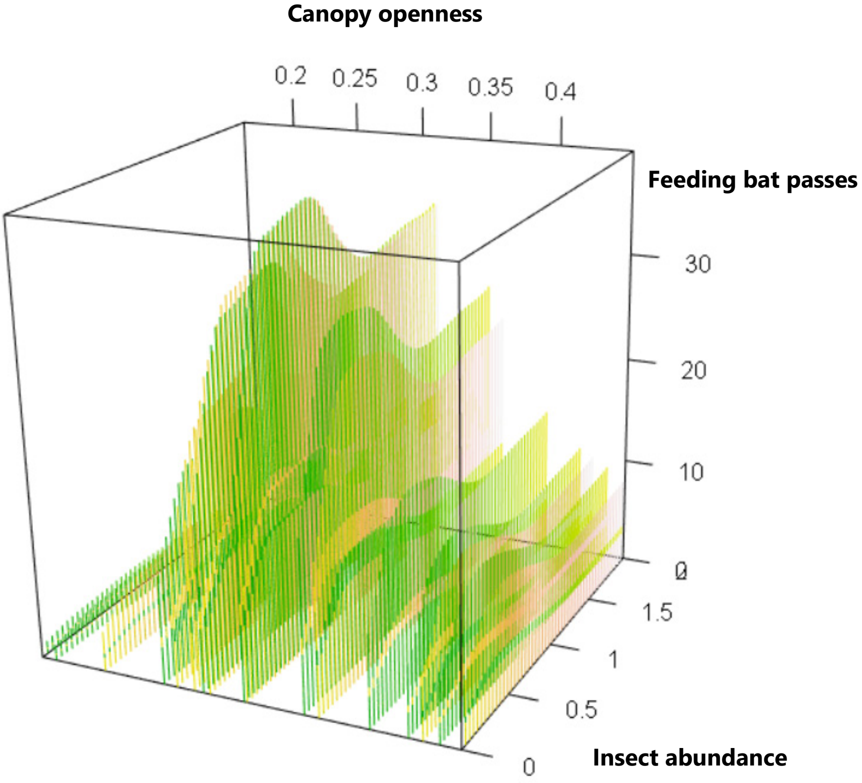

Figure S1. Estimated *Myotis* feeding activity ('Feeding bat passes', that is, number of bat passes per night containing at least one feeding buzz), in response to insect abundance and canopy openness in boreal forest gaps. Model predictions from the GAMM in Table 1, for low soil moisture and mean daylength.

Table S2. Estimates and test statistics from single variable Generalized Additive Mixed Models explaining the relationship between (a). *Myotis* feeding activity and insect abundance, and (b). insect abundance and canopy openness. Site was included as random intercept. Estimated relationships are visualized in Figure S2.

(a). Response: ***Myotis* foraging activity** (deviance explained = 35.1%, n = 364)				
	Estimate	**SE**	**t**	**p**
intercept	3.30	1.57	2.09	0.037
	edf	**Ref.df**	**F**	**p**
s(insect abundance)	6.11	7.25	1.93	0.066
s(Site)	924	10.0	15.61	<0.001
(b). Response: **Insect abundance** (deviance explained = 12.7%, n = 364)				
	Estimate	**SE**	**t**	**p**
intercept	0.20	0.037	5.41	<0.001
	edf	**Ref.df**	**F**	**p**
s(canopy openness)	2.40	2.59	2.59	0.050
s(Site)	6.40	10.0	2.63	<0.001

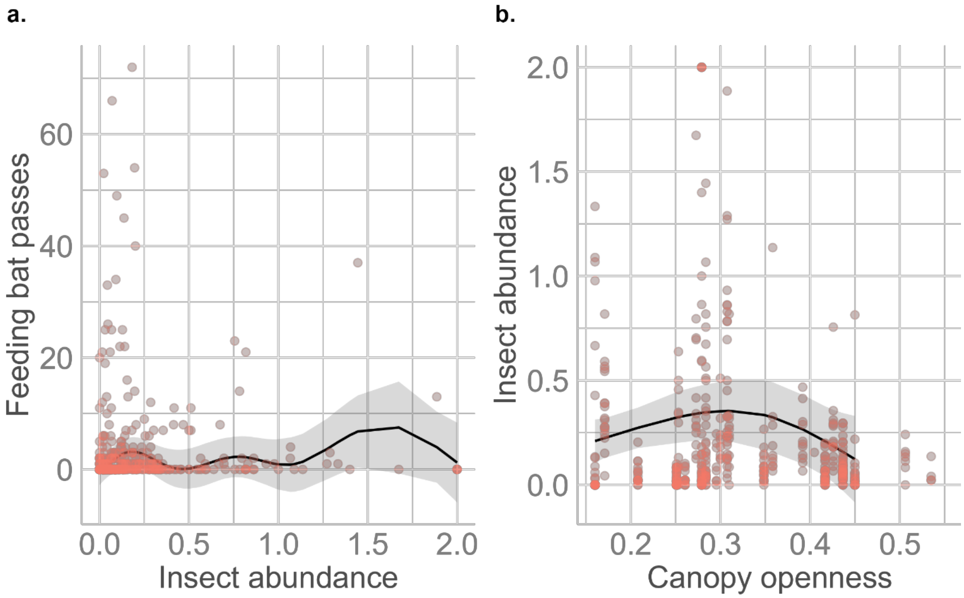

Figure S2. (a). Estimated feeding activity of *Myotis* bats hunting in forest gaps, in response to insect abundance. (b). Estimated insect abundance in forest gaps, in response to canopy openness. Estimated lines and associated 95% confidence limits from the single variable GAMMs in Table S2. Points are observed values.

Table S3. Estimates and test statistics from Generalized Additive Mixed Models explaining the relationship between insect abundance and temperature and Julian night. Site was included as random intercept. Sample sizes differ between because of missing data for temperature in the beginning of the season at some sites due to a delay in deployment of the TSM-4 dataloggers. Predictions are visualized in Figure S3.

Explanatory terms				
Temperature (deviance explained = 12.9%, n = 354)				
	Estimate	SE	t	p
intercept	0.20	0.038	5.2	<0.001
	edf	Ref.df	F	p
s(Temperature)	1.09	1.18	3.37	0.049
s(Site)	7.71	10.0	3.84	<0.001
Julian night (date) (deviance explained = 23.2%, n = 364)				
	Estimate	SE	t	p
intercept	0.20	0.032	6.2	<0.001
	edf	Ref.df	F	p
s(Julian night)	4.56	5.57	10.0	<0.001
s(Site)	8.30	11.0	4.09	<0.001

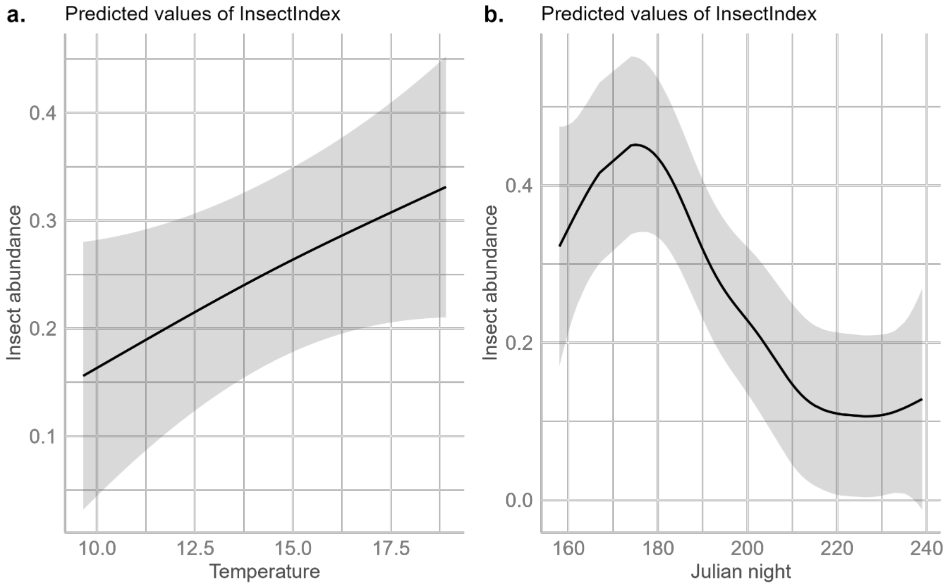

Figure S3. Relationship between insect abundance and (a) temperature (°C) and (b) date (Julian night = night after 1 January; 160 = 9 June, 180 = 29 June, 22 = 8 August). Lines and polygons are estimated relationships and 95% CIs from single variable GAMMs in Table S3.

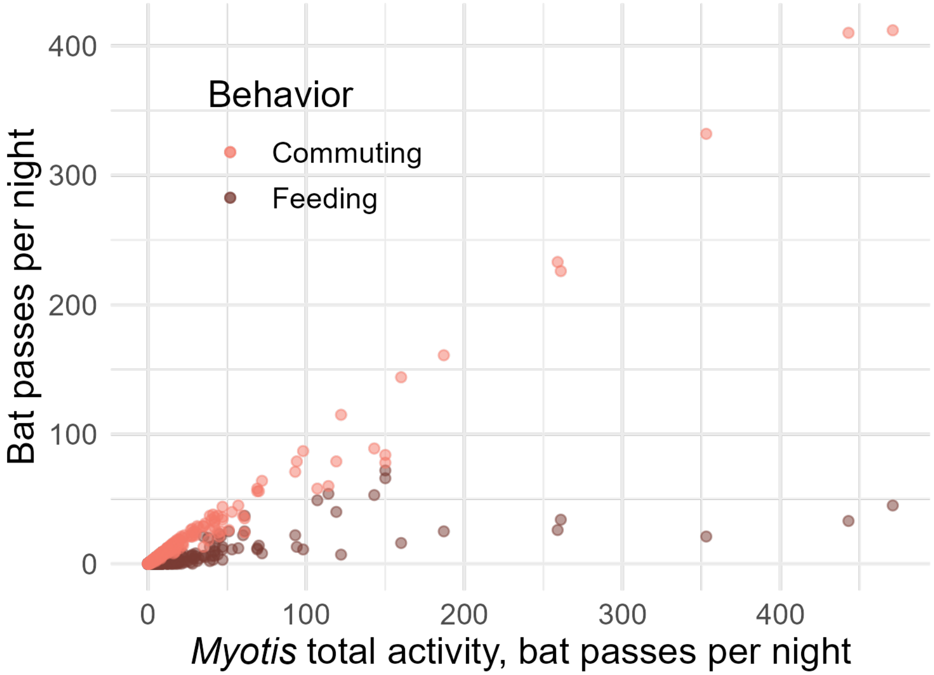

Figure S4. Scatterplot of total *Myotis* activity versus feeding activity (Pearson's product moment correlation: *r* = 0.75 [95% CI: 0.68-0.77], p <0.001) and commuting activity (*r* = 0.99 [95% CI: 0.987- 0.991], p <0.001). Sample size n = 401 observation nights.

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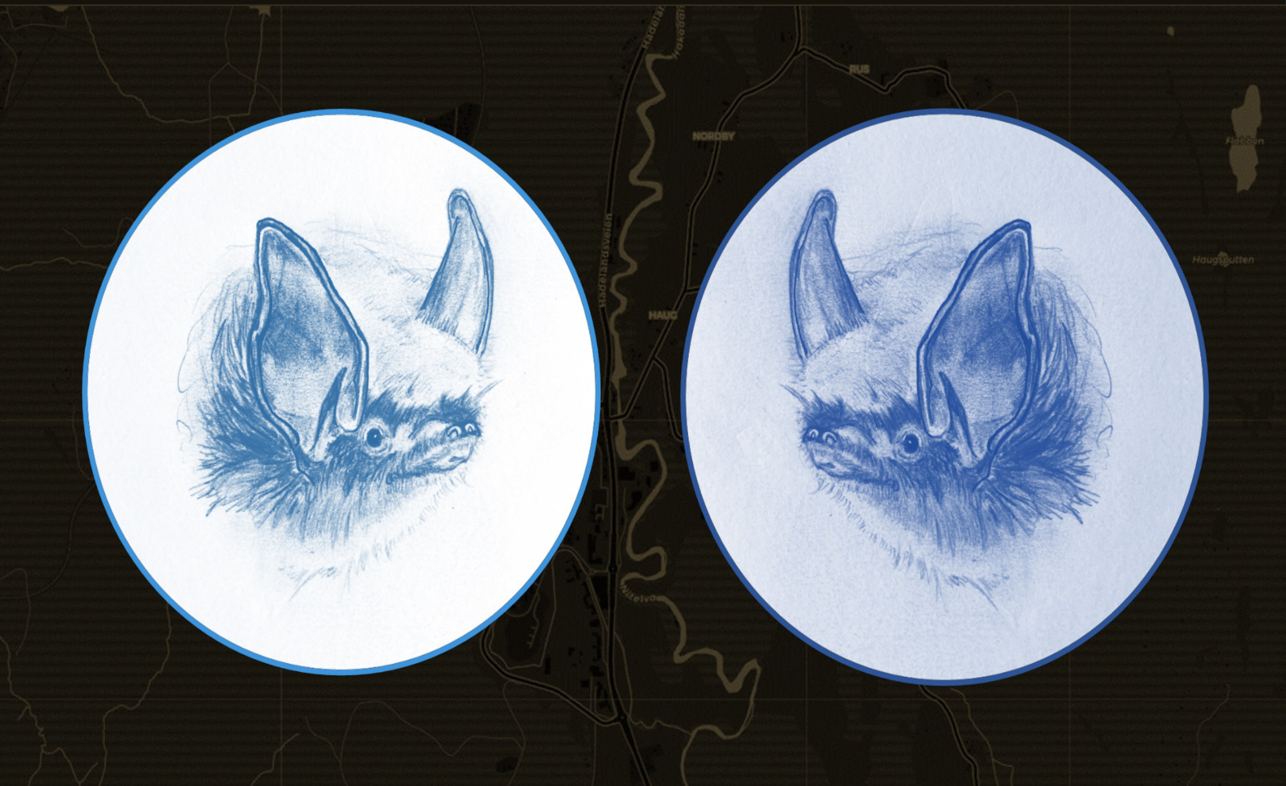
Paper IV

Foraging ecology of two morphologically similar sympatric bat species



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Abstract

The Brandts' bat (*Myotis brandtii*) and the whiskered bat (*M. mystacinus*) are cryptic species from distinct taxonomic clades with overlapping ranges in distribution. What, if any, resource partitioning that exists between them is not well understood, especially at the northern extent of their ranges. This study aims to compare the foraging ecology and diet of *M. brandtii* and *M. mystacinus* during summer in Southeastern Norway. Adult female *M. brandtii* (n = 9) and *M. mystacinus* (n = 11) from neighboring colonies were captured using mist nets and radio-tagged for VHF radiotelemetry surveys. We collected and successfully sequenced 47 fecal samples from *M. brandtii* (n = 16), and *M. mystacinus* (n = 31). Molecular genetic analysis of feces from bats was used to verify in-hand identification and to explore the diet of the *M. brandtii* and *M. mystacinus*. We compared foraging habitat use of *M. brandtii* and *M. mystacinus* using a resource selection function analysis with 3-dimensional vegetation structure descriptions of habitat from airborne laser scanning data as explanatory variables. We found that *M. brandtii* selected continuous forest foraging habitat with low canopy density while *M. mystacinus* selected patchier habitats of more varied densities. *M. brandtii* had mean home ranges that were 4 times larger than *M. mystacinus*. The diet of both species was dominated by Diptera and Lepidoptera. However, we found evidence of higher prey richness within a given sample (alpha diversity) for *M. brandtii* than *M. mystacinus* and that the two bat species had differences in beta diversity of the arthropods found in their respective diets. We conclude that there is considerable overlap in habitat use and diet but there was also evidence for resource partitioning between *M. brandtii* and *M. mystacinus* in our study system.

Introduction

Cryptic species can be defined as two or more species that are or have previously been designated as "a single nominal species because they are at least superficially morphologically indistinguishable" (Bickford et al. 2007). The discovery and study of cryptic species has grown immensely with the increased accessibility of genetic tools; revealing genetically distinct, sympatric and highly similar species around the world (Struck and Cerca 2019). Studying the ecological roles of such species can be inherently difficult but nevertheless important for evaluating species specific conservation and management needs. Understanding the ecological roles of species distinctly is the basis of most efforts to conserve wildlife and is necessary for evaluating what is required to maintain species diversity in different systems. As the field of bat research has expanded alongside advancing methodologies in genetics, bioacoustics, and morphology, new, cryptic species of bats have been gradually discovered at a higher rate (Jones & Barlow, 2004; Srinivasulu et al., 2019). Methodologies assessing beyond morphological differences are fundamental in particular for echolocating bats for which speciation pressure may be stronger through acoustic and dietary mechanisms (Jacobs et al., 2007; Jones, 1997).

The Brandt's bat, *Myotis brandtii* and whiskered bat, *M. mystacinus* are sympatric throughout Eurasia (IUCN 2022) and are difficult to distinguish from each other morphologically, even in the hand for experienced bat workers (Dietz and Kiefer 2016). Before 1970, *M. brandtii* and *M. mystacinus* were classified as a single species. A detailed review of morphological features revealed *M. brandtii* and *M. mystacinus* to be distinct (Baagøe 1973; Gauckler and Kraus 1970; Hanák 1970). Further research with the use of genetic methods found that *M. mystacinus,* as it was described before 1970, consisted of at least five *Myotis* species found throughout Europe that share very similar morphological features (Benda and Tsytsulina 2000; von Helversen et al. 2001). *M. brandtii* and *M. mystacinus* are not currently considered sibling species (Knowlton 1986), as they are not closely related to one another phylogenetically. *M. brandtii* is currently placed in the same clade as *Myotis* species found in the Americas whereas *M. mystacinus* is situated in a clade of European *Myotis* species (Bickham et al. 2004; Ruedi and Mayer 2001). Given their distant genetic relatedness, the morphological similarities between these two species are even more striking. Today, *M. brandtii* and *M. mystacinus* are still considered cryptic species (Berge 2007; Boston et al. 2010; Lučan et al. 2011; Roswag et al. 2019).

Beyond their physical resemblance, *M. brandtii* and *M. mystacinus* also produce very similar echolocation calls such that it is not advised to distinguish between them in acoustic studies where both species are found (Russ, 2021). These species are also grouped together in hibernacula surveys because species level identification would require an unacceptable amount of disturbance. We are aware of two studies comparing in-hand identification of *M. brandtii* and *M. mystacinus* to molecular genetic analysis which have found that a combination of physical characteristics are required for reliable in-hand identification, including the ability to recognize diagnostic features in penis shape, dentition, forearm length, tragus shape, and pelage coloration

(Berge 2007; Lučan et al. 2011). However, incorrect field identification was made in both studies; even with experts it can be difficult to distinguish between *M. brandtii* and *M. mystacinus* in the hand. A combination of resource demanding, technical, and time-consuming methods such as capturing, in hand identification, genetic sampling and/or radiotelemetry is often necessary to study *M. brandtii* and *M. mystacinus* separately where the species are sympatric. Therefore, there is limited understanding of the species-specific ecological differences in diet, habitat use and even range distributions of *M. brandtii* and *M. mystacinus* as well as other *Myotis* species in the whiskered bat complex (Budinski and López-Baucells 2023). These knowledge gaps pose practical challenges for managers throughout Europe which rely on species level information to develop conservation plans.

The foraging behavior and spatial use of *M. brandtii* and *M. mystacinus* has been studied separately and in comparison to one another by some previous studies (Albayrak 1991; Berge 2007; Boston et al. 2010; Buckley et al. 2013; Budinski and López-Baucells 2023; Ekman and de Jong 1996; Lučan et al. 2011; Roswag et al. 2019; Taake 1984; Vesterinen et al. 2018; Kurek et al. 2020). The ranges of both bats expand across Europe and into Asia where they have been documented using a wide range of habitats including forests, agricultural lands, wetlands, urban areas, as well as mountains (Budinski and López-Baucells 2023). Previous research of the habitat selection of *M. brandtii* and *M. mystacinus* has found that while both species are frequently found in forests, there is some evidence which suggests that *M. mystacinus* is more associated with cultural landscapes while *M. brandtii* appears to be more dependent on forested landscapes (Berge 2007; Buckley et al. 2013; Taake 1984; Vaughan, Jones, and Harris 1997). The diet of both bat species has been studied using genetic methods as well as macro and microscopic fecal analysis and found a diverse mix of prey items, dominated by Lepidoptera and Diptera (Berge 2007; Roswag et al. 2019; Vesterinen et al. 2018). Moreover, there are few modern studies which give an in-depth comparison of the foraging habitat and diet of the two species.

This study aims to explore the foraging habitat selection of adult, female *M. brandtii* and *M. mystacinus,* as well as the diet of both species from the same population in Southeastern Norway during the summer maternity season. The main ecological niche theories (Elton, 1946, 2001; Grinnell & Swarth, 1913; Hutchinson, 1957) which largely agree that species which share similarities in geographic position and morphology should have different ecological roles to avoid competition. Thus, we predict that *M. brandtii* and *M. mystacinus* should have some form of resource partitioning to account for their close geographic and morphological similarities. We expected that (i) *M. brandtii* and *M. mystacinus* would select for different habitat within the same areas. Furthermore, we explore (ii) what, if any, differences in the diet exist between *M. brandtii* and *M. mystacinus* and (iii) if differences in habitat selection are apparent from the differences in diet.

Methods

Study area

Data collection took place in Nittedal, Norway (60°4′22′′N, 10°52′0′′). Field work was focused east of the river Nitelva in the Nittedal valley. The bottom of the valley was composed of a mosaic of cultural landscapes and riparian forests with the slopes of the valley dominated by spruce and mixed forests as well as rocky terrain. The varied landscape and topography (elevation range: 10-447 m above sea level) in this area provided the opportunity to study bats in different habitats.

Bat captures and in-hand species identification

Trapping occurred in flight corridors where it would be possible to funnel the bats toward nets and harp-traps such as over water bodies or along forest paths (Kunz and Parsons 2009). Trapping also took place near maternity colonies when it was necessary to follow the movements of bats specifically from these colonies or during periods when it was challenging to capture target species on the landscape. The trapping efforts began at sunset and continued until bat activity dropped, for up to 5 hours after sunset. Bats were identified to species, evaluated for reproductive status, sexed, aged and forearm length as well as weight were measured. Several morphological features need to be taken into consideration to ensure a relative level of certainty in distinguishing between *M. brandtii* and *M. mystacinus* in the hand (Berge 2007; Dietz and Kiefer 2016; Lučan et al. 2011). The primary characteristics used in this study were dentition along with forearm length, pelage and skin coloration, and tragus shape. When assessing males, penis shape was also used to distinguish between species.

Fecal sample collection

A total of 50 fecal samples were collected at mist net sites in the summer (June – September) of 2017 (n = 16 samples) and between June 13th and July 11th in 2018 (n = 34 samples), from clean cloth bags where an individual bat was temporarily held. Samples were collected from male and female bats identified in hand as *M. brandtii* and *M. mystacinus*. Each sample is associated with an individual bat capture. The feces were removed from the bat bags and placed in 2 ml tubes of 100% ethanol where they were stored for a minimum of 24 hours and up to a year before being transferred on to dry, odorless wipes and stored in individual 50 ml falcon tubes that were filled to approximately ⅓ with silica beads.

Radiotelemetry

Adult females of target species, *M. mystacinus* and *M. brandtii*, were selected for tagging during trapping efforts (supplementary materials, Table i) between 5 June and 14 August 2018. Reproductive individuals and those of higher weights were prioritized to locate colony sites as part of parallel research efforts; heavily pregnant individuals were not tagged. Very high frequency (VHF) radiotelemetry tags used in this study were Biotrack PIP4 tags that weighed 0.31 or 0.32 g. The transmitter was attached to the back of the bat just below the interscapular area using skin binding glue (Medical latex glue, Sauer Hautkleber, Manfred Sauer, Germany); a small patch of hair was trimmed from this area before adhering the transmitter. More information about the capture data related to radio-tagged bats is found in the supplementary materials (supplementary materials, Table ii).

Sika receivers (Biotrack, UK) were used with handheld flexible 3 element and 5 element YAGI antennae (Biotrack, UK). In total 9 *M. brandtii* and *12 M. mystacinus* adult females were radio-tagged and tracked for a mean 7.9 (SD ± 1.6 days) and 6 days (SD ± 2.4 days) respectively (Table 1). An additional 10th *M. brandtii* was tagged but no precise foraging locations were collected on this individual, so it was not included in further analyses. Once the tagged bat was released, an individual researcher or a team would follow the bat on foot or by car. For 40% of the tagged bats, the tracking effort was ended due to a transmitter being shed or otherwise failing. Another 40% were deprioritized when they had been tracked for at least one week. The remaining 20% of tagged bats were no longer tracked due to signal loss, or because the field season ended.

A combination of techniques was utilized to study the foraging behavior of tagged bats. Photoperiod fluctuates dramatically throughout the summer in this region and the longest day of the year, the summer solstice, is 18 hours and 53 minutes long (https://www.timeanddate.no) in our study area. The shortened night periods and light northern summer nights, in addition to the legal ability to move through the landscape with limited restriction for crossing privately owned land in Norway (Klima- og miljødepartementet 1957) made it possible for our research team to physically follow bats as they foraged to collect precise foraging locations. Primarily, crew members would 'home in' on an individual bat (Amelon et al. 2009); directly pursue a tagged bat to get near and record foraging locations. The VHF equipment was tested as part of previous research conducted within the same research project (Siljedal 2018) to determine the range of the instruments in the study area which found that any observation made of a bat when the signal being received was at least 45 gain strength, would place the bat within approximately 25 m of the observer. Any observation gathered with 45 gain strength or lower, is classified as a "fix".

When it was not possible to stay in close enough proximity to collect fixes, other techniques were used such as triangulation, cross bearings, and a telemetry tower to recover the signal and inform crew members where to try and home in on tagged bats. The telemetry tower consisted of a 5-element YAGI antenna that was attached to a 6 m tall pole that could be erected, usually at higher elevations, to pick up signal from transmitters up to approximately 2 kilometers away.

Laboratory procedures for analyses of fecal samples

DNA extraction from the fecal samples as well as the genetic analysis took place in the autumn of 2019 at the Konrad-Lorenz Institute of Ethology in Vienna, Austria. This included 16 samples from bats identified in the field as *M. brandtii* (n = 3 (2017), n = 13 (2018)) and 31 from *M. mystacinus* (n = 11 (2017), n = 20 (2018)).

DNA was extracted from all fecal samples using QIAamp® PowerFecal® DNA Kit (Catalog number 12830-50, QIAGEN, Hilden, Germany) following the instruction provided in the manual (version August 2016). Several modifications to the manual were made to fit the purposes of this research in the following steps:

> 1.) Approximately 1-2 pellets (10-50 mg) were used as starting material. 5.) Instead of a Vortex Adapter tube holder, we used a TissueLyser LT by QIAGEN at 50 oscillations per second for 10 minutes. 17.) The sample was centrifuged for 2 minutes at 13000 x g. 19.) 100 μl AE buffer was used and allowed to stand in the spin column for 10 minutes before the final centrifuge step.

Extraction negative controls were included in each round of extraction to detect contamination.

Bat species identification

The SFF primer pair (SFF-145f: 5′-GTHACHGCYCAYGCHTTYGTAATAAT-3′ and SFF-351r: 5′-CTCCWGCRTGDGCWAGRTTTCC-3) described by Walker et al. (2016) was selected for amplifying bat DNA in a polymerase chain reaction (PCR). PCRs contained 5 μl of undiluted DNA in a 20 μl reaction with a final concentration of 2.5 μl 10x Buffer (Solis BioDyne), 2.5 μl, magnesium chloride [25 mM], 2.5 μl dNTP's [2 mM], 0.5 μl of each primer [10 μM], 0.3 μl BSA [50 mg/ml], 11 μl PCR water, 0.2 μl firepol [5 U/μl] (Solis BioDyne). The thermal conditions of this PCR are as follows: 95 °C for 5 minutes, followed by 35 cycles – 95 °C for 30 seconds, 58 °C for 30 seconds, 72 °C for 30 seconds-, then 72 °C for 5 minutes, and 12 °C indefinitely. PCR products were stored at 4 °C.

All extraction negative samples and a non-template control sample were included in each PCR run to control for contamination free DNA extraction and PCR amplification. All PCR products were checked for amplification on a 1% agarose gel including GelRed (Biotium, Inc.; Hayward, California) following the manufacturer's instructions. All samples that appeared positive on the gel (neither of the control samples did) were sequenced on an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, California) using BigDye Terminator V3.1 (Applied Biosystems, Foster City, California) following the manufacturer's instructions. Forward as well as reverse sequences were run for each sample. A second sequencing reaction was performed to verify the results.

Library preparation for dietary analysis

The primer set ZBJ-ArtF1c and ZBJ-ArtR2c, developed by Zeale et al., (2011) with overhang at the 5′ end (indicated by asterisks) for subsequent indexing PCR (see below) was selected to amplify arthropod DNA for the dietary analysis.

ZBJ-ArtF1c: 5′-*TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG* AGA TAT TGG AAC WTT ATA TTT TAT TTT TGG-3′.

ZBJ-ArtR2c: 5′-*GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA G*WA CTA ATC AAT TWC CAA ATC CTC C-3′.

Each PCR was set up in a 20 μl reaction as followed: 12 μl of undiluted DNA, 5 μl AllTaq Mastermix (Qiagen, Hilden, Germany), 0.5 μl of each primer [10 μM], 0.3 μl BSA [50 mg/ml], 1.7 μl PCR water. The thermal conditions of the touchdown PCR are as follows: 95 °C for 5 minutes, followed by 16 cycles – 94 °C for 5 seconds, 61 °C for 15 seconds, 72 °C for 10 seconds – with a 0.5 °C decrease with each cycle, followed by 24 cycles – 94 °C for 5 seconds, 53 °C for 15 seconds, 72 °C for 10 seconds. PCR products were stored at 4 °C.

To pool all samples in one NGS sequencing run, arthropod PCR products were individually labeled in an indexing PCR using the i7 and i5 primer system (including a seven bases long individual barcode sequence). Each indexing PCR was set up in a 20 μl reaction as followed: 1 μl of arthropod PCR product, 5 μl AllTaq Mastermix (Qiagen, Hilden, Germany), 0.5 μl of each primer [10 μM] and 13 μl PCR water. The PCR temperature conditions are as follows: 95 °C for 2 minutes, followed by 15 cycles – 95 °C for 5 seconds, 55 degrees for 15 seconds, 72 degrees for 10 seconds. Indexing PCR product was stored at 4 °C.

Extraction negative samples and non-template control samples were included in all PCR runs and showed no sign of amplification on agarose gels. To pool all indexed PCRs equimolarly, the SequalPrepTM Normalization Plate (Invitrogen, Carlsbad, California) was used, following the instructions provided in the manual. The advantage of using this normalization plate is the accurate normalization of the PCR product to 1.5 ng/μl and a parallel clean-up of the PCR product. All cleaned products were pooled in one single tube and sent to the Vienna BioCenter for a 150 paired end sequencing run on an Illumina NextSeq550 platform.

Habitat use and spatial movements data analysis

Bat observations and home ranges

There were 5458 observations in the form of radiotelemetry data that were collected from the 22 radio-tagged bats with a total of 146 tracking nights for all bats together. 1502 of the observations were classified as fixes, wherein the bat was within approximately 25 m of the observer (Table 1). For the purposes of analyzing the foraging habitat selection and for calculating home range size of these bats, the 1502 fixes were the only observations used in this study and were included for further analyses. We used the adehabitatHR package (Calenge and

Fortmann-Roe 2023) to calculate the 95% kernel density estimate polygons (KDEs; Izenman, 1991; Silverman, 1998) of individual bat foraging home ranges. We compared the size of the home ranges between each bat species with a Mann-Whitney *U* test (McKnight and Najab 2010). Random points that were equal to 10 times the number of fixes were generated within each home range to represent available foraging locations for each individual bat.

Airborne laser scanning data

Airborne laser scanning (ALS) is a remote sensing method that uses a light detection and ranging (lidar) sensor mounted in an airborne platform to scan the terrain and vegetation below and create a visual representation in form of a point cloud of individual echoes (x, y, z coordinates) of the surfaces detected (Killinger, 2014, Figure 1). ALS is an increasingly popular method used in ecological studies for relating wildlife (Ciuti et al., 2018; Davies & Asner, 2014; Lin & Wiegand, 2021), including bats (Carr et al., 2018; Froidevaux et al., 2016; Hermans et al., 2023; Jung et al., 2012; Rauchenstein et al., 2022; Yoh et al., 2023), to their 3-dimensional environment. However, no studies have used ALS to describe bat foraging habitat using radio-telemetry methods, to our knowledge. ALS data is an especially advantageous and practical tool for comparing the habitat selection of bat species which tend to occur in similar landscape types.

The discrete return ALS data used in this study was collected by Terratec AS between November 15 and November 28, 2015. The main purpose of the data acquisition was to obtain an accurate terrain model as part of a national campaign. Two different sensors flown at approximately 1700 m above sea level to obtain a pulse density of 6.2 points/m^2, namely the Lecia ALS70 and the Optech ALTM Titan sensor. The 3-dimensional point cloud obtained from the ALS was normalized, i.e., converted to vegetation height by subtracting the height from a triangular irregular network created from echoes classified as ground. In the subsequent analysis we only used the first echoes (i.e., the first echo from each pulse) to minimize the impact of the different sensors. For a radius of 50 m around a point we computed vertical and horizontal canopy metrics masking out buildings and power lines using existing maps. The 50 m radius was used for both points used by the bats (fixes), and for random (available) points within the bats' home range (see foraging habitat selection below).

From the ALS echoes, the following vertical canopy metrics were calculated from the height distribution of echoes above one meter following the description of Gobakken & Næsset (2008): the mean height (Hmean), standard deviation of height (Hsd), skewness (Hskew), kurtosis (Hkurt), the coefficient of variation (Hcv) and 10 percentiles of vertical height (H10, H20,...,H90, H95). Furthermore, canopy densities were calculated by first dividing the range between a 95% percentile height and the 1 m threshold into ten vertical layers of equal height. The proportion of echoes above each layer to the total number of echoes were computed, resulting in ten canopy density metrics (D0, D1, ..., D9).

A canopy height model (CHM) using the normalized echoes and smoothed with a Gauss filter was built to calculate metrics of horizontal canopy structure. The methods for constructing the model closely follow the methods described in (Sverdrup-Thygeson et al. 2016). An individual tree crown approach was used to detect treetops and segment crowns. First a 3 by 3 local maxima filter was applied to the CHM and the number of "treetops" (ttops.n) was calculated as well as the mean and standard deviation of local maxima's height. The local maxima were used as seed in a crown segmentation algorithm (Dalponte and Coomes 2016) implemented in the lidR package (Roussel et al. 2020). From the identified crown segments, we computed the average and standard deviation of crown sizes within the radius of the point. The number of gaps, mean area of gaps and standard deviation of gaps were also calculated. A gap was defined by applying threshold (3 m) to the CHM to form a binary image and then identifying unique spatial patches with heights lower than 3. Gaps were calculated using the function "patches" in the R package terra (Hijmans et al. 2023).

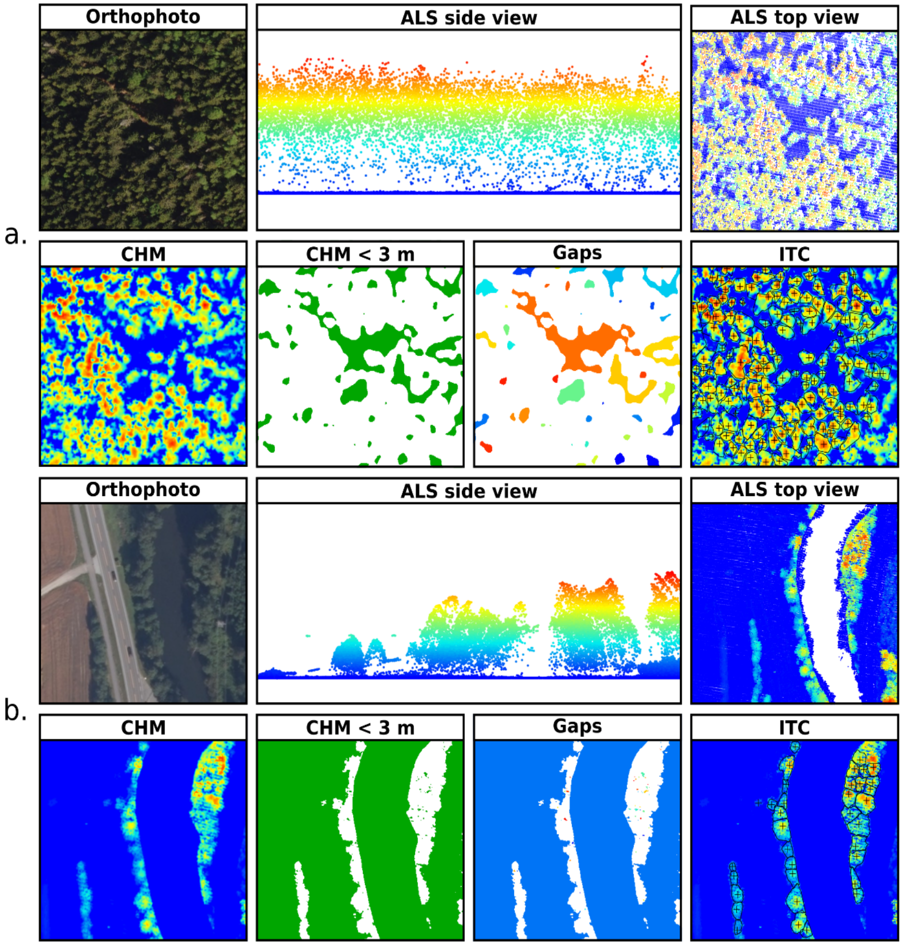


Figure 1. Examples of how ALS metrics can be used to define a forested (a.) and an open, riparian (b.) landscape. Figure showing orthophoto, ALS data as side and top view used to derive height and canopy density metrics: smoothed canopy height model (CHM), the area where CHM < 3 m (CHM < 3 m), the identified individual gaps (Gaps), and the identified treetops and crowns from the individual tree crown (ITC) detection.

Foraging habitat selection

To determine if habitat use differed between *M. brandtii* and *M. mystacinus*, and if the probability of use of a foraging site was influenced by habitat metrics defined from ALS or distance to the nearest water source, we used conditional logistic regression to fit Resource Selection Functions (RSFs) (Chetkiewicz and Boyce 2009). The distance to water was computed as the Euclidian distance from the fix to the water feature in official map data in scale 1:5000. In the RSFs, recorded foraging locations used by the bat (fixes) are compared to the available surrounding landscape (Boyce and McDonald 1999; Johnson et al. 2006; B. Manly et al. 2002; B. F. J. Manly 1985). Availability data were defined by creating random points from within 95% kernel density estimate polygons (KDEs) for each individual bat. For each individual bat, the number of random points was equal to 10 times the number of fixes to effectively cover available area within the KDEs.

The ALS derived metrics were defined by a 50 m radius surrounding all used and available points and were first centered and scaled. The distance to water and all ALS metrics were centered and scaled with the corresponding value from the center subtracted from within each metric. To explore expected collinearity between many of the 38 different ALS metrics, we used the vegan package (Oksanen et al. 2007) to calculate a principal component analysis (PCA) for all points (used and available for all bats) as input data plotted against the first and second principal components. The ordination plots showed that we could separate all ALS metrics into 4 distinct groups which shared a similar influence on the PCA ordination. From each group, we identified the metrics which had the highest scaled eigenvector values (> 2.3) and of those, we chose a single ALS metric which was ecologically meaningful to interpret and communicate findings, and which exhibited low collinearity with the other 3 selected metrics. The 4 ALS metrics we then used in initial RSF models were D0, Hsd, H95, and mean gap area.

We created one set of generalized linear mixed-effect models for each bat species with a binary response variable (1 = used, 0 = available), bat ID as a random intercept and the following explanatory variables: distance to water, D0, Hsd, H95, and mean gap area, assuming a binomial distribution of errors. We used the R package lme4 (Bates et al. 2023) to fit the logistic regression models. All fixed effects had a strong effect on the response for at least one of the two species in this model set. We then calculated the variance inflation factors (VIF) for each bat species model to determine if any of the ALS metrics were highly correlated with each other. We found that H95 had a high VIF value (>5) and chose to drop this term when building the full (most complex) model, which resolved the correlation issues amongst the terms. The exploratory analyses revealed that there was a strong but similar positive relationship between H95, and use of foraging habitat use for both bat species.

The full (most complex) RSF estimated the probability that a point was used, as a function of D0, Hsd, mean gap area, distance to water, bat species, and the interaction between bat species and each of the 4 environmental variables. Again, we used a binary response, included bat ID as a random intercept, and assumed a binomial distribution of errors. To determine if any explanatory variables could be dropped from this model, we carried out model reduction with likelihood ratio tests, comparing models by assessing Akaike information criterion (AIC) values (Burnham and Anderson 2003). The result of the likelihood ratio test suggested that the interaction between bat species and distance to water contributed toward overfitting. We dropped this interaction and then re-ran the likelihood ratio test on the resulting model and found this to be the most parsimonious model. Finally, we used DHARMa package in R (Hartig and Lohse 2022) to produce diagnostic plots to ensure that our final model fitted the empirical data.

Bat diet data analysis

Bioinformatical analysis of arthropod sequences

To use Qiime2 for the analysis of the fecal metabarcoding data, we created a customized database containing the Cytochrome Oxidase I (COI) sequences of all European Insects and Arachnida that are present in the barcode of life database (BOLD). The workflow is based on the work by O'Rourke et al., (2020) using the bioinformatic tool RESCRIPt (Robeson et al. 2020). We used the R packages "bold", "taxize", and "dplyr" to download the sequences and the taxonomic information from BOLD (Chamberlain and Szöcs 2013; Mudalige 2021; Wickham and François 2014).

After duplicate sequences were removed, RESCRIPt was used to filter sequences that contained high numbers of ambiguous sequences and high numbers of homopolymers. Furthermore, extremely short, and redundant sequences were removed. As a last step we used the primer sequences of ZBJ-ArtF1c and ZBJ-ArtR2c to trim and truncate the sequences in our database to the fraction of COI that we amplified. A complete list of all prey taxa found in the diet of *M. brandtii* and *M. mystacinus* is found in the supplementary materials, Table iii.

Fecal metabarcoding analysis

All demultiplexed sequences were downloaded from the Vienna-Bio-Center server and analyzed using the python-based pipeline QIIME2 (Quantitative Insights Into Microbial Ecology 2), version 2021.4 (Bolyen et al. 2019). In brief, we used the plugin "cutadapt" (Martin 2011) to remove the primer sequences, and the plugin "dada2" (Callahan et al. 2015) to denoise the sequences based on the interactive quality plots. The resulting amplicon sequencing variants (ASVs) were classified using the self-made Arthropoda database described above. To remove contaminating ASVs from the dataset, we use the R package "decontam" (Davis et al. 2018) based on frequency of each ASV. ASVs that were not assigned at the order level (only ASVs with very low abundance were affected) were also filtered. As a last step we used the plugin SRS (Beule and Karlovsky 2020); (scaling with ranked subsampling) to normalize the number of ASVs per sample. SRS normalized data was then filtered to remove any ASVs with less than 10 sequence reads (a single DNA fragment identified through sequencing) to reduce the number low frequency artefacts (Drake et al. 2022).

The count of sequence reads per taxa per bat fecal sample does not represent the biomass of prey consumed by the bat that produced the sample due to biases related to biological degradation as well as laboratory procedures. Presence/absence transformed data of diet from metabarcoding studies is considered a relatively conservative alternative to reporting raw sequence reads, but this will also exaggerate the importance of rarely detected taxa (Deagle et al. 2019). . An alternative to presence/absence, or occurrence, type data is to convert the sequence reads to relative read abundance (RRA). RRA is the total number of reads of each detected taxon within a sample, divided by the total number of reads in that sample and then multiplied by 100 to be reported as percentage. RRA can be biased by how the starting material was digested as well as by the primers effectively amplifying certain sequences more so than others (Alberdi et al. 2018). Deagle et al., (2019) proposes reporting presence/absence data alongside RRA to compensate for the biases in both approaches and so in this study, we use a combination of RRA and presence/absence data in reporting differences in the bats' diets, in addition to calculating relative abundance using log-transformation.

Bat Diet – Alpha and beta diversity

The filtered, SRS normalized data was visualized, transformed, and further analyzed for alpha and beta diversity using the R packages "vegan", "phyloseq" and "mircrobiome" in addition to those already mentioned (Lahti and Shetty 2023; McMurdie and Holmes 2013; Oksanen et al. 2007). To get an indication of the overall species richness consumed by a single individual, we calculated alpha diversity with the observed measure of diversity index (richness) for the presence/absence of taxa in each sample. We then applied 3 linear mixed effect models with fecal sample ID as a random intercept and the alpha diversity score as a response to: (M_alpha1) bat species interacting with year as well as the interaction between bat species and year as main effects, (M_alpha2) bat species interacting with year as main effects only and (M_alpha3) bat species only as fixed effects (supplementary materials, Table iv).

To quantify the differences of diets between the two bat species, thus acting as a measure of composition, we calculated beta diversity using a Principal Coordinate Analysis (PcoA) ordination. We calculated both Jaccard distances applied to presence/absence of prey items in samples and Bray-Curtis distances applied to log transformed arthropod prey taxa sequence count abundance. We then used the "adonis2" function in software R with package "vegan"

(Oksanen et al., 2013) To carry out a permutational multivariate analysis of variance using distance matrices (supplementary materials, Table iv).

Bat diet – prey habitat

We explored what landscape-level main habitat types (agriculture, forest, fresh water, wetland, mountain, urban, coastal) were associated with each prey type using data provided by the SLU Swedish Species Information Center (artdatabanken.se; hereafter SLU database). Each prey type was quantified in terms of prevalence (number of times a prey taxa occurred in a sample for each bat species). For the most abundant prey types that were not assigned in the SLU database, we manually inserted habitat data from other sources (Artsdatabanken.no, uk.moths.org.uk, ccw.naturalis.nl). There were a remaining 54 distinct prey taxa that we could not match with habitat characteristics, so no formal analysis was used to compare the differences in prey habitat. However, we visualized and interpreted this data in the context of our other findings to evaluate the relationship between bat diet and habitat use.

Results

Foraging habitat and spatial movements

We found that only 22 locations (1.4% of all used points) were in non-forest areas, with forests defined as locations where H95 was greater than 5 m and D0 was greater than 10%. So, we frame our results with the understanding that both bats primarily used forest habitats. The mean home range size for *M. brandtii* and *M. mystacinus* was 4.00 km^2 (SD = 4.04) and 0.72 km^2 (SD = 0.57), respectively (Mann-Whitney U test: W = 92, p-value = 0.00562, Figure 2).

The final model had moderately powerful abilities to predict bat habitat use (R^2 = 0.129) but the variation amongst individual bats was relatively low (variance = 0.02, SD = 0.14) such that we can be confident that the differences observed between species is not likely due to individual variation (Table 2). We found strong evidence that the influence of gap mean area (Figure 3a), the distance to water (Figure 3b), the canopy density (D0, Figure 3c) and the standard deviation of vegetation height (Hsd, Figure 3d) explain how bat habitat use differed between *M. brandtii* and *M. mystacinus* (Table 2).

M. brandtii selected forests with smaller gaps and lower canopy density compared to *M. mystacinus* (Figure 3). Both *M. brandtii* and *M. mystacinus* selected for foraging habitat with higher standard deviations of vegetation height and habitat near water resources. Proximity to water was a stronger explanatory variable for *M. brandtii* and increasing canopy height variation was a stronger explanatory variable for *M. mystacinus* (Figure 3).

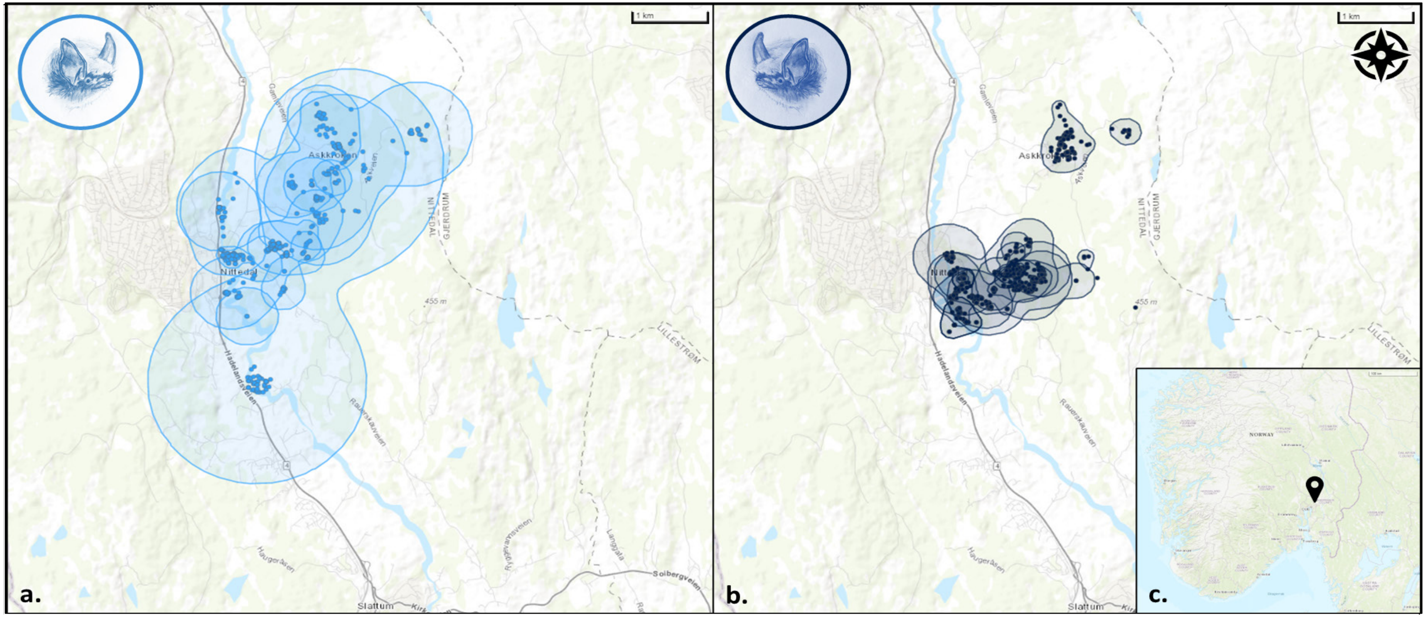


Figure 2. Map of the study area including the home ranges of each individual bat included in the study (n = 21) based on 95% kernel density estimation for each individual bat of *Myotis brandtii* (a., n = 9) and *M. mystacinus* (b., n = 12) located in Nittedal municipality in Southeastern Norway (c.). Base map: Leaflet | Carto DB.Voyager.

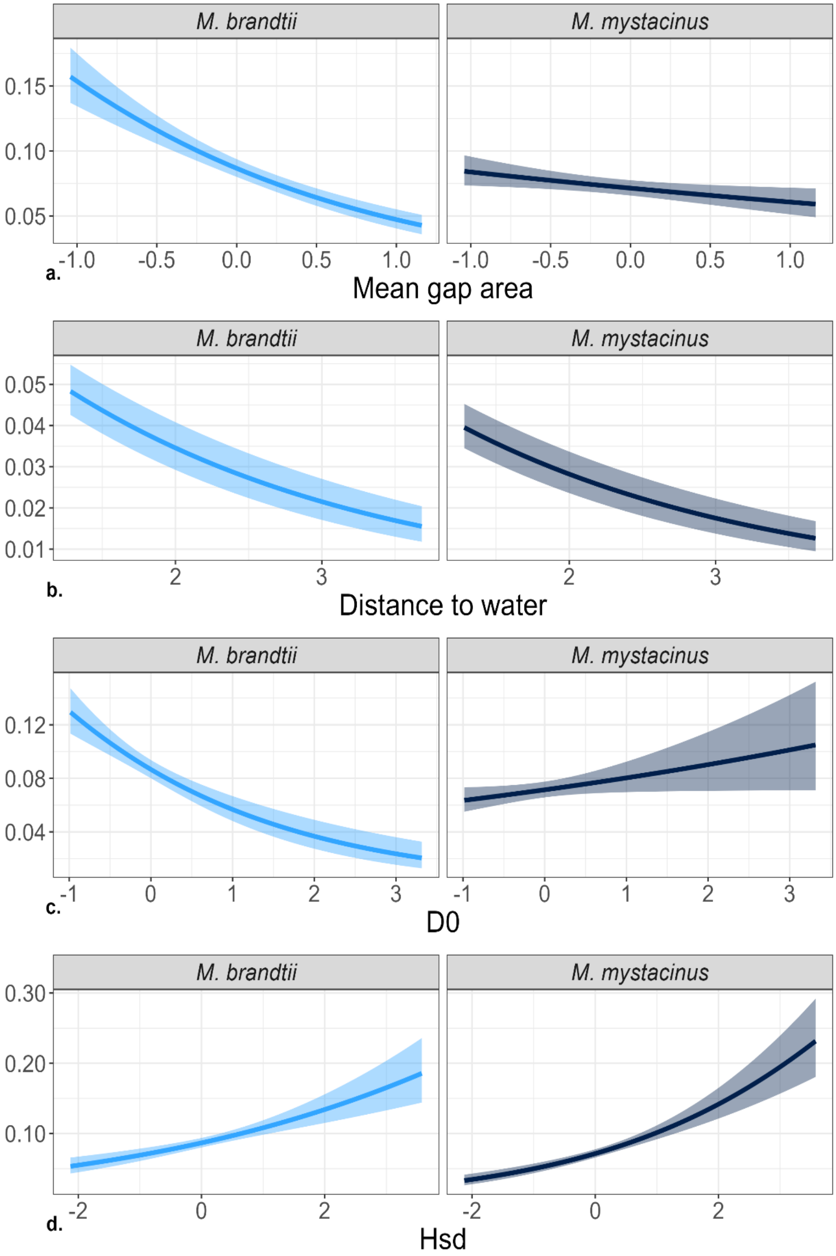


Figure 3. The estimated probability of use of a location within a 50 m radius circle on the landscape for each bat species in relation to amount of a.) mean gap area, b.) the distance to water c.) canopy density (D0), d.) the standard deviation of vegetation height (Hsd). Estimated relationships calculated from the final generalized mixed effect model shown in Table 2.

Table 1. Overview of bats tracked in this study. Date refers to the date of capture in 2018. The reproductive status when captured: NR = Non-reproductive, PR = Pregnant, LA = Lactating, PL = Post-lactating; NR* Indicates bats which were recaptured at other points in the field season with evidence of being reproductive. Days: the number of days each bat was tracked, home range (HR) area based on the 95% kernel density estimations, the number of observations of bats foraging within ~25 m of the observer (N fix), available points (N avail), and total points (N total) use in analyses.

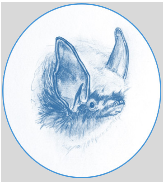
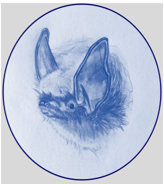
	Bat ID	Date	Repro	Days	N fix	N avail	N total	HR area (m2)
 ***Myotis brandtii***	B1	13.06	NR	7	91	910	1001	0.11
	B2	14.06	NR	7	101	1010	1111	0.83
	B3	5.07	LA	8	49	490	539	5.23
	B4	5.07	LA	8	39	390	429	4.05
	B5	20.07	NR	10	141	1410	1551	1.6
	B6	23.07	PL	8	62	620	682	12.74
	B7	4.08	PL	6	81	810	891	7.59
	B8	4.08	PL	6	39	390	429	1.9
	B9	14.08	NR	11	83	830	913	1.94
Mean (n = 9)				7.9	76.2	762.2	838.4	4.0
 ***Myotis mystacinus***	M1	5.06	NR	6	16	160	176	0.46
	M2	5.06	NR	6	31	310	341	1.24
	M3	11.06	NR	2	8	80	88	0.12
	M4	12.06	NR	4	70	700	770	0.08
	M5	25.06	PR	5	55	550	605	0.3
	M6	25.06	NR*	10	134	1340	1474	0.39
	M7	11.07	PL	4	84	840	924	1.87
	M8	11.07	NR*	9	117	1170	1287	1.52
	M9	16.07	PL	3	28	280	308	0.4
	M10	21.07	PL	9	119	1190	1309	0.57
	M11	20.08	PL	7	90	900	990	1.05
	M12	20.08	PL	7	64	640	704	0.61
Mean (n=12)				6	68	680	748	0.72

Table 2. Summary of the final generalized linear mixed-effect model estimating the probability of use of a location within a 50 m radius on the landscape in relation to distance to nearest water body and the following 3 ALS metrics: the mean open area at 3 m height (mean gap area), the density of the canopy (D0), the standard deviation of vegetation height (Hsd) as well as the interaction of these variables with bat species. The total number of used and available points for both bat species included in the model was n= 16522, marginal R^2 = 0.129.

Explanatory variables	*Estimate*	*CI*	*z*	*p*
(Intercept)	-2.37	-2.49 – -2.25	37.30	**<0.001**
SpeciesM.mystacinus	-0.20	-0.38 – -0.03	-2.30	**0.021**
mean gap area	-0.62	-0.76 – -0.48	-8.68	**<0.001**
D0	-0.44	-0.58 – -0.31	-6.28	**<0.001**
Hsd	0.25	0.16 – 0.34	5.57	**<0.001**
Distance to water	-0.52	-0.59 – -0.45	14.47	**<0.001**
Species×mean gap area	0.43	0.24 – 0.63	4.32	**<0.001**
Species×D0	0.60	0.42 – 0.79	6.29	**<0.001**
Species×Hsd	0.14	0.01 – 0.27	2.13	**0.033**

Random Effects	*Variance*	*Standard deviation*	*n*
Bat ID	0.018	0.136	21

Genetic and dietary analysis

Genetic validation of bat species identification

Of the 50 fecal samples that went through DNA extraction, 47 successfully amplified in a bat species identification PCR. Of those, 43 samples were successfully sequenced in at least one direction. There were two samples for which only the reverse sequence was successful. There was 1 sample with field ID as *M. brandtii* that was revealed to belong to *M. mystacinus*; the remaining samples that were successfully sequenced agreed with their field ID (Table 3). There were 4 samples which belonged to *M. mystacinus* that were also radio-tagged in 2018 (M1, M2, M5, M8). Of those, only one was not successfully sequenced (M8) while the others agreed with their in-field species identification.

Table 3. Overview of the number of fecal samples that were successfully sequenced in each year for the bat DNA metabarcoding analyses, as well as the total number of samples that were successfully sequenced (Seq.) for each species and the number of samples that agreed with the original in-field species identification.

Bat DNA				
Species	2017	2018	Seq.	Correct ID
M brandtii	3	13	14	13
M. mystacinus	13	21	29	29[1]
Total	16	33	43	42

[1] There was one sample for which the original identification of the bat was ambiguous; but was initially identified as *M. brandtii*. This bat was also radio-tagged (M2) and was subsequently recaptured shortly after the initial capture, at which time it was determined the field ID was changed to *M. mystacinus*. The metabarcoding analysis confirmed that this individual was in fact *M. mystacinus*.

Bat diet

We successfully sequenced 45 fecal samples for arthropod DNA. This included 14 samples from *M. brandtii* bats (3 from 2017, 11 from 2018) and 31 from *M. mystacinus* bats (12 from 2017, 19 from 2018) of which 39 genetic verification of the bat species was possible (*M. brandtii,* n = 13, *M. mystacinus,* n = 26). Our dataset included a total of 177,711 reads; the median number of reads per sample was 3950 (min = 3857, max = 4000). We identified 156 distinct prey taxa across 113 genera, 50 families and 9 orders of arthropods (Figure 4, Table iii, supplementary materials) in the combined diet of *M. brandtii* (66 prey taxa total) and *M. mystacinus* (126 prey taxa total). The two bat species had 36 prey taxa in common, with 30 prey taxa that were unique to *M. brandtii* and 90 that were unique to *M. mystacinus.* The diet of both *M. brandtii* and *M. mystacinus* was dominated by Diptera and Lepidoptera prey (Figure 5, Table 4). All 4 radio-tagged bats for which we had fecal samples (M1, M2, M5, M8 also samples 50, 34, 63, 66 respectively; Figure 5) were successfully sequenced and included in diet analyses.

Alpha diversity

We found evidence for higher prey richness within a given sample for *M. brandtii* than *M. mystacinus* and a significant Species×Year interaction (supplementary materials, Table iv). However, the differences in mean values of alpha diversity between the two bat species and years was small (Figure 6). The coefficient of variance for observed alpha diversity for *M. brandtii* and *M. mystacinus* was 26.5 and 24.0, respectively.

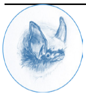
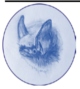
Beta diversity

We found differences in Beta diversity (i.e., differences in the community composition of arthropods found in the diet between *M. brandtii* and *M. mystacinus*) in all models for presence absence data as well as relative abundance data (supplementary materials, Table iv). P values were consistently lowest in models that explained differences in prey species diversity between *M. brandtii* and *M. mystacinus* using presence/absence of prey taxa compared to models which used relative abundance of prey taxa. However, the first two principal components of the PCoA based on prey taxa abundance better explained variation in the data than the presence-absence PCoA (Figure 7). It was clear from both analyses that there is much overlap in the diets of both bat species.

Bat Diet – Prey habitat

Prevalent prey taxa of both bat species were associated with forest, wetlands, and freshwater habitats but prey found in aquatic systems were more dominant in the diet of *M. mystacinus* (Figure 8). Crane flies, typically associated with aquatic habitats, feature heavily in the top prey taxa found in both bat diets, but account for nearly twice as much of the relative read abundance for *M. mystacinus* than for *M. brandtii* (Table 4). Moth species associated with forest habitats as well as *Hemerobius pini,* a lacewing highly associated with coniferous forests, were a more prevalent part of *M. brandtii* than of than *M. mystacinus* diet.

Table 4. The top 10 prey taxa found in the diets of *M. brandtii* and *M. mystacinus* and the abundance of sequence reads for each prey Order according to relative read abundance (RRA) calculated separately for each bat species. Prey taxa that could not be assigned to species level were assigned to lowest taxonomic level that was possible.

	Prey Taxa	**Abundance**	**Prey Order**	**Abundance**
 *M. brandtii*	*Ula* spp.	15.74	Diptera	48.05
	Epinotia tedella	12.41	Lepidoptera	39.85
	Argyresthia conjugella	10.40	Neuroptera	7.85
	Hemerobius pini	7.39	Hymenoptera	3.57
	Simulium vernum	6.64	Trichoptera	0.68
	Pseudatemelia josephinae	6.24		
	Eloeophila submarmorata	5.30		
	Tipula spp.	4.95		
	Rhipidia maculata	3.86		
	Campoplex tibialis	3.30		
 *M. mystacinus*	*Ula* spp.	21.88	Diptera	59.38
	Ula bolitophila	9.27	Lepidoptera	34.12
	Rhipidia maculata	8.81	Neuroptera	4.07
	Epinotia tedella	4.99	Orthoptera	0.72
	Phiaris bipunctana	4.96	Araneae	0.62
	Pseudatemelia josephinae	4.66	Trichoptera	0.57
	Argyresthia conjugella	4.62	Psocodea	0.24
	Tachinidae	2.70	Hymenoptera	0.21
	Tipula spp.	2.18	Coleoptera	0.08
	Hemerobius pini	2.12		

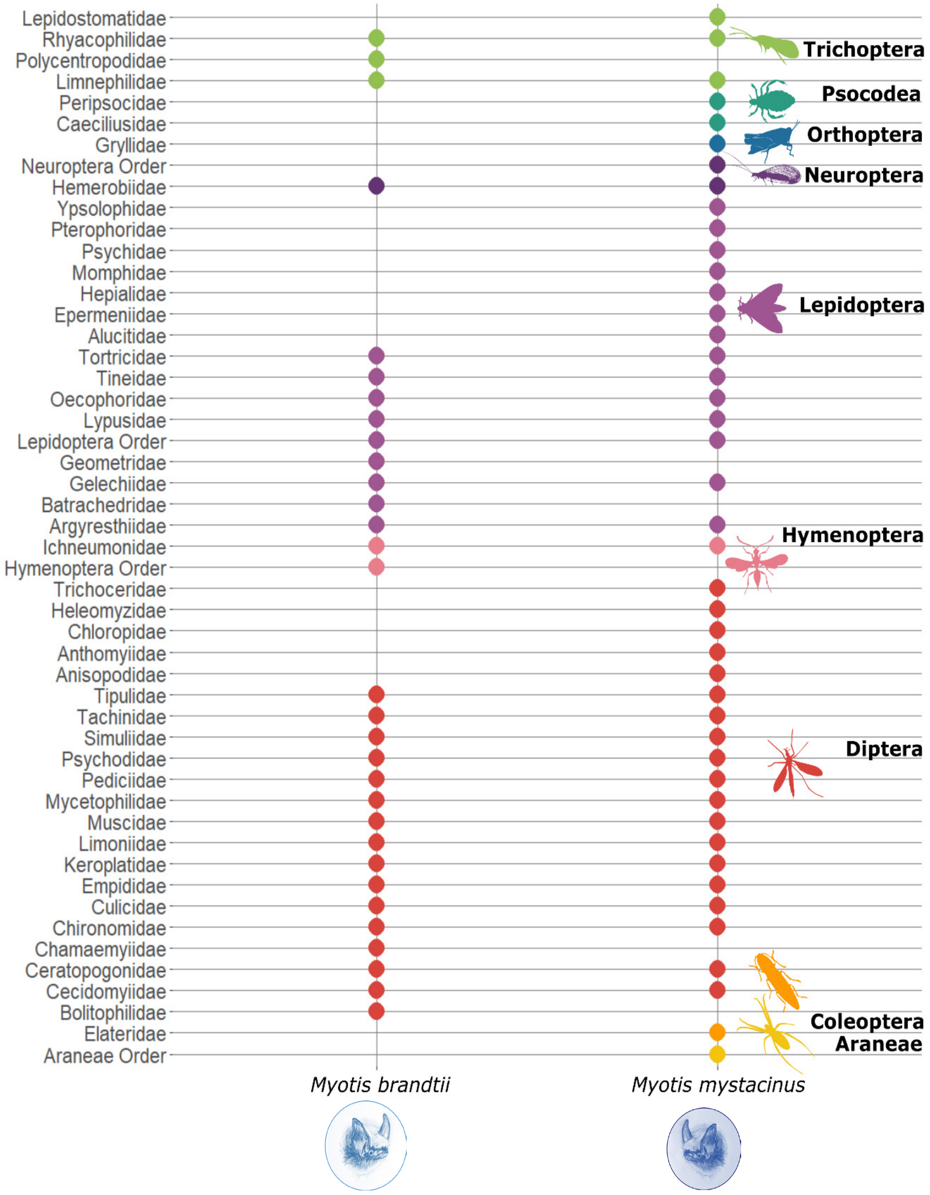


Figure 4. Presence and absence of different prey families, organized by prey order, found in the diet of *Myotis brandtii* and *M. mystacinus*. Prey taxa that could not be assigned to Family level are assigned to Order level.

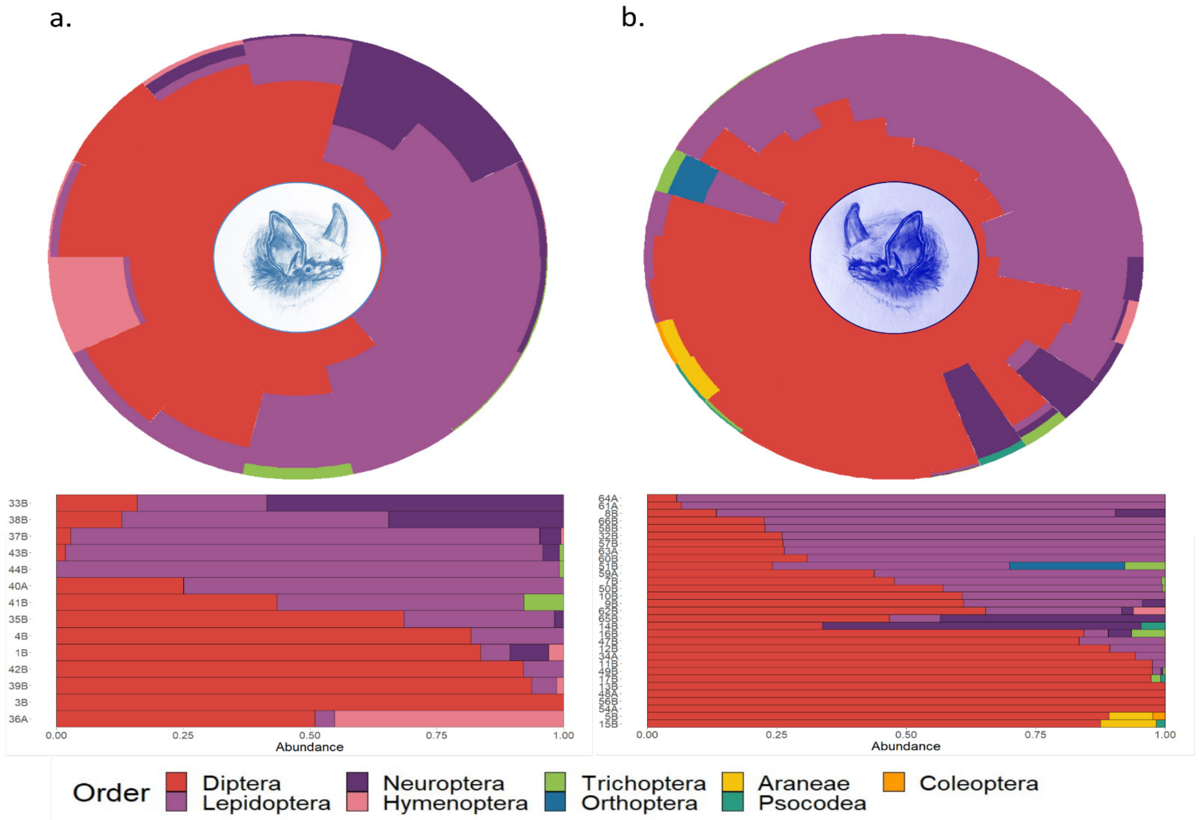


Figure 5. The relative abundance of different prey taxa orders for *Myotis brandtii* (a.) and *Myotis mystacinus* (b.) calculated on the prey Order level for each bat species separately. Iris plots (top) depict relative abundance calculated using PCA ordination with a centered log ratio transformation of sequence reads per sample and composition bar charts (bottom) wherein the relative abundance of reads is shown for each sample.

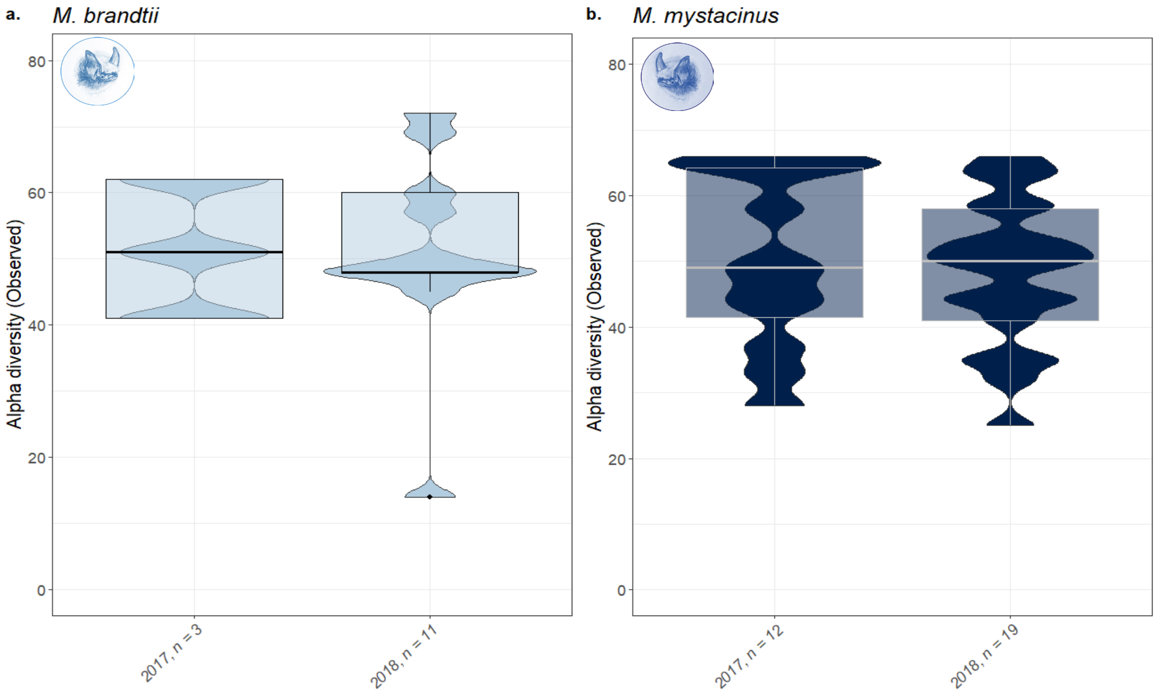


Figure 6. Violin plots overlayed with box plots of the alpha diversity calculated from the Observed Features (richness) diversity index of the arthropod taxa found in fecal samples from *Myotis brandtii* (a., n =14) and *Myotis mystacinus* (b., n = 31).

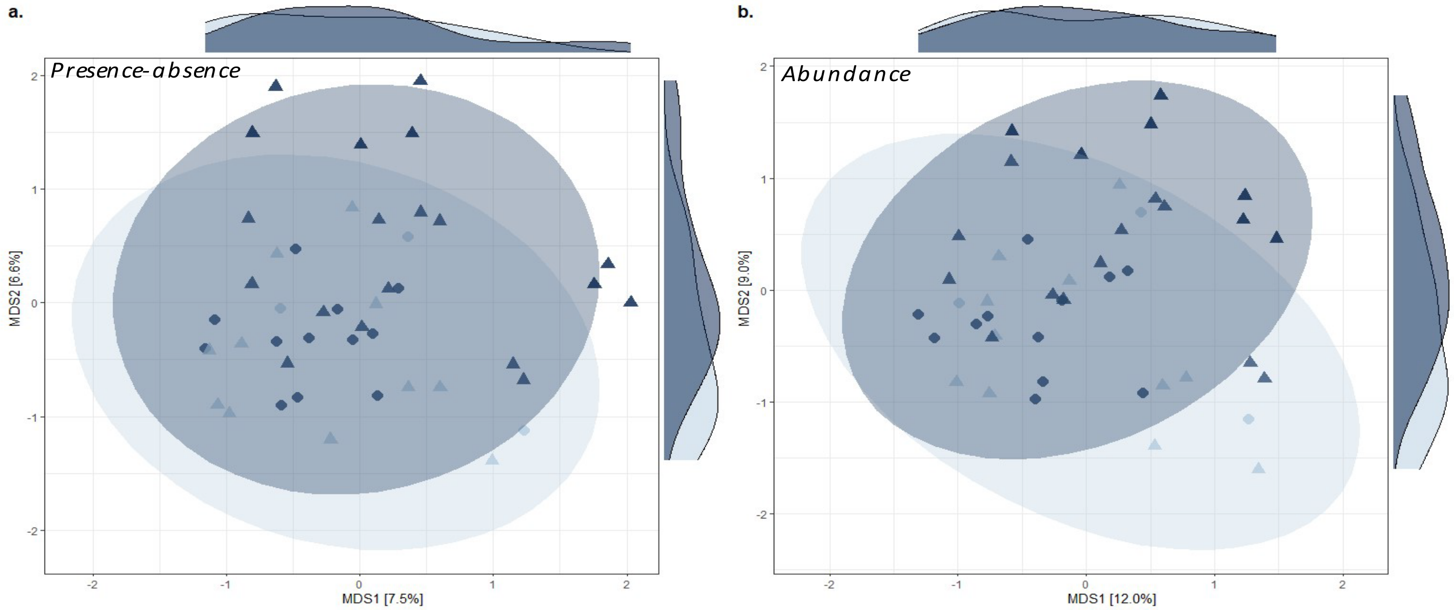


Figure 7. Principal coordinate analysis (PCoA) ordination of the degree of overlap in prey taxa detected in fecal samples of *Myotis brandtii* (light blue) or *M. mystacinus* (dark blue) collected in the summer of 2017 (circle) or 2018 (triangle) calculated with presence-absence of prey taxa using Jaccard distances (a.) and Bray – Curtis distances of log transformed arthropod prey taxa abundance (b.). Density plots along the x and y axes represent how samples were distributed in relation to axis scores. Prey taxa are grouped on species level of amplicon sequence variants (ASV) and each point is a fecal sample of a single individual.

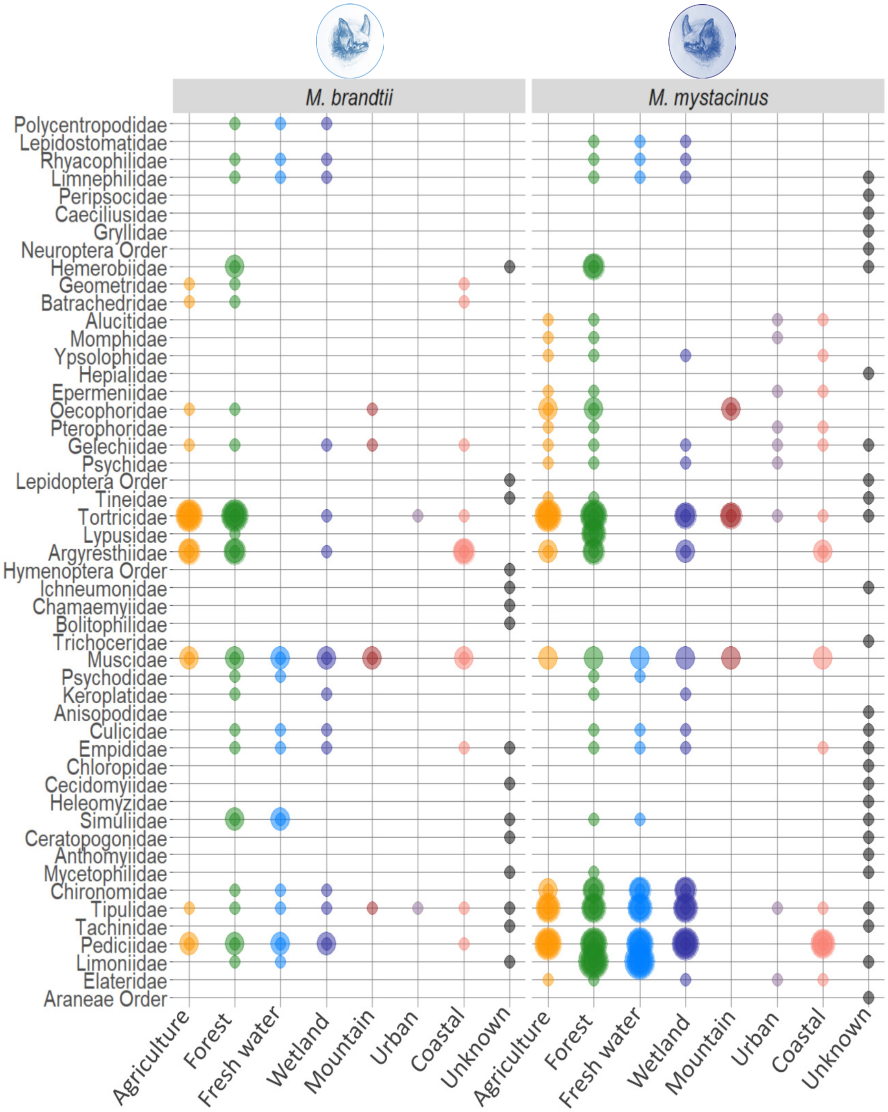


Figure 8. The prevalence (number of times the taxa occurred in a fecal sample for each bat species) of different prey taxa categorized by the habitats associated with different prey. Dot size corresponds to prevalence of the prey (1-7), the darkness of the dots corresponds to the number of repeated occurrences for a given taxa within the same family for each bat species.

Discussion

In our study, *M. brandtii* selected for continuous forests with low canopy density. *M. mystacinus* foraging in the same valley selected for more varied habitat that would include forests with higher canopy density and larger gap area which we interpret as forests with more varied 3-dimensional vegetation structure. Both species selected foraging habitats with variation in vegetation height and habitats closer to water bodies. *M. brandtii* and *M. mystacinus* had partly overlapping diets but we found evidence that individual *M. brandtii* had higher alpha diversity than *M. mystacinus* and that the beta diversity of the diet of the two species was significantly different when measured using presence/absence as well as abundance measurements of prey taxa. We found some evidence that the diet of *M. mystacinus* was more associated with aquatic environments while the diet of *M. brandtii* was more strongly associated with forest habitats.

Habitat use and home range size

To our knowledge, this is the first study to use 3-dimensional data describing vegetation structure in relation to bat foraging habitat using radiotelemetry methods. Previous studies have used ALS to describe bat foraging habitat using acoustics (Froidevaux et al. 2016; Hermans et al. 2023; Jung et al. 2012; Rauchenstein et al. 2022; Yoh et al. 2023) or bat roost selection with radiotelemetry methods (Carr et al. 2018). Earlier research on the habitat selection of *M. brandtii* and *M. mystacinus* have relied on 2-dimensional, categorical descriptions of habitat which lack finer scale and structural complexity of 3-dimensional descriptions that small, echolocating bats are likely to respond to. Even so, our own findings generally agree with the notion previously reported that *M. mystacinus* is associated with a variety of landscape types including forests, residential areas, and cultural landscapes whereas *M. brandtii* is more closely associated with forest habitats.

We can report that the *M. mystacinus* in our study area selected for varied forests with both high canopy density and large gap areas. In the context of our study area, this would include forest patches neighboring residential areas and agricultural lands. *M. brandtii* was more associated with forest habitats with a variation in vegetation height that had low gap area and low canopy density, suggesting a selection on mature and diversely aged, continuous forests. Habitat with heterogenous vegetation height (Hsd, i.e., forest with diverse canopy heights) were important for both bat species, but we found a stronger positive relationship between *M. mystacinus* use and Hsd, which also provides evidence for their appeal toward more varied habitat (Table 2, Figure 3).

Amount of gap area decreased with probability of habitat use for both species, but this relationship was much stronger for *M. brandtii* than *M. mystacinus* (Figure 3) suggesting *M. brandtii* forages in more intact forests than *M. mystacinus*. Earlier studies have found that *M. brandtii* appears to be more dependent on forested landscapes (Berge 2007; Buckley et al. 2013; Kurek et al. 2020; Roswag et al. 2019; Taake 1984; Vaughan, Jones, and Harris 1997). Berge (2007) found that *M. brandtii* was more associated with coniferous woodlands, and that *M. mystacinus* was more frequently recorded using gardens or park areas.

We found that proximity to water had the highest explanatory power for habitat use of all direct effects for both bat species (Table 2, Figure 3). Distance to water had a slightly more negative relationship for *M. brandtii* than *M. mystacinus*. In our study area where one river and several creeks were the main water resources, riparian habitat can also be considered an important foraging area for both *M. brandtii* and *M. mystacinus* in this study. Aquatic insects were dominant in the diet of both bat species, but this was most obvious for *M. mystacinus*. Berge (2007) and Taake (1984) both agreed that riparian areas were more important for *M. brandtii* than *M. mystacinus*. Aquatic habitats bordering forests such as swamps and wetlands have been identified as important habitat for *M. brandtii* (Budinski and López-Baucells 2023). Vernal pools which appear in a broad variety of landscapes can also be an important bat foraging habitat (Marteau et al. 2023), which could be part of how *M. mystacinus* targeted its aquatic prey in our study area.

Roswag et al., (2019) compared the habitat use of *M. brandtii* and *M. mystacinus* using stable isotopes and found that *M. mystacinus* was also more closely associated with aquatic environments. Conversely to our findings and other previous research, the authors of this study reported that *M. brandtii* was less associated with forests and more so with open habitats than *M. mystacinus*.

How much *M. mystacinus* relies on a particular type of habitat varies throughout its range and can include deserts, mountains as well as urban areas (Albayrak 1991; Budinski and López-Baucells 2023; Piksa 2008). In Ireland, Buckley et al. (2013) found that diverse habitats including arable land, woodlands as well as riparian areas were important foraging areas for *M. mystacinus*. The study of Buckley et al. (2013) took place in a landscape mosaic with varied habitats available, similar to our own study area.

The more generalist habitat use of *M. mystacinus* may explain why *M. mystacinus* travelled shorter distances than *M. brandtii* in our study area which was composed of a mosaic of landscape types. *M. brandtii* perhaps had to travel further to access more continuous forest habitats. The larger home ranges reported in *M. brandtii* for our study are contributed from bats that travelled longer distances to reach specific foraging patches that were far apart from each other (Figure 1).

Diet

Ula spp. were the most abundant prey taxa for both *M. brandtii* and *M. mystacinus*. Top prey taxa for *M. brandtii* were dominated by moth and lacewing species associated with forests whereas *M. mystacinus* top prey taxa were more so composed of aquatic and generalist Diptera. Top prey taxa for both bat species included *Epinotia tedella, Argyresthia* *conjugella, Pseudatemelia josephinae,* and *Hemerobius pini* which all feed heavily on tree species that are important for forestry or agriculture (Table 4).

The species richness within a given fecal sample was slightly higher for *M. brandtii,* though our study included over twice as many samples for *M. mystacinus.* As such, it is not surprising that we detected nearly twice as many different taxa in the pooled diet of *M. mystacinus* compared to *M. brandtii*. The two bat species had very similar diets in terms of the Order of prey taxa but there were only 36 out of the 156 prey taxa detected that were found in the diet of both *M. brandtii* and *M. mystacinus.* Both bats, and especially *M. mystacinus,* preyed heavily on arthropods associated with aquatic ecosystems (Figure 8). This generally agrees with our findings from the resource selection function analysis. While *M. brandtii* had a slightly higher tendency to select habitat near water, *M. mystacinus* was more associated with open habitats which could include wetlands or ephemeral water resources such as vernal pools in our study area. Vernal pools were not included in the distance to water bodies metric used in the RSF because we could not be sure if or when the pools were dried during the study period. However, only 4 radio-tagged bats were also included in the diet analyses so drawing direct comparison between the diet analyses and spatial analyses is inherently limited.

M. brandtii and *M. mystacinus* are frequently categorized as some variation of edge-space aerial foragers (Froidevaux et al. 2016; Norberg and Rayner 1987; Müller et al. 2013) and are both considered dietary generalists (Roswag et al. 2019). Previous studies have found that the diet of both *M. brandtii* and *M. mystacinus* is dominated by Lepidoptera, Diptera, and may also contain large proportions of Coleoptera and Araneae (Beck 1995; Berge 2007; Roswag et al. 2019; Vesterinen et al. 2018). However, only one of these earlier studies directly compares *M. brandtii* and *M. mystacinus* alone (Berge, 2007) and the two latter (Roswag et al. 2019; Vesterinen et al. 2018) used genetic methods to describe bat diets but the number of samples for each species made it difficult to compare *M. brandtii* and *M. mystacinus* directly. There remains a lack of detailed comparisons of the diet of *M. brandtii* and *M. mystacinus* in the Fennoscandian region using molecular methods. Vesterinen et al., (2018) studied the diet of *M. brandtii* and *M. mystacinus* in combination with three other common bat species in Finland but had 10 times more samples of *M. brandtii* than *M. mystacinus;* they found that Lepidoptera was the most dominant part of the diet for *M. brandtii* and *M. mystacinus* and reported no strong differences in the prey communities between the species. Lepidoptera were a dominant part of the diet for both bats in our study, but Diptera prey were far more abundant for both bats and especially *M. mystacinus* (Table 4). We found Araneae and Coleoptera only in the diet of *M. mystacinus,* though this may simply be due to our low sample size.

We found that Neuroptera was the third most abundant prey order for both bat species but made up 7.9 % of the prey taxa detected in *M. brandtii* and only 4.1 % for *M. mystacinus* (Table 4). To our knowledge, Neuroptera have not been previously reported as important in the diet of *M. brandtii* and *M. mystacinus*. Perhaps in our study area, Neuroptera was more abundant and therefore opportunistically more heavily preyed upon. Given that there are special constraints placed on bats at higher latitudes in terms of reduced darkness, shortened night periods and a cooler climate, it may be the case that bat species living at northern latitudes are reliant on more energy rich prey and more intensive foraging to compensate for time lost during short summer nights (Boyles et al. 2016; Kaupas and Barclay 2018). Many species of Neuroptera will hatch into adults in large numbers simultaneously. In such cases, Neuroptera could have been an important ephemeral prey resource that bats can exploit. Future studies, especially those at far northern latitudes, should consider how energy richness as well as ephemerality of arthropods influences prey choice in bats. This could be of vital importance as climate change influences range shifts and phenological cycles of arthropods as well as insectivores (Bolduc et al. 2013; Vafidis, Smith, and Thomas 2019).

In our study, between-species differences in beta diversity of prey in the diet of *M. brandtii* and *M. mystacinus* were difficult to detect from visualizations using ordination (Figure 7) but bat species had a consistent strong explanatory power of prey community composition (supplementary materials, Table iv). More samples from diverse populations over a longer period would provide further clarity as to how much prey species diversity varies between *M. brandtii* and *M. mystacinus*.

Resource partitioning

The differences in habitat selection and diet found in this study show consistent differences between *M. brandtii* and *M. mystacinus*, which suggests some degree of resource partitioning. There was still much overlap in areas used for foraging as well as in diet for the bats in our study. An important limitation of the study is that the bats included in the resource selection function analysis were not all the same individuals as those included in the diet analyses, and our sampling was focused on bats found foraging within one valley. Additionally, we could only confirm the species identification for 3 of the radio-tagged bats using genetic methods. However, of the 42 fecal samples that were successfully sequenced for bat DNA, only one had an incorrect in-field identification so we are confident in our ability to differentiate the two species in hand. Also, all the bats included in the spatial analyses were adult females, most of which were reproductive, so the habitat use reported in our study is probably related to the high energy demands connected to pregnancy and lactation. The limitations in time and space as well as sample size for our study mean that our findings do not provide conclusive evidence of the existence of resource partitioning in *M. brandtii* and *M. mystacinus*. Our findings do, however, provide important insights about the foraging ecology of *M. brandtii* and *M.*

mystacinus living in the northern extent of their ranges.

Other studies that explore resource partitioning between *Myotis* species have found that prey size is an important feature to consider (Divoll et al. 2022; Vesterinen et al. 2018). It was outside of the scope of this study to use prey size as an explanatory variable for differences in diet but given the similarity in size of *M. brandtii* and *M. mystacinus* as well as their similarities in echolocation, we did not expect prey size to be an important feature describing their differences. When Vesterinen et al., (2018) compared prey size between *M. brandtii* and *M. mystacinus,* they found no strong evidence of difference.

The hypothesis that the ecological roles of *M. brandtii* and *M. mystacinus* should be distinct from one another is in large part due to their lack of genetic relatedness (Bickham et al. 2004; Ruedi and Mayer 2001). However, there is some debate as to whether or not *M. brandtii* may be more closely related to European species than previously thought (Korstian et al. 2022). Regardless of the genetic relatedness of *M. brandtii* and *M. mystacinus*, it may be the case that these two species have flexible ecological roles which allow them to live in sympatry with limited competition, which would also explain their broad range distributions.

More modern theories on evolution question the abilities of classic theories of the ecological niche to account for the nuanced relationships between species and their environments that genetic studies frequently reveal (Holt 2009; Odling-Smee et al. 2013). Others have postulated that the concept of a niche is not useful at all (Kimura 1991; McInerny and Etienne 2012). Perhaps low levels of competition where *M. brandtii* and *M. mystacinus* co-occur have led to sympatric or neutral relationships which over time has been expressed in similar morphological features. Bickford et al., (2007) theorized that cryptic species may more often occur when evolving under extreme environmental constraints which limited their ability to evolve diverse physical traits. Following this logic, it may be the case that *M. brandtii* and *M. mystacinus* are sharing an ecological niche, with little or no resource partitioning between them. When competition is low but environmental stressors are high and diverse, the diversification of morphological traits may be reduced while allowing the two species to live in sympatry as adaptive generalists.

Conclusion

Combining ALS descriptions of habitat use by radio-tagged *M. brandtii* and *M. mystacinus* and combining this method of studying foraging habitat selection as well as genetic metabarcoding diet analyses provides unique insights on potential resource partitioning of these two sympatric species that are commonly pooled in bat surveys. Our study is also amongst the first to compare the foraging ecologies of this cryptic pair of species in detail at the northern extent of their ranges. The results of our resource selection function analysis provide further evidence that *M. brandtii* is more associated with continuous forest habitats whereas *M. mystacinus* selects foraging habitats in less continuous forests bordering a variety of landscapes. The differences in the diet of these two species suggest that *M. mystacinus* may be more associated with aquatic systems while *M. brandtii* consumed a higher proportion of moths and lacewings associated with forest habitats. We found considerable overlap in the diet and habitat use with some evidence for resource partitioning between the two species. Future studies can draw on our findings to further explore differences in the foraging ecology between *M. brandtii* and *M. mystacinus*.

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Author contributions

Reed April McKay: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Franz Hoelzl:** Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Jeroen van der Kooij:** Conceptualization (supporting), Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Rune Sørås:** Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Hans Ole Ørka:** Formal analysis (supporting); Investigation (supporting); Resources (supporting); Visualization (supporting); Writing – review and editing (supporting). **Steve Smith:** Methodology (supporting); Resources (supporting). **Clare Stawski**: Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Katrine Eldegard:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – review and editing (supporting).

Ethics statement

All wildlife included in this study were handled with the appropriate permits and ethical considerations. Capturing, handling, and marking of wildlife were all in accordance with permitted authorizations from the Norwegian Environment Agency (Miljødirektoratet) and the Norwegian Food Safety Authority (Mattilsynet).

Data availability statement

The workflows for analyses are available on GitHub: https://github.com/airmckay/ForagingEcology2SimilarSympatricBatSpecies. The data will be stored in a repository such as Dryad when this manuscript is accepted for publication in a scientific journal. Inquiries about the data and how it was analyzed or managed are welcome and can be addressed to Reed April McKay (reed.april.mckay@nmbu.no).

Supplementary materials

Table i. Summary of the 10 sites where tagged bats were captured. Bat individuals with "*" indicate a recapture in the summer of 2018. Individuals that were recaptured during studies in 2019 are indicated by "**".

Site ID	Captured	Site Description	Bat ID	
			M. brandtii	***M. mystacinus***
N1	05.06	Riparian forest edge		M1, M2
N2	07.06	Pond in cropland	B0	
HM	11.06	House – *M. mystacinus* colony		M3, M4, M2*
	25.06			M5, M6
HB	13.06	House – *M. brandtii* colony	B1, B2	
N3	03.07	Coniferous forest edge	B3, B4	
N4	11.07	Mixed forest edge		M7, M8
H2	16.07	*M. mystacinus* colony		M9
	20.08			M10
N5	20.07	Coniferous forest, logging road	B5	M11
N6	21.07	Coniferous forest, logging road		M12
	22.07		B6	
N7	04.08	Pond in coniferous forest	B7, B8	
	14.08		B9	

Table ii. Summary of the body weight, transmitter weight as well as the percent body weight added by the tag and the days tracked for each bat. B0 was not included in spatial analyses because no fixes (observations within ~25 m) were collected from this individual.

	Bat ID	Bat weight	Transmitter weight	% of bodyweight	Days tracked
M. brandtii	B0	5.8	0.31	5.34	3
	B1	6.91	0.32	4.63	7
	B2	8.5	0.32	3.76	7
	B3	7.6	0.32	4.21	8
	B4	5.7	0.32	5.61	8
	B5	6.18	0.31	5.02	10
	B6	5.62	0.31	5.52	8
	B7	5.44	0.31	5.70	6
	B8	6.51	0.32	4.92	6
	B9	6.23	0.31	4.98	11
M. mystacinus	M1	4.3	0.31	7.21	6
	M2	5.0	0.31	6.20	6
	M3	5.6	0.31	5.54	2
	M4	6.1	0.31	5.08	4
	M5	7.3	0.31	4,25	5
	M6	7.3	0.32	4,38	10
	M7	5.0	0.31	6.20	4
	M8	5.6	0.32	5.71	9
	M9	6.26	0.31	4.95	3
	M10	5.56	0.31	5.58	9
	M11	4.93	0.31	6.29	7
	M12	4.95	0.31	6.26	7

Table iii. Overview of the different pray taxa found in the diet of *M. mystacinus and M. brandtii* from fecal samples collected from individual bats in Nittedal, Norway in the summers of 2017 and 2018. When the taxa were found in the diet of both bat species, “Both” is indicated, otherwise the arthropod taxa were found in only one of the bat diets.

Prey Order	**Prey Taxa**	**Bat Species**
Araneae	*Araneae*	*M. mystacinus*
Coleoptera	*Denticollis linearis*	*M. mystacinus*
Diptera	*Aedes communis*	Both
Diptera	*Bolitophila* spp.	*M. brandtii*
Diptera	*Bolitophila cinerea*	*M. brandtii*
Diptera	*Cecidomyiidae*	Both
Diptera	*Chamaemyiidae*	*M. brandtii*
Diptera	*Coelosia silvatica*	*M. brandtii*
Diptera	*Culicoides impunctatus*	Both
Diptera	*Eloeophila submarmorata*	Both
Diptera	*Empididae*	*M. brandtii*
Diptera	*Epiphragma* spp.	*M. brandtii*
Diptera	*Leia subfasciata*	*M. brandtii*
Diptera	*Macrocera angulata*	Both
Diptera	*Mycetophila fungorum*	*M. brandtii*
Diptera	*Mycetophilidae*	*M. brandtii*
Diptera	*Mycomya trivittata*	Both
Diptera	*Ormosia ruficauda*	*M. brandtii*
Diptera	*Palpomyia lineata*	*M. brandtii*
Diptera	*Paratanytarsus natvigi*	*M. brandtii*
Diptera	*Polypedilum albicorne*	*M. brandtii*
Diptera	*Polypedilum convictum*	Both
Diptera	*Psychoda phalaenoides*	Both
Diptera	*Rhamphomyia* spp.	*M. brandtii*
Diptera	*Rhamphomyia nigripennis*	Both
Diptera	*Rhipidia maculata*	Both
Diptera	*Simulium* spp.	Both
Diptera	*Simulium vernum*	Both
Diptera	*Tachinidae*	Both
Diptera	*Tanytarsus longitarsis*	Both
Diptera	*Thricops semicinereus*	*M. brandtii*
Diptera	*Tipula* spp.	Both
Diptera	*Tipula maxima*	*M. brandtii*
Diptera	*Tipula repanda*	*M. brandtii*
Diptera	*Tipula varipennis*	*M. brandtii*
Diptera	*Tricyphona alticola*	Both
Diptera	*Ula bolitophila*	Both
Diptera	*Ula spp.*	Both

Diptera	*Actia pilipennis*	*M. mystacinus*
Diptera	*Aedes* spp.	*M. mystacinus*
Diptera	*Aedes sticticus*	*M. mystacinus*
Diptera	*Anthomyiidae*	*M. mystacinus*
Diptera	*Chironomidae*	*M. mystacinus*
Diptera	*Chironomus lugubris*	*M. mystacinus*
Diptera	*Chloropidae*	*M. mystacinus*
Diptera	*Dicranomyia frontalis*	*M. mystacinus*
Diptera	*Dicranomyia modesta*	*M. mystacinus*
Diptera	*Erioptera* spp.	*M. mystacinus*
Diptera	*Helina* spp.	*M. mystacinus*
Diptera	*Hilara quadrifasciata*	*M. mystacinus*
Diptera	*Limonia nubeculosa*	*M. mystacinus*
Diptera	*Limoniidae*	*M. mystacinus*
Diptera	*Linnaemya picta*	*M. mystacinus*
Diptera	*Macropelopia notata*	*M. mystacinus*
Diptera	*Metriocnemus eurynotus*	*M. mystacinus*
Diptera	*Molophilus* spp.	*M. mystacinus*
Diptera	*Mycetophila signatoides*	*M. mystacinus*
Diptera	*Mycomya levis*	*M. mystacinus*
Diptera	*Mycomya ruficollis*	*M. mystacinus*
Diptera	*Nephrotoma* spp.	*M. mystacinus*
Diptera	*Nephrotoma tenuipes*	*M. mystacinus*
Diptera	*Neuratelia* spp.	*M. mystacinus*
Diptera	*Ormosia lineata*	*M. mystacinus*
Diptera	*Orthocladius frigidus*	*M. mystacinus*
Diptera	*Polylepta guttiventris*	*M. mystacinus*
Diptera	*Polypedilum quadriguttatum*	*M. mystacinus*
Diptera	*Rhamphomyia geniculata*	*M. mystacinus*
Diptera	*Rhamphomyia umbripennis*	*M. mystacinus*
Diptera	*Rheotanytarsus pentapoda*	*M. mystacinus*
Diptera	*Stenochironomus gibbus*	*M. mystacinus*
Diptera	*Suillia bicolor*	*M. mystacinus*
Diptera	*Sylvicola cinctus*	*M. mystacinus*
Diptera	*Tanytarsus eminulus*	*M. mystacinus*
Diptera	*Thienemannimyia carnea*	*M. mystacinus*
Diptera	*Tipula iberica*	*M. mystacinus*
Diptera	*Tipula lunata*	*M. mystacinus*
Diptera	*Tipulidae*	*M. mystacinus*
Diptera	*Trichocera regelationis*	*M. mystacinus*
Diptera	*Ula mixta*	*M. mystacinus*
Hymenoptera	*Campoplex tibialis*	Both
Hymenoptera	*Hymenoptera*	*M. brandtii*
Hymenoptera	*Ichneumonidae*	*M. mystacinus*
Lepidoptera	*Ancylis diminutana*	*M. brandtii*

Lepidoptera	*Ancylis myrtillana*	Both
Lepidoptera	*Argyresthia brockeella*	*M. brandtii*
Lepidoptera	*Argyresthia conjugella*	Both
Lepidoptera	*Argyresthia glabratella*	Both
Lepidoptera	*Argyresthia retinella*	Both
Lepidoptera	*Batrachedra pinicolella*	*M. brandtii*
Lepidoptera	*Carpatolechia fugitivella*	Both
Lepidoptera	*Carpatolechia proximella*	*M. brandtii*
Lepidoptera	*Cnephasia asseclana*	*M. brandtii*
Lepidoptera	*Denisia stipella*	Both
Lepidoptera	*Epinotia tedella*	Both
Lepidoptera	*Eupithecia tantillaria*	*M. brandtii*
Lepidoptera	*Lathronympha strigana*	*M. brandtii*
Lepidoptera	*Lepidoptera*	Both
Lepidoptera	*Montescardia tessulatellus*	*M. brandtii*
Lepidoptera	*Orthotaenia undulana*	Both
Lepidoptera	*Pseudatemelia josephinae*	Both
Lepidoptera	*Syndemis musculana*	Both
Lepidoptera	*Zeiraphera ratzeburgiana*	*M. brandtii*
Lepidoptera	*Acompsia cinerella*	*M. mystacinus*
Lepidoptera	*Adoxophyes orana*	*M. mystacinus*
Lepidoptera	*Aethes margaritana*	*M. mystacinus*
Lepidoptera	*Alucita hexadactyla*	*M. mystacinus*
Lepidoptera	*Ancylis badiana*	*M. mystacinus*
Lepidoptera	*Apotomis turbidana*	*M. mystacinus*
Lepidoptera	*Argyresthia bergiella*	*M. mystacinus*
Lepidoptera	*Argyresthia sorbiella*	*M. mystacinus*
Lepidoptera	*Capua vulgana*	*M. mystacinus*
Lepidoptera	*Celypha lacunana*	*M. mystacinus*
Lepidoptera	*Chionodes electella*	*M. mystacinus*
Lepidoptera	*Chionodes lugubrella*	*M. mystacinus*
Lepidoptera	*Eana argentana*	*M. mystacinus*
Lepidoptera	*Epermenia illigerella*	*M. mystacinus*
Lepidoptera	*Epinotia pygmaeana*	*M. mystacinus*
Lepidoptera	*Epinotia ramella*	*M. mystacinus*
Lepidoptera	*Epinotia signatana*	*M. mystacinus*
Lepidoptera	*Epinotia tenerana*	*M. mystacinus*
Lepidoptera	*Eulia ministrana*	*M. mystacinus*
Lepidoptera	*Gillmeria pallidactyla*	*M. mystacinus*
Lepidoptera	*Helcystogramma rufescens*	*M. mystacinus*
Lepidoptera	*Korscheltellus fusconebulosa*	*M. mystacinus*
Lepidoptera	*Lobesia reliquana*	*M. mystacinus*
Lepidoptera	*Lobesia virulenta*	*M. mystacinus*
Lepidoptera	*Metendothenia atropunctana*	*M. mystacinus*
Lepidoptera	*Mompha subbistrigella*	*M. mystacinus*

Lepidoptera	*Morophaga choragella*	*M. mystacinus*
Lepidoptera	*Nemapogon cloacella*	*M. mystacinus*
Lepidoptera	*Nemapogon nigralbella*	*M. mystacinus*
Lepidoptera	*Pandemis cinnamomeana*	*M. mystacinus*
Lepidoptera	*Phiaris bipunctana*	*M. mystacinus*
Lepidoptera	*Pseudargyrotoza conwagana*	*M. mystacinus*
Lepidoptera	*Stictea mygindiana*	*M. mystacinus*
Lepidoptera	*Taleporia tubulosa*	*M. mystacinus*
Lepidoptera	*Thyraylia nana*	*M. mystacinus*
Lepidoptera	*Ypsolopha parenthesella*	*M. mystacinus*
Neuroptera	*Hemerobius* spp.	*M. brandtii*
Neuroptera	*Hemerobius perelegans*	Both
Neuroptera	*Hemerobius pini*	Both
Neuroptera	*Wesmaelius concinnus*	Both
Neuroptera	*Hemerobiidae*	*M. mystacinus*
Neuroptera	*Hemerobius contumax*	*M. mystacinus*
Neuroptera	*Hemerobius fenestratus*	*M. mystacinus*
Neuroptera	*Neuroptera*	*M. mystacinus*
Orthoptera	*Gryllus bimaculatus*	*M. mystacinus*
Psocodea	*Peripsocus subfasciatus*	*M. mystacinus*
Psocodea	*Valenzuela despaxi*	*M. mystacinus*
Trichoptera	*Limnephilus coenosus*	Both
Trichoptera	*Plectrocnemia conspersa*	*M. brandtii*
Trichoptera	*Rhadicoleptus alpestris*	Both
Trichoptera	*Rhyacophila fasciata*	Both
Trichoptera	*Halesus tessellatus*	*M. mystacinus*
Trichoptera	*Lepidostoma hirtum*	*M. mystacinus*
Trichoptera	*Limnephilus fuscicornis*	*M. mystacinus*

Table iv. Summaries of the models used to describe the relationship between alpha and beta diversity indices with bat species and year associated with the fecal samples. a.) The first three model summaries are of linear mixed-effect models describing the relationship between sample alpha diversity, bat species and year (M_alpha1, M_alpha2, M_alpha3). b.) The following summaries describe permutational multivariate analysis of variance (PERMANOVA) outputs for the models describing the relationship between beta diversity defined by the Jaccard measures of community dissimilarity calculated with presence/absence of prey taxa (J_beta1, J_beta2, J_beta3) and Bray-Curtis measure of community dissimilarity calculated with the logarithmic-scaled read abundance of prey taxa (B_beta1, B_beta2, B_beta3).

a. Alpha diversity

Linear mixed-effect models		*Estimate*	*T*	*SE*	*p*	*DF*
M_alpha1	(Intercept)	85.849	46.148	1.860	(<0.001)	8135
	Bat species	122.848	-59.065	2.080	(<0.001)	41
	Year	9.345	4.453	2.099	(<0.001)	41
	Bat species * Year	-10.157	-4.212	2.412	(<0.001)	41
M_alpha2	(Intercept)	91.892	77.613	1.184	(<0.001)	81135
	Bat species	130.402	-123.848	1.053	(<0.001)	42
	Year	1.653	1.599	1.034	(0.117)	42
M_alpha3	(Intercept)	93.191	108.205	0.861	(<0.001)	81135
	Bat species	130.688	-125.945	1.038	(<0.001)	43

b. Beta diversity

PERMANOVA		*SumOfSqs*	*R^2*	*F*	*Pr(>F)*	*DF*
J_beta1	Bat species	0.650	0.033	1.512	0.005	1
	Year	0.616	0.032	1.433	0.011	1
	Bat species * Year	0.651	0.033	1.515	0.003	1
	Residual	17.616	0.902			41
	Total	19.532	1.000			44
J_beta2	Bat species	0.645	0.033	1.493	0.006	1
	Year	0.616	0.0315	1.416	0.016	1
	Residual	18.267	0.9352			42
	Total	19.532	1.000			44
J_beta3	Bat species	0.6495	0.033	1.480	0.013	1
	Residual	18.8825	0.967			43
	Total	19.532	1.000			44
B_beta1	Bat species	0.613	0.034	1.578	0.034	1
	Year	0.642	0.036	0.650	0.022	1
	Bat species * Year	0.667	0.037	1.716	0.019	1
	Residual	15.942	0.892			41
	Total	17.864	1.000			44
B_beta2	Bat species	0.613	0.034	1.551	0.042	1
	Year	0.642	0.036	1.622	0.02	1
	Residual	16.609	0.930			42
	Total	17.864	1.000			44
B_beta3	Bat species	0.613	0.034	1.529	0.041	1
	Residual	17.251	0.966			43
	Total	17.864	1.000			44

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