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Abstract. This study explores the spatial distribution of bats around lakes in valleys around 62° N in western Norway. Stationary ultrasound detectors were used to record ultrasound at various distances from the shores of lakes during the bats late pregnancy and lactation period. In this landscape, northern bat was the most commonly recorded species, followed by *Myotis* bats (pooled) and the soprano pipistrelle. None of the other European bat genera were present. There was a clear non-linear distribution pattern, with a steep increase in bat activity close to the shores. This is similar to what is found in fiords and thus could be a general pattern in landscapes with complex topography. Both climate and topography are factors likely to contribute to this pattern.

Key words: climate, *Eptesicus nilssonii*, GAM, habitat, *Myotis*, *Pipistrellus pygmaeus*, topography, valley

Introduction

Bat diversity and behaviour in latitudinal gradients is influenced by light conditions and temperature (e.g. Rydell 1992, Kaufman & Willig 1998, Ulrich et al. 2007, Michaelsen et al. 2011, Frafjord 2012a). With increasing latitude, summer gets shorter, temperatures drop, nights become brighter and darkness is eventually no longer available to bats during the summer months. Still, several bat species cope with such difficulties through morphological, physiological and ecological adaptations (e.g. Rydell 1992, Frafjord 2012a, Haarsma & Siepel 2013, Michaelsen 2016a). Hunting in bright summer nights may be risky due to diurnal avian predators (e.g. Rydell 1992, Speakman et al. 2000, Frafjord 2012b, Michaelsen et al. 2014), but bats can to some extent reduce this risk by exploiting habitats that provide shade and by maintaining a nocturnal activity pattern (Nyholm 1965, Rydell 1992, Rydell & Speakman 1995, Rydell et al. 1996, Duverge et al. 2000, Russo et al. 2007, Michaelsen et al. 2011, 2014, Lima & O'Keefe 2013, Michaelsen 2016a).

At northern latitudes in Scandinavia, knowledge about spatial variation in habitat use is still limited for several species (but see Rydell 1992, 1993, Speakman et al. 2000, Frafjord 2012a, Michaelsen 2016a). Bat distribution is governed by several features and their interactions with other variables (e.g. Piksa et al. 2013, Bruckner 2016, Ciechanowski et al. 2016, Maxinová et al. 2016, Michaelsen 2016c, Ijäs et al. 2017). This means that a variable such as habitat may show considerable variation in bat activity. In general, many bat species show an affinity for hunting over or near aquatic habitats (see Salvarina 2016 for a review). Woodlands in the vicinity of aquatic habitats potentially hold more insects with limnic larvae stages compared to more distant woodlands. For several bat species, this distinction is likely to be highly important and cannot be ignored. Particularly at northern latitudes, where some bats seek out habitats that provide shade (e.g. Michaelsen et al. 2011), insect rich woodlands close to freshwater could be particularly important.

To the north in Europe, bats can be observed throughout the bright summer nights. In U-shaped fiords and valleys, if the observer is positioned properly, some bat species can be observed over large areas using binoculars, similar to how one would study birds in flight. In Norwegian fiords with low salinity surface layer, bat activity produces a non-linear patterns with a steep increase near the shores (Michaelsen 2016a). Based on visual observations, similar patterns as those found in fiords is to be expected also around freshwater in valleys in this part of Scandinavia. Here, it is assumed that areas close to freshwater provides high densities of insects compared to areas

more distant from lakes. The purpose of this study is to quantify bat activity and analyse the spatial distribution patterns of common bats in deciduous woodland in valleys at northern latitudes in Norway. If a steep increase in bat activity close to shores is confirmed in these valleys, it would suggest that some simple rules can be applied in bat conservation, where a limited portion of the landscape might have a very high importance to foraging bats. Such a pattern would also suggest great variation within habitats, indicating that discrete habitat variables are not ideal in analysis and that interaction terms between variables must be considered.

Material and Methods

Study area

This study was carried out in valleys in western Norway, between 61°44′54″ N-06°48′50″ E and 62°36′20″ N-8°10′17″ E (Fig. 1) and includes valleys with lakes in Sogn og Fjordane and Møre og Romsdal counties. Locations used in this study are in well-preserved woodlands, with little or no recent human influence, and include nature reserves and landscape protection areas. In some areas, narrow roads go through these woodlands, but such man-made structures were avoided when detectors were deployed. Images from the study area can be found as supplementary material (S1). At these latitudes most bat species form maternity roosts in lowlands where mean July temperatures reach 13-14 °C (Michaelsen 2016c). In this landscape, maternity roosts are found only in the south facing slopes (Michaelsen et al. 2014, Michaelsen 2016b) where the sun heats the roost site for much of the day (see Olseth et al. 1995 for solar mapping in this landscape). Due to the relief of these valleys and the limited distribution of most bats in an altitudinal gradient, the distance (as the crow flies) from roosts to the bottom of valleys with rivers or lakes, is usually short.

Data collection with ultrasound detectors

Seven D500x detectors (Pettersson Elektronik AB, Sweden) were used to automatically record ultrasounds of passing bats on nine nights between 1 July and 28 July 2015. All units (with software version 2.2.5) were given the following settings; sampling frequency = 500, pre-trigger = off, recording length = 3 seconds, high pass filter = yes, t-sense = medium. Input gain was set to 30, trigger level to 28 and continuous recording was allowed (no pause between each recording). Recording time was set to start at 21.00 hours (minimum of 2 h 5 min before sunset) and

end at 05.00 hours (minimum 53 min after sunrise) local time. This should cover the activity period of all bats in this region, including early emerging soprano pipistrelles (Michaelsen et al. 2011).

Only areas with deciduous forests were included in this study. The dominant tree species are birch *Betula pubescens/Betula pendula*, rowan *Sorbus aucuparia*, alder *Alnus incana*, hackberry *Prunus padus* and goat willow *Salix caprea*. Fairly common deciduous species are elm *Ulmus glabra*, ash *Fraxinus excelsior* and small-leaved lime *Tilia cordata*. Detectors were deployed in open woodland where the canopy was not continuous and bats could fly freely in open spaces between the trees. Such woodland is common on partly overgrown and stable screes in this type of landscape. Within each of the seven locations, the first detector was deployed at approximately 3-5 meters from the shoreline, followed by six detectors distributed up the hillsides up to 180 m from the shores. The aim was to deploy the detectors 20 m (+/–5 m) distant (as the crow flies) in a straight line up these slopes. However, due to variation in woodland composition (some areas had too dense woodland to be accepted) deployment would frequently exceed this distance. In such cases, where no suitable site could be found after walking 20 m up the hillside, the nearest suitable tree at distances greater than 20 m distant was used. Details on distribution of ultrasound detectors are presented in Table 1 and a map with the locations is shown in Fig. 1.

The detectors were fitted horizontally approximately 2 m above the ground on the stem of trees without

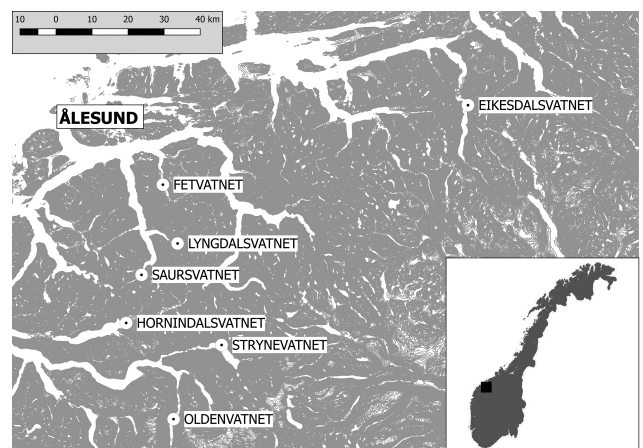**Fig. 1.** The map shows the seven valleys where ultrasound detectors were deployed in 2016. The main city in the region (Ålesund) is shown on the map as a reference point. The inset (lower right) shows the study areas position (black square) in Norway. The figure was produced with QGIS (QGIS Development Team 2016). The map is available from The Norwegian Mapping Authority (Creative Commons 4.0 international (CC BY 4.0)).

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Table 1. The table gives information about the seven lakes where detectors were deployed during this study. The angle of the slope was calculated automatically using the free map-server GISLink (www.gislink.no). Temperature and wind conditions were retrieved from e-klima, the Norwegian Meteorological Institute's free web-client (www.eklima.no). Here, the weather station Brusdalsvatnet in Ålesund municipality in the centre of the study area was selected.

Locality	Date	Coordinates	Slope (%)	Distance shore (min-max), meters	Mean temperature (range), °C	Wind, m/s
Oldenvatnet	1 July 2015	61°44′54″ N-06°48′50″ E	66	4-180	20.8 (13.2-29.4)	< 5
Strynevatnet	4 July 2015	61°57′2″ N-06°59′50″ E	76	3-139	16.8 (12.2-21.4)	< 5
Hornindalsvatnet	10 July 2015	61°58′17″ N-06°29′14″ E	55	4-156	12.9 (6.8-17.6)	< 5
Saursvatnet	16 July 2015	62°5′48″ N-06°32′35″ E	59	5-135	12.4 (8.0-17.7)	< 5
Lyngdalsvatnet	20 July 2015	62°10′33″ N-06°43′54″ E	25	3-137	14.1 (11.0-17.7)	< 5
Fetvatnet	25 July 2015	62°19′19″ N-06°35′22″ E	24	5-156	14.6 (10.6-19.1)	< 5
Eikesdalsvatnet	27 July 2015	62°36′20″ N-8°10′17″ E	34	4-143	14.6 (11.4-17.9)	< 5

any vegetation blocking the microphone. With this design, the detectors were expected to pick up bats flying in open woodland as well as bats circling above the treetops. Activity was monitored only one night per location, thus all data within each location is comparable in terms of climatic conditions, insect activity and other random factors. Detectors were deployed only on nights with suitable weather forecasts, including no precipitation or strong winds. On two nights however, unexpected heavy rain occurred during the time interval when the detectors were recording. These were excluded from any further analysis and no data from these nights are included in this study. Temperature and wind conditions for all nights included in this study are presented in Table 1.

Ultrasound analysis
Recordings were first processed using Kaleidoscope version 3.1.6. (Wildlife Acoustics, U.S.A.). Automatic species identification was made using classifier version "Bats of Europe 3.1.3". All recordings were later manually inspected using the Kaleidoscope viewer included in the software package. This includes all audio files suggested to contain only noise and all files where ultrasound was confirmed by the software, but without an automatic identification to species. Manual species identification was made directly in the viewer. Such manually added information is automatically saved in a csv-file together with all data produced by Kaleidoscope during automated analysis. Decibel gain was set to a high level (+50) and all pulses that were clearly visible at this setting were inspected further. Here the decibel gain was adjusted downwards to reduce noise. Other settings specified prior to analysis were FFT size 512 and window size 64. General literature on echolocation and social calls from European bats (Ahlén & Baagøe 1999, Skiba 2003, Middleton et al. 2014, Barataud 2015) was used to identify these recordings to species or genus. Recordings determined to contain noise or only social calls (see Middleton et al. 2014) are omitted from this study.

Statistics
The statistics software R (R Core Team 2015) was used for all statistics and in the production of all figures. A Wilcoxon signed rank test was used to test if the detector closest to the shore would produce more bat recordings than detectors deployed at greater distances from the shores. Generalised Additive Models (GAM) were applied to analyse spatial distribution patterns mainly for two reasons. First, inspection of the data (plots) suggested non-linearity in the relationship between number of bats recorded and distance from the shore. Second, the aim of this study is to explore patterns in bat distribution, not predict specific values of recordings per time unit at various distances from the shore. The mgcv library was used for all GAM models (Wood 2017, see also Zuur 2012). Here, the GAM was allowed to automatically find the proper amount of smoothing (cross-validation with GCV). The unit used in the analysis is the proportion of recordings made by each detector of the total number of recordings that particular night, with a range of 0 (no recordings were made by the particular detector that night) to 1 (all recordings were made by the particular detector that night). Predicted values from the GAMs are imposed on plots of the proportions to visualise the smoother. To avoid conclusions based on very small sample sizes, at least 10 recordings of each species/genus had to be recorded each night (an *a priori* decision). If this limit was not reached, the data from that night would be excluded for the species/genus in question.
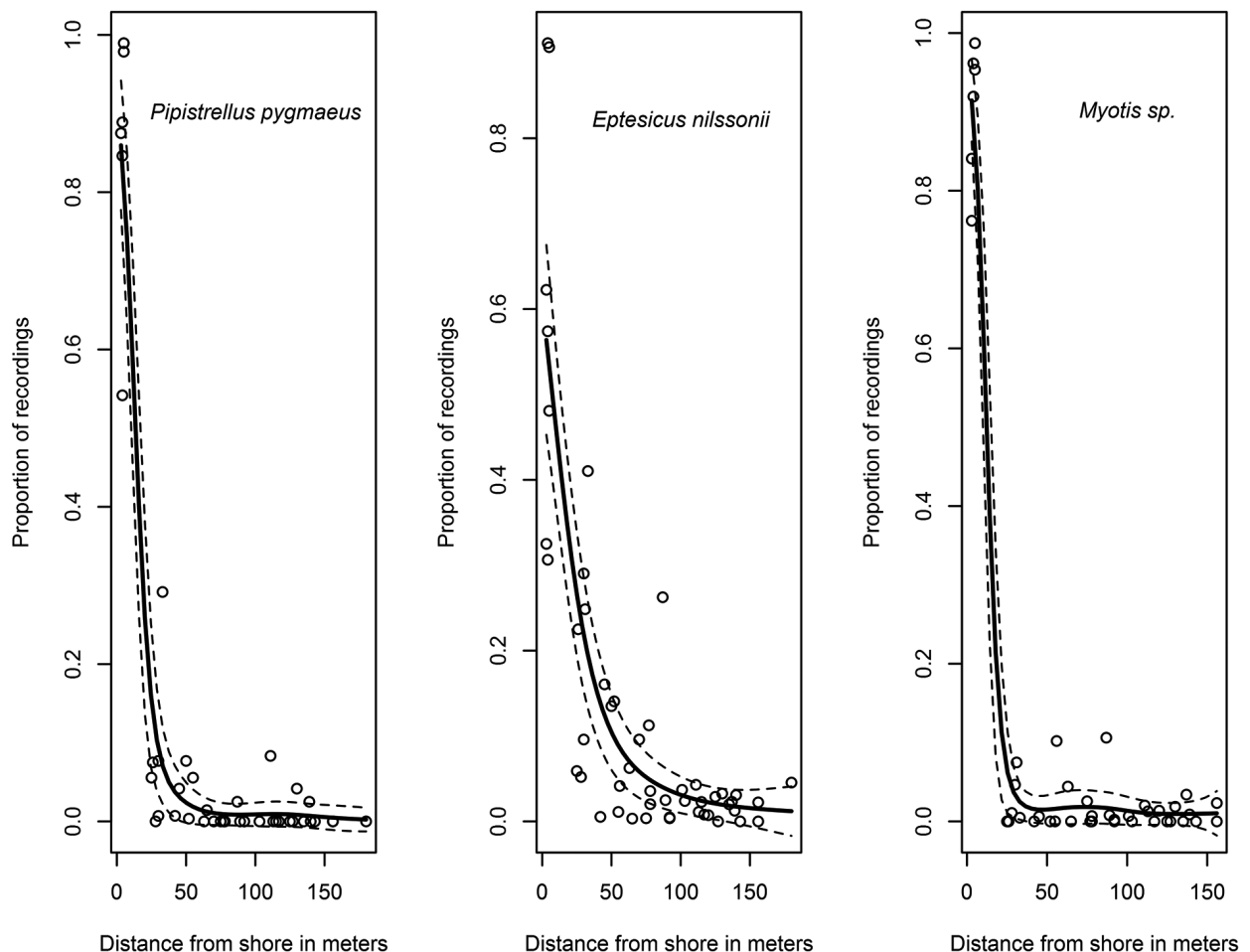
Fig. 2. Bat activity relative to the distance from the shores. Each circle represent the proportion of recordings of bats (y-axis) of the soprano pipistrelle (left), the northern bat (centre) and the *Myotis* genus (right) in deciduous woodlands at various distances from the shore (x-axis) of lakes in valleys in western Norway. The solid lines show estimated smoothers based on Generalised Additive Models. Dotted lines are 95 % pointwise confidence bands.

Results

Diversity

A total of 11813 recordings were made on nights without rain and only these are included in further analysis. Bat calls that could be determined to species or genus were present in 9342 recordings. Additional twelve recordings contained pulses of a single species that were not possible to determine to species or genus. The remaining 2459 recordings contained noise or social calls without the presence of any pulses emitted by bats in search flight. The northern bat was by far the most common bat and was present in 8643 recordings (93 %). *Myotis* bats and soprano pipistrelles followed with ultrasound present in 1497 (16 %) and 808 (9 %) recordings respectively. No attempt was made to determine bats of the *Myotis* genus to species level.

Spatial pattern

On all the nights, the detector nearest the shore recorded more bats than all the other detectors combined (Wilcoxon signed rank test; V = 28, *p* = 0.0156), suggesting a strong affinity for the areas close to lakes. The detector nearest the shore (n = 7 detector nights) made 5597 recordings where one or more bat species were confirmed, whereas the remaining detectors combined (n = 42 detector nights) produced only 3745 recordings. Soprano pipistrelles and *Myotis* bats yielded less than 10 recordings at one locality each. These nights were excluded from analysis of spatial distribution of soprano pipistrelles and *Myotis* bats. The GAM models suggest that a smoother for distance was justified for the soprano pipistrelle (n = 42, df = 3.313, F = 28.01, *P* < 0.0001), the northern bat (n = 49, df = 2.242, F = 31.26, *P* < 0.0001), and bats in the *Myotis* genus (n = 42, df = 4.264, F = 36.81, *P* < 0.0001). The models with this single predictor explain an estimated 88 %, 72 % and 93 % of the variation, respectively. All models predict a relatively steep increase in the activity towards the shore, starting with a distance of below 30-60 meters (Fig. 2).

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Discussion

The northern bat was present in more recordings than any other species in these valleys. This is different from low salinity marine fiords, where the soprano pipistrelle can be the most frequently recorded bat (Michaelsen 2016a). This difference is also supported by previous studies showing that soprano pipistrelles are more frequently found in low salinity marine fiords compared to any other water source at these latitudes (Michaelsen et al. 2011). Bats in the *Myotis* genus seem to occur in numbers fairly similar to what is found in low salinity marine fiords (Michaelsen 2016a). In such fiords, the Daubenton's bat hunts just above the water and takes prey from the surface, similar to the behaviour over freshwater (Michaelsen et al. 2002). Both Daubenton's bats and whiskered bats are common or fairly common in the study area and both are likely to have contributed to the calls recorded during this study (Michaelsen 2016c). Unfortunately, it is at present difficult to discriminate between the different species within this genus based on evidence from statistical classification models (Walters et al. 2012, but see Barataud 2015 for a subjective approach). The brown long-eared bat is rarely recorded by detectors due to short range of its ultrasound (Barataud 2015, see also Baagøe 2001). The exception is some types of social calls frequently recorded in autumn. Several colonies of brown long-eared bats have been found in this study area and the species is occasionally trapped when using acoustic lures (Michaelsen et al. 2013). Thus, the lack of recordings in this study is likely to be related to methodological shortcomings.

The spatial patterns found in this study fit well with patterns displayed by the same species and genera along fiords at similar latitudes (Michaelsen 2016a). This suggests that non-linear patterns with a steep increase in activity near the shores could be present over large areas in glacially carved fiords and valleys in Scandinavia. It may also be present elsewhere in mountainous regions, but this possibility has not been explored. Recent advances in technology, where stationary ultrasound detectors collect huge amounts of data, and statistical pattern recognition tools that deals with such data, provide researchers with new methods to understand bat behaviour. Stationary ultrasound detectors also make it possible to record bats in pristine habitats with steep and dangerous terrain. Attempting radio telemetry projects in the woodlands investigated in this study would not only be risk prone behaviour, but would also fail due to significant restrictions on movement.

The conclusion that freshwater is of high importance to bats is no new discovery (e.g. Bruckner 2016, see also Salvarina 2016), whereas the sustained importance of woodlands near lakes throughout summer for all common species in this region, is. At northern latitudes, those parts of the landscape close to lakes (this study) and low salinity marine fiords (Michaelsen 2016a) are highly important in late summer and through the period when females are lactating. This may to some extent be explained by differences in climate, where hatching of insects with limnic larva stages occurs later at northern latitudes compared to southern latitudes. However, other factors may also play a decisive role. Light conditions at northern latitudes are likely to affect habitat use to the north and anti-predator considerations may limit bats from seeking out the most insect rich habitats (e.g. Rydell 1992). At latitudes around 62° N, shade from tall mountains or lack thereof even affect distribution of bats (Michaelsen et al. 2011), as well as their behaviour (Michaelsen et al. 2014, Michaelsen 2016a). In all areas where detectors were deployed during this study, tall mountains block out the sun in the evening and provide shade throughout the night. Thus, spatial activity patterns of bats may not only be affected by latitude, but also by topography. In this regard, bats may here find sufficient shade during the darkest part of the night to adopt a fairly similar behaviour to that found in central and southern Scandinavia, where bats seek out more open habitats such as lakes (e.g. Rydell 1986, 1992, de Jong & Ahlén 1991). This study does not include information on exactly when bats shift to hunt in open landscapes (over lakes), but this should be further explored. Studies that identify the exact location of bats, in open space or not, coupled with estimates of insect densities in those habitats, would be particularly valuable (see Salvarina 2016).

Also, the relief of the landscape itself may play an important role in local distribution of bats. Due to the steep slopes of these valleys, the distance from roosts to the shoreline of lakes or rivers is never long. Roosts are always found in the warmest parts of the landscape, generally in lowlands and in hillsides facing south (Michaelsen 2016b). Here, the flight time from roosts to the areas around the shoreline should be a matter of seconds. This is not necessarily the case in the more flat landscapes found in much of Europe, where long flight to lakes may outweigh the energetic benefits of exploiting such insect rich habitats. Such differences should be appreciated when considering the broader validity of this study (see also Bruckner 2016).

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Another interesting result from this study is the suggestion that discrete variables such as habitat, may not contribute with significant information unless additional features are considered (distance from shore). The massive variation in bat numbers within a habitat, with a non-linear increase towards the shores within a habitat, clearly shows that habitat use can only be understood in relation to the distance to other nearby landscape elements (lakes). Therefore, an interaction term between habitat and distances to other landscape elements may explain much of the variance in models and should always be explored if this freshwater is within the range of the bats nightly hunting bout. Data collection in this study was made (by design) in similar habitats with deciduous woodland, thus exclusion of the habitat variable is justified. Future studies of bat distribution with a similar design, but where data is collected in many different habitats, could provide more information on this methodologically important issue.

The pattern displayed by northern bats, and the lower explanatory value of the GAM model compared to soprano pipistrelles and Daubenton's bats, may suggest that it is more flexible in its use of the landscape. In this region of Scandinavia, the northern bat covers all landscapes from treeless coastal plains to the alpine habitats (Michaelsen 2016c), where it is more common and more widely distributed compared to any other bat species (low salinity fiords is the exception, see Michaelsen 2016a). The various bat species have different ultrasound range, and calls from the northern bat can be detected around twice the distance of the soprano pipistrelle (Barataud 2015, see also Baagøe 2001). The difference in range is even greater for the Daubenton's bat and the whiskered bat. On the other hand, northern bats generally fly higher than *Myotis* bats and soprano pipistrelles. Thus, the number of recordings presented in this study may not reflect the true composition of the bat fauna and this should be appreciated when interpreting the results (e.g. Collins & Jones 2009).

Conservation impact
Roads in this type of landscape in Norway are generally constructed near the shores of lakes and rivers. This study highlights the importance of giving bats due weight in development projects close to freshwater, including woodland adjacent to freshwater.

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Supplementary online material

Images from the study area (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/Michaelsen_Supplementary_material_S1.pdf).