In anthropogenic landscapes, aerial insectivores are often confronted with variable habitat complexity, which may influence the distribution of prey. Yet, high mobility may allow aerial insectivores to adjust their foraging strategy to different prey distributions. We investigated whether aerial-hunting common noctules Nyctalus noctula adjust their foraging strategy to landscapes with different habitat complexity and assumingly different prey distribution. We hypothesized that the movement behaviour of hunting common noctules and changes of movement behaviour in reaction towards conspecifics would depend on whether they hunt in a structurally poor cropland dominated landscape or a structurally rich forest dominated landscape. We tracked flight paths of common noctules in northeastern Germany using GPS loggers equipped with an ultrasonic microphone that recorded foraging events and presence of conspecifics. Above cropland, common noctules hunted mainly during bouts of highly tortuous and area restricted movements (ARM). Bats switched from straight flight to ARM after encountering conspecifics. In the forested landscape, common noctules hunted both during ARM and during straight flights. The onset of ARM did not correlate with the presence of conspecifics. Common noctules showed a lower feeding rate and encountered more conspecifics above the forested than above the cropland dominated landscape. We conjecture that prey distribution above cropland was patchy and unpredictable, thus making eavesdropping on hunting conspecifics crucial for bats during search for prey patches. In contrast, small scale structural diversity of the forested landscape possibly led to a more homogeneous prey distribution at the landscape scale, thus enabling bats to find sufficient food independent of conspecific presence. This suggests that predators depending on ephemeral prey can increase their foraging success in structurally poor landscapes by using social information provided by conspecifics. Hence, a minimum population density might be obligatory to enable successful foraging in simplified landscapes.

Keywords: competition, eavesdropping, GPS tracking, movement, Nyctalus noctula, public information
Introduction

The human impact on ecological patterns and processes is apparent worldwide (Ellis 2011, Boivin et al. 2016). A particular strong driver of changes in biodiversity patterns is habitat degradation through human landuse regimes (Bianchi et al. 2006, Barnes et al. 2014). In 2017, cropland and forested land covered 63% of the area of the European Union (FAO 2019). Landscapes dominated by cropland and managed forests are particularly dynamic landscape mosaics because of their temporal patterns of seeding and harvesting. Yet, temporal fluctuations vary between these two landscape types owing to differences in harvest cycles. Whereas biomass fluctuations are rapid in cropland dominated landscapes (USDA 2010), thus making resource distribution difficult for animals to predict, biomass fluctuations in landscapes dominated by managed forests are comparably slow (Moog and Borchert 2001). In addition to increased temporal dynamics, human landuse also results in changes in the total amount of biomass available to wildlife (Haberl et al. 2007).

Further, humans also modify the spatial distribution of resources. When resource-rich areas that provide forage are patchily distributed in the landscape, animals must on average commute longer distances between foraging patches, which ultimately leads to larger home ranges, added energy expenditure (Ullmann et al. 2018), and possibly also higher predation risk. Agricultural landscapes characterised by large fields and few ecotones possess low compositional and configurational habitat complexity (Robinson and Sutherland 2002). In such simplified landscapes, abundance and diversity of animals is often reduced (Fahrig et al. 2015, Newbold et al. 2015, Redlich et al. 2018). A potential underlying mechanism might be that on the landscape scale resource heterogeneity increases with decreasing habitat complexity, making it more difficult for consumers to find food resources (Mueller and Fagan 2008).

Nevertheless, individuals may be able to adjust their behaviour to persist in human-influenced landscapes. Behavioural adjustments manifest in various ways, including changes in movement patterns (Salinas-Melgoza et al. 2013, Tucker et al. 2018), or changes in the social systems and interactions with conspecifics (Banks et al. 2007). Especially aerial insectivores may compensate for human-induced changes in prey abundance and distribution through their high mobility (Kniowski and Gehrt 2014), and thus may be able to exploit a multitude of landscapes. Yet, aerial insectivores that depend on ephemeral, patchily distributed prey, may suffer from difficulties in locating profitable foraging grounds in structurally poor landscapes such as intensively used farmland (Mueller and Fagan 2008, Batáry et al. 2017). In such landscapes, insect prey is often associated with relatively rare structures such as hedges, forest edges (Grüebler et al. 2008, Froidevaux et al. 2019), water bodies or other areas showing relatively low human impacts (Wickramasinghe et al. 2003, de Araújo et al. 2015, Treitler et al. 2016, Froidevaux et al. 2017). In contrast, structurally richer landscapes such as forests may provide more prey-rich patches, leading to a higher probability for aerial insectivores to encounter such patches during undirected search movements (Mueller and Fagan 2008).

Insectivorous bats play a major role in food webs (Kalka et al. 2008). In agricultural landscapes, they are crucial for the control of insect pests (Boyles et al. 2011, Ghanem and Voigt 2012, Main and Boyles 2015). However, the range at which bats can detect prey items with ultrasonic echolocation calls is generally shorter than ten meters (Holderied and von Helversen 2003, Stilz 2004, Jones and Siemers 2011). Thus, a common strategy to detect insect aggregations is the use of inadvertently provided social information (Danchin et al. 2004) via eavesdropping on hunting calls of other bats. These may originate from conspecifics (Gillam 2007, Dechmann et al. 2009, Übernickel et al. 2013) or heterospecifics with similar prey preferences (Dorado-Correa et al. 2013, Roeleke et al. 2018a).

Recently, Cvikel et al. (2015) showed that aerial hunting bats may fly within hearing range of each other in order to eavesdropping on each other’s hunting calls, and may therefore inadvertently work as a sensory array during prey search. Similar behaviour has been described for swallows which likewise depend on ephemeral prey (Brown 1988). These observations suggest the occurrence of facilitation through social hunting (Bruno et al. 2003). However, such a social foraging strategy may only increase foraging effectiveness if resources are patchily distributed (Ryer and Olla 1995, Egert-Berg et al. 2018) because the aggregation of hunting bats at distinct prey patches may also result in increased competition, either for a limited number of prey items or for undisturbed hunting space (Voigt-Heucke et al. 2010, Corcoran and Conner 2014, Roeleke et al. 2018a). Thus, bats face a trade-off between finding prey and avoiding competition when foraging on patchily distributed prey. We therefore expect that the use of a social foraging strategy will differ between individuals of the same species that live in landscapes with different resource abundance and distribution.

Here we asked whether hunting activity and the influence of conspecifics on movement behaviour of an aerial hunting insectivoru bat, the common noctule Nyctalus noctula, differ between the two most prominent landscapes in Europe, i.e. cropland dominated landscapes and forest dominated landscapes. The common noctule bat is a highly mobile species adapted to the rapid pursuit of insects flying in the open space (Norberg and Rayner 1987, Jones 1995, Schnitzler and Kalko 2001). Food items of common noctules can be quite diverse, ranging from small Diptera to large Lepidoptera or Coleoptera (Eichstädt 1995, Gloor et al. 1995, Jones 1995, Vaughan 1997, Rydell and Petersons 1998). Consequently, common noctules can be categorised as food and habitat generalists that hunt opportunistically above water bodies (Roeleke et al. 2016, Voigt et al. 2020), open fields (Mackie and Racey 2007, Roeleke et al. 2018c), forest edges (Rachwald 1992, Kauch et al. 2008, Heim et al. 2018) or even urban areas (Kronwitter 1988, Gaisler et al. 1998).

We hypothesised that foraging strategies of common noctules (i.e. the combination of movement behaviour, feeding activity and the reaction towards conspecifics) is influenced by the underlying landscape (Nakano et al. 1999). To locate
hunting grounds, bats will use inadvertently provided social information by eavesdropping on conspecific hunting calls in a cropland dominated landscape where we assume prey to be hard to find for a single bat, due to patchy and ephemeral insect distribution. We predict that common noctules concentrate their feeding activity in small areas performing so-called area restricted movements (ARM, Fig. 1a) and that the onset of such movements is triggered by encounters with conspecifics (Fig. 1b) in structurally poor cropland dominated landscapes (Fig. 1c). In contrast, we assume a more even distribution of insect prey in a comparably complex forest dominated landscape mosaic. We predicted that bats in this landscape do not spatially concentrate their feeding activities (Fig. 1d). Also, bats would not depend on eavesdropping on conspecifics and therefore the probability of initiating ARM would not be affected by encounters with conspecifics (Fig. 1e) in the forest dominated landscape (Fig. 1f).

**Material and methods**

**Animal tracking**

In mid-summer (July) 2016–2018, we equipped 27 (15 and 12 at two different study sites) subadult common noctule bats *Nyctalus noctula* with combined GPS and ultrasound loggers. This period coincides with the onset of independent foraging by subadult noctule bats. Mothers usually abandon the maternity roosts during this time, whereas subadult bats stay for about one more month in mixed sex groups. In the early morning, we obtained subadult noctule bats from artificial bat boxes. At each of our two study sites (cropland dominated and forest dominated landscape mosaics, described below), bats were taken from one to three different boxes at a time. All boxes belonged to the same roost box cluster (each cluster consisting of approx. 25 boxes) with distance between boxes ranging from 10 to 30 m. From unpublished data, we know that bats regularly switch between boxes within the roost box clusters. We used latex-based surgical skin glue to attach loggers to the dorsal fur of each bat. The procedure of tag deployment took about 30 min, after which bats were returned to their roosting boxes. Loggers (weight 3.5 g) were packed in latex balloons together with VHF transmitters (weight 0.3 g) to facilitate retrieval. The complete packages weighed 4.5 g. Given an average bat mass of $28.5 \pm 1.5$ g (median $\pm$ median absolute deviation MAD), the attached packages accounted for $15.8 \pm 0.01\%$ (median $\pm$ MAD) of the bats’ body masses. Despite the relative high mass of the tracking devices, we considered the effect on the health of the bats and their flight behaviour to be negligible, since...
devices stayed on the bats only for a short period of time (retrieval after 2 ± 1.5 days, median ± MAD). Emergence time, flight distance and flight duration were in the expected range (Kronwitter 1988, Kanuch 2007, Mackie and Racey 2007). Further, similar studies did not reveal adverse effects on bats that were tagged with similar loggers (Cvikel et al. 2015, Roeleke et al. 2016, 2018b, Egert-Berg et al. 2018, Voigt et al. 2020). From sunset to sunrise, loggers recorded 3-dimensional GPS positions every 31 s. Loggers included an ultrasonic microphone, which recorded ultrasonic bat calls for a duration of 1.5 s every 10 s (i.e. duty cycle of 15%), at a sampling rate of 160 kHz. We used subadults only in this study to ensure that foraging behaviour was not based on individual experience from the last year. Eavesdropping behaviour of subadults might be more pronounced than eavesdropping behaviour of adults that may have knowledge on the location of predictable food patches.

Study sites

We compared movement and foraging behaviour of bats at two study sites representing two different anthropogenic landscapes. We tracked 15 subadult *Nyctalus noctula* (five males and ten females) that roosted in a small mixed forest patch within an intensively used agricultural area in northeastern Germany, about 100 km north of Berlin. This area was dominated by fairly large fields used for intensive wheat and corn cropping, and thus offered little structural heterogeneity (Ullmann et al. 2018). The area provided only few semi-natural structures like small forest remnants and shallow bodies of water (Fig. 2b).

We further tracked 12 subadult *N. noctula* (nine males and three females) that roosted in a pine stand about 125 km south of the previously mentioned study site, and about 40 km south-east from the city centre of Berlin. This landscape was dominated by a river and lake system and monocultural pine forest (66% of forest area), interspersed by mixed and deciduous forest patches, clear cuttings and smaller agricultural areas (Fig. 2a).

Both landscapes are rather flat, with elevation ranging roughly from 20 to 80 m asl and 30 to 70 m a.s.l. in the cropland dominated and forest dominated landscape, respectively. Average precipitation throughout the year does not differ between study sites and equals 62 and 65 mm in June at the cropland dominated and the forest dominated landscape, respectively. Median temperature throughout the year

![Figure 2](https://via.placeholder.com/150)

Figure 2. Landuse maps of the two study sites forested landscape (a) and cropland (b) with movement tracks from 27 common noctules *Nyctalus noctula*, recorded by GPS loggers. Different colors depict different individuals. The locations of the roosting box clusters are depicted by the stars. The location of the study sites within Germany are depicted by the two circles in the overview map; lower green circle: forest dominated landscape in panel a; upper orange circle: cropland dominated landscape in panel b.
is 0.5°C higher in the forest dominated (17.0°C in June) than in the cropland dominated landscape (16.5°C in June) (<https://de.climate-data.org/>).

### Analysis of ultrasound recordings

We used the software Avisoft-SASLab Pro ver. 5.2.09 to analyse the recordings made on-board of the combined GPS- and ultrasound loggers. Recordings were displayed as spectrograms (Fast Fourier Transition, FFT length 1024 or 512). Signal strength, call frequency and pulse trains allowed us to identify whether recorded calls originated from the tagged bat or from adjacent conspecifics. We further identified hunting events by distinct characteristics of pulse trains that bats emit when pursuing airborne insect prey, so-called feeding buzzes (Griffin et al. 1960, see Supplementary material Appendix 1 for a detailed description and examples of analysed recordings). Since we scanned the ultrasonic environment three times more often than we estimated spatial positions via GPS, we annotated every GPS position with the pooled data from the past three ultrasound recordings. The maximum number of clearly distinguishable call sequences from conspecifics in any of the pooled recordings was used to estimate the number of surrounding conspecifics. The summarized number of recorded feeding buzzes from the focal bat over the past three recordings was used as a proxy for feeding activity.

### Analysis of movement and foraging behaviour

Since all bats performed their longest consecutive flight during the first half of the night, we solely analysed the first trip of each bat, assuming a similar motivation of the bats (i.e. foraging), to allow better comparison of behaviours across individuals. GPS locations were annotated with the number of feeding events since the last GPS fix, the maximum number of conspecific bats recorded in one of the past three recording intervals, and the underlying landuse class (meadows or grasslands, forest or wood plantation, cropfields, water, urban areas, shrubs or bushes) extracted from aerial infrared images (Land Brandenburg 2013). We used hidden Markov models (R package moveHMM, Michelot et al. 2016) to identify two different movement modes derived from step lengths and turning angles of subsequent GPS locations. We used distinct models for each study site to allow potential effects of the respective landscapes on movement characteristics. However, initial values were the same for both models (gamma distribution of steplength with mean ± standard deviation = 50 ± 50 m and 200 ± 200 m equalling a flight speed of 1.7 m s⁻¹ and 6.7 m s⁻¹ respectively, van Mises distribution of turning angles with mean and concentration = π rad and 1 and 0 and 1). Exemplary changes of initial values had no effect on the outcome of the models. We defined the movement mode characterised by short step lengths and uniformly distributed turning angles as area restricted movement (ARM), and the movement mode characterised by long step lengths and small turning angles as directed movement (DM).

Whenever a minimum of 10 consecutive GPS locations (i.e. duration of at least 5 min) were defined as ARM, we used these locations to calculate a kernel-based density (R package adehabitatHR, Calenge 2006). We used the areas enclosed by the 90% isopleth of these kernel density estimations to create what we hereafter call ARM patches.

We then used a binomial generalised mixed model (R package lme4, Bates et al. 2015) to explain whether a given GPS point belonged to an ARM patch by the number of conspecifics, the number of feeding buzzes, the underlying landuse class and each of these explanatory variables in interaction with study site. We used the sampling year, the day of the year and the individual bat as random factors. We confirmed that explanatory variables were not correlated (Pearson product-moment correlation, coefficient < 0.08, p < 0.01). Since the model yielded significant correlations between response and explanatory variables, we reiterated the hidden Markov model with conspecifics, feeding buzzes and landuse class as covariates to examine their influence on the switching probability between movement modes.

We calculated another binomial generalised mixed model to examine whether the probability to meet conspecifics differed based on the interaction of movement mode (i.e. ARM or DM) and study site, with random effects again being sampling year, day of the year and individual bat.

### Comparison of study sites

To compare the structural diversity of the two study sites (cropland and forest) at an ecologically relevant scale from the bats’ point of view, we used the shapes of the previously built ARM patches to sample the habitat classes of the two different landscapes. We randomly distributed each of the obtained shapes nine times within the respective landscapes. The distance of the random patches to the common roosting area was taken from the empirical distance distribution between roost and all realised ARM patches in the respective landscape, whereas the bearing from roost to random patch was chosen randomly. We thus simulated how bats could potentially use the available space based on their normal flight behaviour. We then extracted the relative areas of the underlying landuse classes (bushland, forest, open habitats such as arable fields and grassland, urban areas, water) as provided by a classification based on aerial infrared photography (Land Brandenburg 2013), and calculated the Shannon diversity indices for the respective patches using the relative amount of landuse classes within the respective patches. We compared the Shannon diversities of the two landscapes using a Mann–Whitney-U test. We further calculated the edge length of landuse classes per patch area and compared these measures between the two landscapes using a Mann–Whitney-U test. We defined the edges as borders between distinct polygons of the landuse map. Accordingly, edges could occur between different landuse classes, but also between similar landuse classes, e.g. when polygons are divided by footpaths, hedges or streets, or when two forest polygons differ in successional status or predominant tree species.
Results

Movement and foraging behaviour

Flight time (117 ± 49 km median ± MAD), total flight distance (25.3 ± 15.5 km median ± MAD) and maximum distance from the roost (5.2 ± 2.0 km median ± MAD) did not differ for common noctules that were tracked above the cropland dominated or the forest dominated landscape (Mann–Whitney-U tests, n = 27, p > 0.2; Supplementary material Appendix 3 Table A1). We recorded on average 61 ± 39 hunting events (feeding buzzes) for bats above cropland, and 34 ± 13 feeding buzzes for bats above forested landscape. Feeding activity per minute flight time was higher above cropland (0.50 ± 0.22 recorded feeding buzzes per min flight, median ± MAD) than in the forested landscape (0.26 ± 0.14 recorded feeding buzzes per min flight, Mann–Whitney-U test, n = 27, U = 146, p = 0.02). The recorded numbers of feeding buzzes stem from non-continuous sound recordings (1.5 s recording every 10 s). Correcting for this by assuming continuous recording, the number of feeding buzzes would have ranged from 136 to 1758 (2.5–97.5% quantile) per flight trip.

Bats in the forested landscape were more likely to meet conspecifics than bats in the cropland dominated landscape. About one third of GPS points in the forested area, but only about one fifth of GPS points in the agricultural area contained recordings of conspecifics. This pattern was independent of the movement mode, but most pronounced during directed movements. During directed movements, the probability that individuals met conspecifics was two times higher in the forested landscape than in the cropland dominated landscape (Fig. 3, see Supplementary material Appendix 2 for model statistics).

The median time bats spent within spatially well-defined foraging patches (ARM patches) did not differ between the two study sites and averaged 30 ± 21% (median ± MAD) of their nightly flight time. ARM patches in the forested landscape were smaller and closer to the roost than ARM patches above cropland (Mann–Whitney-U tests, n = 66; ARM patch size: forested landscape = 1.4 ± 1.6 ha, cropland = 3.8 ± 4.5 ha, U = 320, p = 0.004; distance roost to ARM patch: forested landscape = 1.9 ± 1.8 km, farmland = 3.6 ± 1.1 km, U = 336, p = 0.007). ARM patches in both landscapes were distributed in all directions from the roost. In the cropland dominated landscape, the proportion of the landscape area covered by patches to the sum of patch areas was 0.90, in the forest dominated landscape that proportion was 0.84.

Above farmland, feeding activity of tagged bats occurred mostly in ARM patches, whereas no significant relation was observed between feeding activity and movement behaviour in the forested landscape (Fig. 4a). For both study sites, we found a strong positive correlation between ARM patch use and the number of adjacent conspecifics (Fig. 4b), i.e. the more conspecifics were recorded, the more likely it was that bat activity was restricted to small areas. Whenever bats in the cropland dominated landscape used bushland, the probability for ARM was comparably high (Fig. 4c). However, bushland accounted only for a small portion of the landscape and made up only for 4 ± 2% (median ± MAD) of the ARM patches (Table 1).

For bats in the cropland dominated landscape, we observed a slight rise in the probability to switch from DM (directed movement) to ARM after individual feeding activity increased. In the forested landscape, we did not observe an effect of recent feeding activity on the switching probability between movement modes (Fig. 5a). For bats flying above cropland, the likelihood to switch from directed DM to ARM increased strongly with the number of conspecifics encountered recently (i.e. during the last 30 s). In the forested landscape, the switching probability from DM to ARM increased only slightly with the number of recent conspecific encounters (Fig. 5b). The underlying landuse class had comparably little effect on the switching probability between movement modes (Fig. 5c). Please see Supplementary material Appendix 4 for model statistics.

Comparison of study sites

At the scale of ARM patches, the structural diversity of patches randomly distributed over the cropland dominated landscape was lower than that of patches randomly distributed in the forested landscape (cropland: Shannon index 0.19 ± 0.23...
Table 1. Proportion of landuse class categories at the two study sites. Median values for the use of landuse categories by common noctules tracked in the respective study sites are given.

| Habitat | Cropland dominated landscape | Forest dominated landscape |
|---------|------------------------------|---------------------------|
|         | Proportion in colony MCP     | Proportion of GPS points (median ± MAD) | Proportion in ARM patches (median ± MAD) | Proportion in colony MCP | Proportion of GPS points (median ± MAD) | Proportion in ARM patches (median ± MAD) |
| open    | 0.88                         | 0.83 ± 0.14               | 0.85 ± 0.23               | 0.34                     | 0.30 ± 0.22               | 0.26 ± 0.33               |
| bush    | 0.04                         | 0.04 ± 0.03               | 0.04 ± 0.02               | 0.01                     | 0.01 ± 0.01               | 0.00 ± 0.00               |
| forest  | 0.05                         | 0.05 ± 0.05               | 0.00 ± 0.00               | 0.57                     | 0.47 ± 0.11               | 0.32 ± 0.29               |
| urban   | 0.02                         | 0.02 ± 0.01               | 0.00 ± 0.00               | 0.03                     | 0.03 ± 0.03               | 0.00 ± 0.00               |
| water   | 0.01                         | 0.04 ± 0.05               | 0.00 ± 0.00               | 0.05                     | 0.14 ± 0.15               | 0.24 ± 0.36               |
Movement and foraging behaviour

Common noctules emitted fewer feeding buzzes above the forest dominated than above the cropland dominated landscape. Foraging trips in the forested landscape thus seemed to be less efficient than above cropland. Since we observed similar numbers of ARM patches in the forested landscape and in the cropland dominated landscape, yet without an increase of feeding activity, we argue that foraging efficiency of common noctules in the forested landscape might have been impaired by intraspecific competition. Indeed, the overall higher conspecific encounter rate of common noctules in the forested landscape in the cropland dominated landscape suggests that the overall density of common noctules was higher in the forested landscape. Another, not mutually exclusive explanation for the comparable low feeding buzz rate may be that even distribution of prey items across the forest dominated landscape led to lower prey density at small scales, when compared to insect rich patches above the cropland dominated landscape. Both explanations suggest that common noctules flying above the forested landscape may have mainly competed for prey (Cvikel et al. 2015, Roeleke et al. 2018a), whereas bats flying above cropland might have been limited by the search for scarce food patches, but not by the competition for single food items within such insect rich patches.

Bats in both landscape spent about one third of their flight time performing ARM, a behaviour that is in many animals associated with concentrated feeding within patches of high resource abundance (Smith 1974a, b, Kronwitter 1988, Weimerskirch et al. 2007, Watanabe et al. 2014). However, we observed a strong correlation between ARM and the number of feeding buzzes only in the cropland dominated landscape. Insects might have been more abundant and more evenly distributed in the relatively complex forested landscape than in the simplified cropland dominated landscape (Thies and Tscharntke 1999, Ferguson et al. 2003, Tscharntke et al. 2005, Grüebl et al. 2008, de Araujo et al. 2015, Nguyen and Nansen 2018). Different distributions of insect prey above forested area and cropland dominated landscapes are in line with our findings that bats in the forested landscape hunted during ARM and DM alike, while bats in the cropland dominated landscape rarely hunted during DM. We speculate that the proposed patchy distribution of insects above the cropland dominated landscape restricted bats to forage during ARM in insect rich patches. For our study, it remains unclear which factors determined the spatial distribution of prey patches within the cropland dominated landscapes. Although insect distribution often was found to be influenced by landuse classes in agricultural landscapes (Brack Jr. and Laval 1985, Tscharntke et al. 2005, Grüebl et al. 2008, Nguyen and Nansen 2018), we found only minor influence of landuse classes on the movement behaviour of common noctules, and thus exclude visual or acoustic sampling of the landuse classes for finding prey patches.

However, looking at the foraging strategies of common noctules flying above the cropland dominated landscape, we found support for our prediction that common noctules eavesdrop on conspecifics to locate ephemeral prey patches. Above cropland, bats encountered conspecifics mainly when foraging in ARM patches. A local enhancement of foraging bats has often been documented with experiments broadcasting playbacks of conspecific echolocation calls and feeding buzzes (Gillam 2007, Dechmann et al. 2009, Überrnickel et al. 2013). Although in our case the presence of conspecifics could have been a mere correlation driven by high prey availability, our findings that bats were also more likely to switch from DM to ARM after recent encounters with conspecifics suggests

![Figure 5](image-url)
that this change in movement behaviour was indeed driven by the presence of conspecifics. Further, the even distribution of ARM patches around the roost, and thus low overlap of ARM patches, argues against certain alternative hypotheses on how bats located prey patches. If prey was predictably distributed or information on prey aggregations were shared between bats in the roost (‘information-centre hypothesis’, Ward and Zahavi 1973), one would expect that most ARM patches would lie in the same direction from the roost and would have a high overlap. Since the effect of conspecifities on movement behaviour was more pronounced than the effect of own recent feeding activity or landuse class, we suggest that the presence of conspecifities is a better indicator of plentiful prey patches than individual detection of single prey items or landuse class. Indeed, eavesdropping on hunting conspecifics should provide reliable information on prey availability, since the receiving bat uses inadvertently provided social information on behaviour which cannot easily be manipulated by the sender (Danchin et al. 2004). Eavesdropping is probably a crucial foraging strategy that facilitates hunting success when prey patches are hard to find, e.g. if prey are temporarily and spatially unpredictable (Templeton and Giraldeau 1995, Rafacz and Templeton 2003, Cortés-Avizanda et al. 2014).

We found strong support for our hypothesis that bats use different foraging strategies above cropland dominated and forest dominated landscape mosaics, possibly driven by differences in prey distribution and the competitive environment. In the forested landscape, feeding activity was not correlated with the use of ARM patches. Moreover, the probability to switch from DM to ARM increased only slightly with the number of recently encountered conspecifics, arguing against the use of social information via eavesdropping in the forested landscape. We propose two reasons for the different reactions towards conspecifics for common noctules flying above the cropland dominated landscape or above the forested landscape. First, the overall higher bat density in the forested landscape increased the probability of encountering conspecifics during commuting flights. Thus, the presence of conspecifics in the forested landscape could not be used to predict food availability. Second, the even distribution of diverse landscape elements may have led to a homogeneous distribution of prey insects in the forested landscape. Paired with an overall high intraspecific competition, homogeneous prey distribution, group hunting may have resulted in increased competition while foraging with conspecifics (Ryer and Olla 1995). Indeed, past studies showed that foraging efficiency of bats can be impaired at high densities (Amichai et al. 2015). Bats might thus avoid aggregations of conspecifics (Roeleke et al. 2018a) or even engage in agonistic behaviour when competing for prey (Voigt-Heucke et al. 2010, Corcoran and Conner 2014). Interestingly, an individual’s recent feeding activity had no influence on the probability to switch from DM to ARM. In combination with the observation that feeding activity was not significantly higher in ARM patches than during DM, it seems as if foraging in both movement modes was equally profitable for bats in the forested landscape.

Future directions

Although the observed patterns of conspecific encounters and feeding activity during the use of ARM patches strongly substantiated our hypotheses, we must acknowledge that these patterns constitute correlations, and potential reasons for that, such as prey distribution, competition or landscape effects, are hard to disentangle. Yet, increased switching probability towards ARM after encountering conspecifics indicates that bats above cropland indeed based their decisions on social information, while other factors such as recent feeding success or underlying landuse class were less important. To substantiate our hypotheses, we suggest additional playback studies combined with tracking of individual bats and insect catching to experimentally test if bats are attracted by conspecific feeding activity irrespective of other external factors such as landuse class or prey availability. Such studies could be conducted in landscapes with differing complexity and insect distributions to proof that the use of a social foraging strategy depends on the difficulty to find ephemeral insect patches in simplified landscapes, rather than on the landscape itself or unknown biological variables.

Conclusion

Here we complement and expand recent findings on social foraging in bat species (Egert-Berg et al. 2018). Our results indicate that the use of social information by bats is not only species-specific, but that the degree to which eavesdropping during foraging is used within a species can be flexibly adjusted to different resource landscapes and competitive environments. Our results further suggest the presence of a component Allee effect, i.e. that a minimum density of prey-searching conspecifics might be necessary for a local population to ensure sufficient prey-search efficiency when prey is scarce and patchily distributed (Jackson et al. 2008), thus making such local populations especially vulnerable to landscape simplification, irrespective of the landscape type. We further suggest that similar foraging strategies, i.e. that individuals exploit inadvertently provided information from conspecifics on prey occurrence, may be crucial for animal species other than insectivorous bats. The use of social information may be beneficial for several species depending on ephemeral and patchily distributed forage, such as insectivorous birds (Brown 1988), scavenging birds (Harel et al. 2017), fishing birds that hunt over the open sea (Thiebault et al. 2014a, b) or marine foragers (Ryer and Olla 1992, Coolen et al. 2005).

Data availability statement

GPS tracking data is stored in the movebank tracking data repository (<www.movebank.com>) under the study ID 622521340 and at <www.doi.org/10.4228/ZALF.DK.112>. (Roeleke et al. 2020).

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**Conflict of interest** — The authors declare no conflict of interest.

**Author contributions** — MR and CCV conceptualised the study. MR, TB, TT and UH carried out field work. MR, CCV and US conceptualised data analyses. MR and LM analysed the data. CCV acquired funding and provided material. MR and CCV wrote the manuscript. All authors revised the manuscript. TB, UH, LM and UES are listed strictly alphabetically.

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Supplementary material (available online as Appendix oik-07158 at <www.oikosjournal.org/appendix/oik-07158>). Appendix 1–4.