Foraging strategies of an aerial-hawking insectivore, the Common noctule bat *Nyctalus noctula*

Inaugural-Dissertation

to obtain the academic degree

Doctor rerum naturalium (Dr. rer. nat.)

submitted to the

Department of Biology, Chemistry and Pharmacy

of Freie Universität Berlin

by

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2018

This dissertation was conducted between October 2015 and December 2018 at the Leibniz Institute for Zoo- and Wildlife Research in the Forschungsverbund Berlin e.V. under the supervision of PD Dr. Christian C. Voigt.

1st Reviewer:	PD Dr. Christian C. Voigt (Leibniz Institute for Zoo- and Wildlife Research in the Forschungsverbund Berlin e.V., and Freie Universität Berlin)
2nd Reviewer:	Prof. Dr. Britta Tietjen (Freie Universität Berlin)
Date of defense:	12.06.2019

Acknowledgements

Many thanks to my supervisor Christian C. Voigt for his longstanding support, his trust, his enthusiasm, and his company during many exciting field trips. Thanks to the whole BioMove group for pushing forward movement ecology, thus making this research possible, and thanks for intellectual and administrative support. Thanks to the DFG for funding. Special thanks to Florian Jeltsch for his relentless enthusiasm. Many thanks to my colleagues and friends Oliver Lindecke and Cedric Scherer for discussing science and sharing the usual ups and downs of PhD life. Thanks to Viktoriia Radchuk for statistical advice. Thanks to the colleagues who helped revising this work. Many thanks to Anja Fritz and Rolf Struikmans for support in the field and discussions. Thanks to Gernot Verch and the crew from the Zalf field station in Dedelow for administrative support during field work. Thanks to all members of the batlab and many spontaneous helpers without whom fieldwork would not have been possible. Thanks to Friederike Klingler for sharing data, to Lilith Johannsen for extensive help with the playback experiments, and to Maris Pärn for help with the insect samples. Thanks to Britta Tietjen for reviewing this thesis. Special thanks to Torsten Blohm, Uwe Hoffmeister, and Tobias Teige for their longstanding engagement in bat conservation, for sharing their knowledge about bats, and for their eager support.

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SUMMARY

Movement is a key signature of life. Yet, the integration of movement ecology and biodiversity concepts was only recently formalize. In this framework, an individual's movement path and the underlying drivers are used to explain interactions between individuals and eventually species coexistence. Interactions influence the individual's environment including species assemblage, and thereby feed back on the individual's movement path. Foraging represents one of the most common movements of many animals, and thus has been of interest for ecologists ever since. Yet, classical foraging ecology predominantly focused on optimality models to explain the behaviour of single foragers, but rarely took into account the interactions between moving individuals.

The overarching question of the three studies in this thesis thus was "**How can different foraging strategies support coexistence?**". Being highly mobile and showing a large niche overlap with several other species, the insectivorous Common noctule bat *Nyctalus noctula* (Schreber, 1774) is an ideal model species to study intra- and interspecific interactions during foraging movements. I therefore investigated movement behaviour and space use of *N. noctula* during aerial foraging, and evaluated the potential role of different foraging strategies for the coexistence of competing bat species in the light of different competitor densities and prey distributions.

In **chapter one**, I asked whether foraging *N. noctula* adjust their space use to abiotic factors (i.e. moonlight) which might be linked to prey distribution. I used GPS (global positioning system) loggers to investigate the habitat use of nine *N. noctula* during high and low moonlight intensities.

During moonlit nights, *N. noctula* hunted preferentially over open fields, whereas they avoided open fields in dark nights. I suppose that foraging activity followed changes in insect activity triggered by the lunar cycle. The results suggest that *N. noctula* might be able to predict cyclic changes in prey distribution. The exploitation of prey aggregations in lit habitats might be an advantage towards competing bat species that are less light tolerant.

In **chapter two**, I asked whether the use of social foraging by *N. noctula* depends on season, possibly as a response to changes in insect availability. I quantified *N. noctula* activity at foraging sites in early and late summer during acoustic playbacks of either hunting conspecifics or heterospecifics.

N. noctula activity increased during heterospecific playbacks in early summer, but decreased in late summer. There was no clear reaction towards conspecific playbacks, irrespective of the season. The results suggest that external factors determine the strengths of intraspecific and interspecific competition, but that insectivorous bats mitigate different competitive pressures through flexibility in foraging strategy and fine scale space use. I argue that conspecific might impair each other by acoustic interference of echolocation calls and competition for flight space. However, niche segregation might make social foraging with heterospecifics beneficial, given that there is low competition for prey items.

In **chapter three**, I asked whether the foraging strategy of *N. noctula* depends on the combination of conspecifics density and landscape features that might determine prey distribution. I used combined GPS-ultrasound loggers to record the nightly foraging movements and hunting activity of 27 *N. noctula* above farmland and forested landscape. Acoustic records also allowed quantification of nearby conspecifics. I deduced two movement states - area restricted movement and directed movement - from the GPS tracks.

Above farmland, *N. noctula* switched to area restricted movements after encounters with conspecifics, and foraging activity was highest during those movements. Above forested landscape, encounters with conspecifics had little influence on the movement behaviour of *N. noctula*, and foraging activity occurred during directed and area restricted movements alike. *N. noctula* encountered more conspecifics above the forested landscape than above farmland. I argue that *N. noctula* was able to integrate prey distribution and competitive pressure when deciding whether or not to pursue a social foraging strategy. The use of a social foraging strategy might be a prerequisite for survival in agricultural landscapes where prey is patchily distributed and ephemeral. In contrast, solitary foraging might be the optimal strategy in forested landscapes that offer evenly distributed prey and support larger populations.

In **conclusion**, the results showed that *N. noctula* integrated environmental factors that probably influenced prey distribution, adverse effects from intra- and interspecific competition, and public information about prey availability provided by hunting con- and heterospecifics. N. noctula used this compiled information to decide where to forage and whether to forage solitary or socially. The studies highlighted that *N. noctula* can adjust its foraging strategy context dependently. This flexibility was achieved through dynamic feedbacks between the movement paths and the perceived environment. These dynamic feedbacks may play a pivotal role in promoting the coexistence of competing species. In particular, the similarity of movement behaviours and resulting foraging strategies among conspecifics might stabilize species assemblages through intraspecific competition, while slight differences in the movement behaviour among heterospecifics might allow fine-scale niche segregation and thereby equalize the fitness of coexisting species. I propose that dynamic foraging behaviour might act stabilizing and equalizing not only in insectivorous bats but on assemblages of highly mobile predators in general.

ZUSAMMENFASSUNG

Bewegung ist ein Hauptmerkmal allen Lebens. Dennoch gibt es erst seit kurzem ein formelles Rahmenwerk, welches Bewegungsökologie und Biodiversitätsforschung miteinander verflechtet um das Zusammenleben von Arten zu erklären. In diesem Rahmenwerk werden der Bewegungspfad und die dem Pfad zugrunde liegenden Faktoren benutzt um Interaktionen zwischen mehreren Individuen zu erklären. Diese Interaktionen beeinflussen wiederum die Umwelt des einzelnen Individuums sowie die lokale Artengemeinschaft, und somit letztlich auch wieder die Bewegung des einzelnen Individuums . Es entsteht ein dynamischer Kreislauf. Die tägliche Futtersuche ist eine der alltäglichsten Bewegungsformen von Tieren, und steht daher schon lange im Fokus von Ökologen. Dennoch hat sich die klassische Nahrungssuch-Ökologie bisher hauptsächlich mit Optimalitäts-Modellen für einzelne Individuen beschäftigt, aber selten die Interaktionen von Individuen während der Nahrungssuche einbezogen.

Die übergeordnete Frage in den drei Studien dieser Dissertation war daher: “**Wie ermöglichen verschiedene Strategien der Nahrungssuche das Zusammenleben konkurrierender Arten?**”. Eine ideale Modell-Art zur Untersuchung dieser Frage ist der Große Abendsegler *Nyctalus noctula* (Schreber, 1774). Er ist eine sehr mobile, insektenfressende Fledermaus, und weist einen hohen Nischen-Überlapp mit anderen Fledermäusen auf. Ich untersuchte daher Bewegungsverhalten und Raumnutzung Großer Abendsegler, und bewertete den Einfluss verschiedener Jagdstrategien auf das Zusammenleben konkurrierender Fledermaus-Arten unter Einbezug der Dichte von Konkurrenten und der Verteilung von Beuteinsekten.

In **Kapitel eins** untersuchte ich die Anpassung der Raumnutzung Großer Abendsegler an abiotische Faktoren (hier Mondlicht), welche möglicherweise die Beuteverteilung beeinflussen. Dazu nahm ich mit Hilfe von GPS Datenloggern die nächtliche Habitatnutzung von neun Großen Abendseglern während niedriger und hoher Mondlicht-Intensität auf.

Während heller Nächte jagten große Abendsegler bevorzugt über offenen Feldern, mieden solche Felder aber während dunkler Nächte, eventuell als Reaktion auf schwankendes Insektenvorkommen. Diese Anpassung des Jagdverhaltens deutet darauf hin, dass Große Abendsegler wiederkehrende räumliche Muster der Beuteverteilung voraussagen können. Die Fähigkeit der

Großen Abendsegler in relativ hellen Lebensräumen zu jagen könnte ein Vorteil gegenüber lichtscheueren Konkurrenten sein.

In **Kapital zwei** untersuchte ich ob die Anwendung einer sozialen Jagdstrategie, also das Jagen in Gemeinschaft, bei Großen Abendseglern saisonal schwankt, möglicherweise als Reaktion auf unterschiedliche Beuteverfügbarkeit. Dazu maß ich die akustische Aktivität Großer Abendsegler in Reaktion auf akustische Simulationen jagender Artgenossen oder andersartiger Fledermäuse.

In Reaktion auf andersartige Fledermäuse erhöhte sich die Aktivität der Großen Abendsegler im Frühsommer, verringerte sich aber im Spätsommer. Unabhängig von der Saison reagierten Große Abendsegler nicht auf jagende Artgenossen. Die Ergebnisse zeigten, dass äußere Faktoren das Ausmaß inner- und zwischenartlicher Konkurrenz beeinflussen können. Insektenfressende Fledermäuse können starkem Konkurrenzdruck aber möglicherweise durch Anpassung von Jagdstrategie und Raumnutzung entgegenwirken. Wahrscheinlich behindern sich Artgenossen bei der Jagd gegenseitig, da sie den gleichen Flugraum und die gleichen akustischen Frequenzen zur Echoortung von Beute verwenden. Einnischung könnte die Jagd in Gemeinschaft mit anderen Arten dahingegen begünstigen, sofern die Konkurrenz um einzelne Beuteinsekten gering ist.

In **Kapitel drei** untersuchte ich ob die Kombination aus Dichte von Artgenossen und Landschaftsmerkmalen, welche sich wiederum auf die Verteilung von Beuteinsekten auswirken können, bestimmte Jagdstrategien fördert. Dazu bestückte ich 27 Große Abendsegler mit kombinierten GPS-Ultraschall-Loggern. Akustische Aufnahmen ermöglichten mir die Quantifizierung sowohl von Jagdereignissen als auch von Artgenossen in der Nähe der beobachteten Fledermäuse. Anhand der GPS Aufnahmen konnte ich zwei Bewegungsarten bestimmen: räumliche begrenzte und gerichtete Bewegung.

In der Agrarlandschaft gingen die Großen Abendsegler zu räumlich begrenzten Bewegungen über nachdem sie Artgenossen antrafen. Die Jagdaktivität war während dieser Bewegungen am höchsten. In der Forstlandschaft hatte das Zusammentreffen mit Artgenossen dahingegen keinen Einfluss auf die Bewegungsart. Die Jagdaktivität unterschied sich nicht zwischen räumlich begrenzter und gerichteter Bewegungen. Insgesamt war die Dichte an Artgenossen in der Forstlandschaft höher als in der Agrarlandschaft. Die

Ergebnisse legen nahe, dass Große Abendsegler Beuteverteilung und Konkurrenzdruck bei der Entscheidung über ihre Jagdstrategie heranziehen. In Agrarlandschaften mit flüchtiger, geklumpter Beuteverteilung könnte soziale Jagd für Große Abendsegler eine Voraussetzung zum Überleben sein. Demgegenüber ist eine solitäre Jagdstrategie wahrscheinlich in Forstlandschaften von Vorteil, da die Beute hier gleichmäßiger verteilt ist und die Konkurrenz durch eine hohe Anzahl an Artgenossen stärker ist.

Zusammenfassend lässt sich sagen, dass Große Abendsegler Umweltfaktoren welche die Beuteverteilung beeinflussen, nachteilige Effekte durch inner- und zwischenartliche Konkurrenz, und Informationen über andere jagende Fledermäuse, bei der Entscheidung ob einer sozialen oder solitären Jagdstrategie einbeziehen. Die Studien in dieser Dissertation unterstreichen, dass Große Abendsegler ihre Jagdstrategien situationsabhängig anpassen können. Diese Flexibilität erreichten die Tiere durch dynamische Rückmeldungen zwischen ihrem Flugpfad und der wahrgenommenen Umwelt. Solche dynamische Rückmeldungen scheinen eine wichtige Rolle für das Zusammenleben konkurrierender Arten zu spielen. Insbesondere könnte das innerartlich gleichartige Bewegungsverhalten zu ähnlichen Jagdstrategien führen, was wiederum zu innerartlicher Konkurrenz führt und somit die lokale Artenzusammensetzung stabilisiert. Zwischenartlich unterschiedliche Bewegungsmuster könnten dahingegen den Nischenüberlapp verschiedener Arten mindern und somit Fitnessunterschiede zwischen Arten ausgleichen. Diese Mechanismen gelten wahrscheinlich nicht nur für insektenfressende Fledermäuse, sondern für Gemeinschaften hoch-beweglicher Räuber im Allgemeinen.

GENERAL INTRODUCTION

MOVEMENT OF ANIMALS

Movement is a key signature of life. Many animals move actively and throughout all life stages, some passively or only during certain life stages. There are several reasons to move. The most prominent one may be dispersal. Dispersal movement is one of the key features shaping local and global biodiversity patterns (Urban *et al.* 2008; Carrara *et al.* 2012). Future biodiversity patterns will be heavily influenced by dispersal movements altered in response to human induced global change (Knowlton & Graham 2010; Caplat *et al.* 2016, Schlägel *et al.* in prep).

Yet, besides dispersal, there are several other movement types (e.g. Barton *et al.* 2015), such as migratory movements dedicated to find suitable niches across yearly seasons, searching for mates, or foraging movements. Generally, single foraging trips are relatively short in length and duration, but constitute the most frequent movements, often performed on a daily basis. The decision when, where, how, and on what to forage can be condensed under the term foraging strategy. The success of an individual’s foraging strategy - in terms of net energy gain - proximately influences the individual‘s survival (e.g. King & Moors 1979; Huey & Pianka 1981; Tiselius *et al.* 1993). The adaptive value of a set of foraging strategies restricts the niche and ultimately plays a key role in the distribution of a species. Accordingly, foraging movements and underlying foraging strategy shape biodiversity patterns and can have cascading effects on species assemblages across trophic levels. Hence, the study of foraging behaviour has always been at the core of ecology, and culminated in a distinct sub discipline – *foraging ecology*.

FORAGING ECOLOGY

A key concept of foraging ecology was first developed by Emlen (1966) and MacArthur & Pianka (1966) and is today known as *optimal foraging theory*. Optimal foraging theory basically proposes that foraging strategies that yield the greatest net energy gain for an individual will be evolutionary stable (Giraldeau & Caraco 2000). Individuals will maximize their net energy gain by adjusting prey choice and space use to prey abundance and distribution. A fundamental sub-model of optimal foraging strategy is the *marginal value* *theorem* developed by Charnov (1976). The marginal value theorem basically predicts that foraging animals should move from the current food patch to another food patch when the food intake rate within the current patch drops below the expected average food intake rate across all available patches. It further accounts for the travel time to reach the next patch. Accordingly, an optimal forager will leave patches the earlier the more resources other patches include, and the closer other patches are to the current one.

Although classic optimal foraging theory still constitutes a comprehensive framework, it has repeatedly been criticized for not complying with empirical observations, which suggests that optimal foraging models are oversimplified (Pyke *et al.* 1977; Iwasa *et al.* 1981; Pierce & Ollason 1987; Nonacs 2001). Firstly, the most severe drawback of optimization models in foraging theory is probably the unrealistic assumption that a forager has omniscient knowledge of the spatial distribution of food items. However, attempts have been made to account for the problem that individual foragers do not possess all information on resource distribution, e.g. by acknowledging the need to sample different food patches in order to assess their quality (Krebs *et al.* 1978; Pyke 1984). Secondly, another major limitation stems from the fact that classic optimal foraging theory focuses on single individuals, and thus does not account for adverse effects of competition or advantageous effects of social foraging. This problem has partially been addressed, leading to the postulation of the *ideal free distribution* hypothesis (Fretwell 1972), which states that the distribution of a group of foragers shall be congruent to the resource distribution. Similarly, enhanced detection of food patches via group hunting has been modelled by Clark & Mangel (1984). Yet, these approaches assume that all predators are equal, and thus do neither account for individual variation within homospecific forager groups nor for variations among heterospecifics forager assemblages. Thirdly, the last limitation of classic optimal foraging theory that I want to stress here is that movement, including different costs and limitations, is rarely modelled explicitly, but generally just incorporated implicitly through time spent travelling between patches which thus cannot be spent for feeding (Charnov 1976).

INTEGRATION OF MOVEMENT AND BIODIVERSITY RESEARCH

Some conceptual limitations of classical optimal foraging strategy have led to the aim to integrate individual movements into foraging ecology (e.g. Turchin, 1991). Finally, the essential role of individual movement behaviour in foraging ecology, but also in a multitude of other ecological processes, has led to the rise of the discipline *movement ecology* (Holyoak *et al.* 2008; Nathan *et al.* 2008), which is flourishing thanks to technical (e.g. Cvikel *et al.*, 2015; Taylor *et al.*, 2017; Toledo *et al.*, 2014; Wikelski *et al.*, 2007) and theoretical endeavours alike (e.g. Benhamou, 2014; Fagan *et al.*, 2013; Fauchald & Tveraa, 2003; Humphries, Weimerskirch, Queiroz, Southall, & Sims, 2012; Thurfjell, Ciuti, & Boyce, 2014). The widely used movement ecology framework of Nathan et al. (2008, green circle in Fig. 1.1) dissects the entities that finally lead to an observable movement path, and the feedback from the movement path on the individual's internal state and its environment. Namely, the authors propose that every individual movement is triggered by the *internal state* (i.e. the motivation of an animal), which in concert with *external factors* leads to a *navigational process* (i.e. decisions where to move), which under the limitations of an animal's *motion capacity* (i.e. the biophysical ability to realize certain movements) finally results in the realized *movement path*. Accordingly, the movement of an individual is the result of the interactions of the environment, an individual's motivation, an individual's decisions, and an individual's previous movements. The study of these interactions can reveal ecological meaningful mechanism that may help to explain large scale phenomena like population dynamics or biodiversity patterns.

Indeed, recently frameworks were developed that aim to integrate modern biodiversity theory (*sensu* Chesson 2000) with movement ecology (Fig. 1.1, Jeltsch *et al.*, 2013, Schlägel *et al.* in prep.). The need for this integration becomes most obvious in the face of human driven global change and its effects on animal movements (e.g. Brown *et al.*, 2017; Gibert, Chelini, Rosenthal, & DeLong, 2016; Kremen *et al.*, 2007; Tucker *et al.*, 2018). Changes in animal movements may lead to changes in animal distributions through altered dispersal and altered competitive environments. Chesson (2000) proposes that so-called *stabilizing* and *equalizing* mechanisms are necessary to reach stable coexistence of competing species. In a nutshell, stabilizing mechanisms can be thought of as density dependant negative feedbacks on populations, since individuals of one species put more competitive pressure on each other than on a heterospecific competitor. Consequently, growth rate and population density will be negatively correlated, which allows rare species to recover from low densities. Equalizing mechanisms on the other hand slow down competitive exclusion by decreasing fitness differences across different species, and thereby mitigate interspecific competition. Jeltsch *et al.* (2013) propose that the movements of individuals can act stabilizing or equalizing (cf. Macandza *et al.* 2012), e.g. through influencing intra- and interspecific interactions.

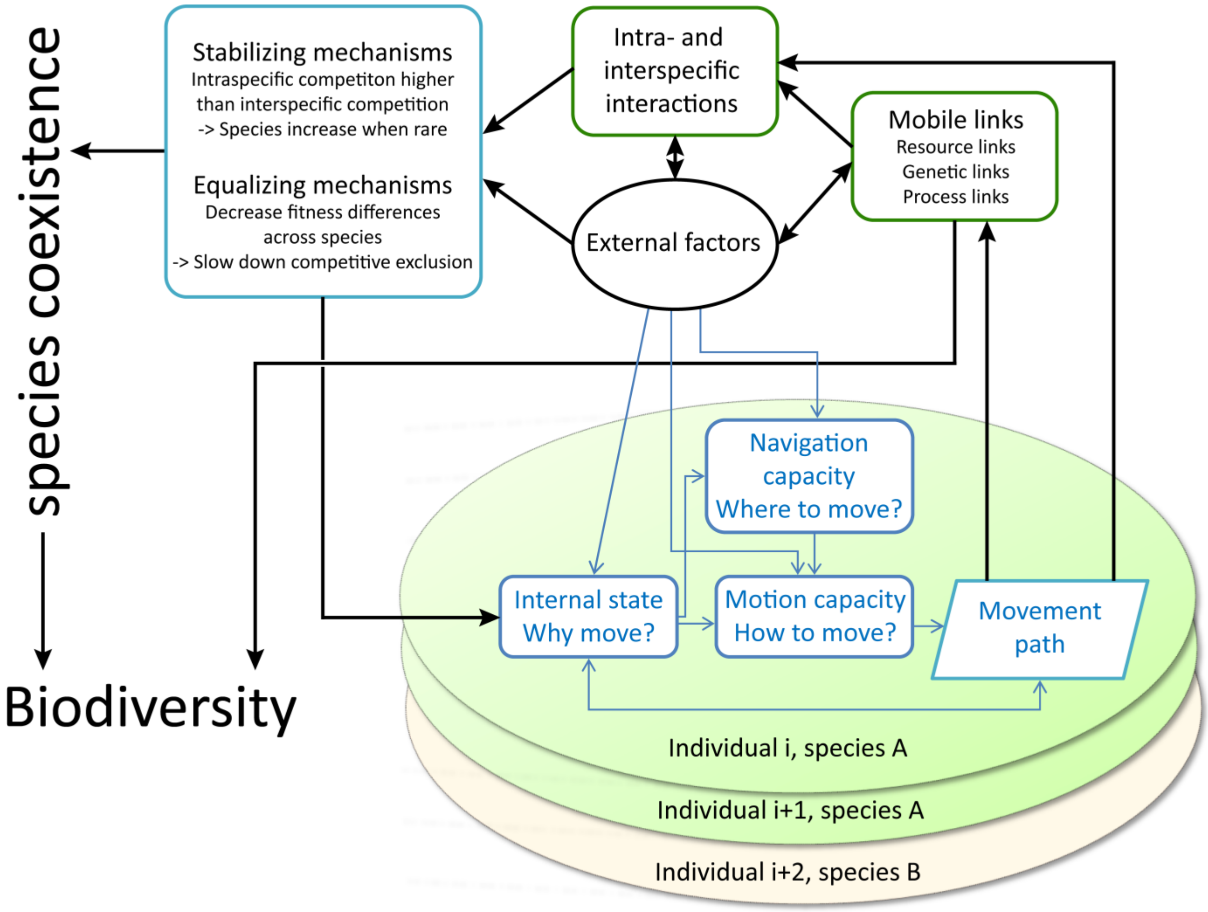

Fig. 1.1 Concept for linking movement and biodiversity research by Jeltsch *et al.* (2013, figure modified)

BATS AS A MODEL FOR MOVEMENT AND BIODIVERSITY RESEARCH

The work presented here aimed to contribute to our understanding of biodiversity patterns by integrating foraging ecology and movement ecology with the study of intra- and interspecific competition. All three studies of this thesis focused on the foraging movements of the insectivorous Common noctule bat *Nyctalus noctula* (Schreber, 1774). *N. noctula* is ideal as a model organism for movement and biodiversity studies in the wild for several reasons.

Importance and generalisability

N. noctula is a representative of the second largest mammalian order. Bats (*Microchiroptera*) are distributed worldwide and comprise well over a thousand species (IUCN Redlist). Besides the intrinsic value of every single species, bats therefore vastly contribute to mammalian biodiversity. They further provide crucial ecosystem services by acting as mobile linkers during their foraging flights, conducting pollination, seed dispersal, and trophic stabilization through suppression of pest insects (Boyles *et al.* 2011; Ghanem & Voigt 2012; Maas *et al.* 2013; Wanger *et al.* 2014; Maine & Boyles 2015). Indeed, most bat species are insectivorous (Hutson *et al.* 2001). Since *N. noctula* is hunting insects during fast flight in mid air, it also represents the guild of aerial hunting insectivores. Aerial insectivores are directly linked to low trophic levels, making them excellent indicators for the condition of ecosystems. Especially in the light of massive decline of insect biomass (Hallmann *et al.* 2017), detecting changes in abundance and behaviour of insectivorous bats may serve as early warning system for nature conservation. Since *N. noctula* occurs in a wide range of ecosystems, the study of its foraging ecology and movement ecology may further elucidate key features that enable species to persist in strongly anthropogenically influenced landscapes.

Study of ecological key mechanisms

Insectivorous bats such as *N. noctula* are known to often hunt within distinct, i.e. spatially well-defined, patches to exploit aggregations of prey insects (Kronwitter 1988; Roeleke *et al.* 2016). Such patchy distribution of prey is one of the core assumptions of foraging ecology. The - at least partial - spatio-temporal unpredictability of the formation of foraging patches presents one of the major problems of optimal foraging theory: How can animals obtain sufficient information about the distribution of prey items to feed successfully? Several studies have shown that insectivorous bats might solve this problem through social hunting, whereby they use the information from specialized ultrasonic hunting call sequences (Griffin *et al.* 1960) of nearby con- or heterospecifics to detect foraging patches (Barclay 1982; Balcombe & Fenton 1988; Gillam 2007; Dechmann *et al.* 2009; Dorado-Correa *et al.* 2013; Cvikel *et al.* 2015; Egert-Berg *et al.* 2018; Gager 2018). However, the aggregation of bats at foraging patches may also lead to increased intra- and interspecific competition, thus challenging the proposition of the ideal free distribution and arising questions on mechanisms enabling coexistence of competing bat species. Yet, flexibility in foraging movements may enable open space foragers like *N. noctula* to exploit a wide range of foraging patches, and thereby mitigate for lacking knowledge on prey distribution or increased competition at distinct patches. Indeed, even upon bats, *N. noctula* is a particular mobile species. Individuals may cover hundreds of kilometres during seasonal migrations (Hutterer 2005; Lehnert *et al.* 2014), or dozens of kilometres during nightly foraging flights (Roeleke *et al.* 2016; Chapter three this thesis). Their wing morphology allows them to exhibit prolonged fast flight at low energetic cost (Norberg & Rayner 1987; Winter & von Helversen 1998). *N. noctula* may thus be able to sample a large area for insect prey, or use foraging patches at large distance from its roost. Therefore, *N. noctula* is an ideal species to study on the one hand movement components of foraging ecology, and on the other hand how movement ecology of a species contributes to local biodiversity patterns.

Research feasibility

Last but not least, the ecology of *N. noctula* allows the study of movement, foraging strategy, and competition in great detail by using recent technological developments. Namely, recent miniaturization of telemetry devices such as global position system (GPS) loggers (Cvikel & Yovel 2014) allows attachment of loggers over short periods of time. GPS loggers can record 3-dimensional positions of animals flying in the open air space at very high spatio-temporal resolution. Combined with additional sensors such as temperature sensors, heart rate loggers, or microphones, miniaturized devices can provide additional information on environmental factors and physiology or behaviour of free ranging animals. Especially bats are able to carry such loggers temporarily, even if the logger masses currently still exceeds 5 % of the animal's body mass, which is the threshold recommended for birds (Aldridge & Brigham 1988). This is because bats are adapted to a wide range of wing loadings which enables them to gain mass before hibernation (Kunz *et al.* 1998) or to fly with unborn young in their uterus that may weight about 20 % of the mother's body mass (Kurta & Kunz 1987).

The combination of GPS and acoustic ultrasound recordings proofed especially useful for studying bats (Cvikel & Yovel 2014), since most insectivorous bats emit ultrasonic echolocation calls at high rates during flight. Characteristics of echolocation calls and call sequences are adapted to the situations that bats encounter and tasks that bats perform during flight. For example, call intervals and frequency range vary with habitat complexity (Schnitzler & Kalko 2001), and the pursuit of single prey items is accompanied by stereotypic ultrasonic pulse trains, so called feeding buzzes (Griffin *et al.* 1960). The combination of movement behaviour reconstructed from GPS records with ultrasound recordings therefore allows the study of foraging strategies and the spatially explicit quantification of hunting activity. For animals which have less suspicious hunting behaviour than bats, it is to date mostly impossible to quantify hunting events remotely (but see Weimerskirch *et al.* 2007; Watanabe *et al.* 2014). Further, in 1982, Barclay implemented a method that is meanwhile a well-established tool for experiments with bats in the wild; he broadcasted ultrasonic bat calls to simulate a group of bats and studied changes in the flight behaviour of bats receiving the broadcasted calls. Today, researchers can construct playbacks that simulate bats in different situation, e.g. during foraging (Gillam 2007) or advertising themselves to potential mates (Voigt-Heucke *et al.* 2016). The response can be quantified via changes in the vocal activity that is simultaneously recorded by ultrasonic microphones placed in the vicinity of the speaker used for the playback (e.g. Gillam 2007). Therefore, bat researchers have a well-established and non-invasive tool to perform experiments that allow the study of social behaviour of bats in the wild.

N. noctula is especially suited for experimental studies, including studies with short term attachment of loggers, because (a) it is upon the largest bats in Europe and thus able to carry loggers, (b) it is easily accessible from artificial bat boxes, and (c) its IUCN conservation status was “least concerned” by the date of this study.

THESIS OUTLINE

In **chapter one** I investigated the effect of moonlight intensity - as an example of varying abiotic factors – on foraging movements of *N. noctula*, and interpreted the observed flexibility in space use at the habitat scale in the light of a suggested co-variation in prey distribution. In **chapter two** I investigated how social foraging of *N. noctula* varied with prey composition, and inferred how flexibility in foraging behaviour promotes bat diversity through flexibility in space use at the local patch scale. In **chapter three**, I investigated the differences in foraging movements and social foraging behaviour across different anthropogenic landscapes, and related these differences to prey distribution and population density.

CHAPTER ONE - ENVIRONMENTAL EFFECTS ON MOVEMENT PATTERNS

Published in Movement Ecology 6 (1), 2018

as

Aerial-hawking bats adjust their use of space to the lunar cycle

by

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https://doi.org/10.1186/s40462-018-0131-7

ABSTRACT

Animals change their habitat use in response to spatio-temporal fluctuation of resources. Some resources may vary periodically according to the moonphase. Yet it is poorly documented how animals, particularly nocturnal mammals, adjust their use of space in response to the moonphase.

Here, we asked if an obligate nocturnal mammal, the aerial-hawking common noctule bat (*Nyctalus noctula*), adjusts its 3-dimensional flight behaviour and habitat use to the lunar period. Using miniaturized GPS loggers, we recorded 3-dimensional flight tracks of *N. noctula* and related these to a canopy height model derived from aerial laser scans to investigate whether bats adjust forest strata use to moonlight intensities.

Noctules frequently foraged above the canopy of coniferous forest at low moonlight intensities, but switched to using open grasslands and arable fields in nights with high moonlight intensities. During the few occasions when noctules used the forest during moonlit nights, they mostly restricted their use of space to flying below the canopy level. The median overall flight altitude of *N. noctula* equalled 13 ± 16 m but reached up to 71 m above ground (97.5 % quantile).

Our findings argue against general lunar phobic behaviour of aerial-hawking bats. We suggest that the preferred use of open fields around full moon may be a strategy of noctules to increase the success of hunting airborne insects at night. Specifically, the adjustment in use of space may allow bats to hunt for insects that emerge and disperse over open fields during bright moonlight.

BACKGROUND

Animals live in heterogeneous landscapes that offer resources for different requirements, such as breeding, shelter, or foraging(Kotliar & Wiens 1990). Such functional heterogeneity within landscapes may occur in space and time alike (Kolasa & Rollo 1991). At the spatial scale, animals will perceive the temporal heterogeneity of resource availability as a change in habitat suitability (cf. Wiens 2002), which may result in distinct temporal patterns of use of space. Temporal changes in habitat suitability may be partially or completely unpredictable, e.g. when they are driven by local weather conditions (Petit 1989), or distinct events like human hunting activities (Béchet *et al.* 2004) or extreme weather conditions (Bailey & Secor 2016). However, temporal changes in habitat suitability may also occur periodically. Periodic changes in habitat suitability and resulting changes in habitat use happen on very different timescales, ranging from hourly (e.g. tidal flooding, Sheppard *et al.* 2009) to daily (e.g. day-night changes or periodic human disturbances, Coppes *et al.* 2017) and seasonal patterns (e.g. snow cover, Rehnus *et al.* 2013). According to the optimal foraging theory (Pyke *et al.* 1977), animals should react towards periodic and thus predictable temporal heterogeneity in habitat suitability with a concordant adjustment of their use of space.

The moon phase presents a highly predictable periodic change in the environment to which various animals respond. Many studies reported so-called lunar phobia in prey species, a term describing the negative response of animals towards bright moonlight by either decreasing overall activity (Cresswell & Harris 1988; Griffin *et al.* 2005) or by adjusting habitat use and behaviour to prevent encountering visually oriented predators (Brown *et al.* 1988; Cresswell & Harris 1988; Kotler *et al.* 1991; Bouskila 1995; Mougeot & Bretagnolle 2000). Predators on the other hand may increase their activity during low or intermediate moonlight levels to enhance foraging success (Van Orsdol 1984; Funston *et al.* 2001; Rockhill *et al.* 2013). This may result in complex temporal and spatial patterns of predator-prey interactions (Palmer *et al.* 2017). Yet, some mammals are predator and prey at the same time, a fact that may result in a trade-off between increasing foraging activity when prey is easy to perceive, and decreasing activity at the same time in order to avoid becoming prey themselves during moonlit nights (Penteriani *et al.* 2013). The optimal strategy thus depends on trading the energetic benefit from increased capture rate when hunting prey which is sensitive to the moonphase against the potential costs of increased predation risk in bright moonlight. One such strategy can be adjustment in use of space according to the anticipated resource distribution and likelihood of predation (Di Bitetti *et al.* 2006; Penteriani *et al.* 2013).

Although bats are commonly perceived as lunar phobic animals (Prugh & Golden 2014), the picture within the order of bats is complex (Saldaña-Vázquez & Munguía-Rosas 2013). Thus far, lunar phobia has been described exclusively in some tropical bat species (Börk 2006; Lang *et al.* 2006; Appel *et al.* 2017), yet with different reasoning for the underlying causes, such as predator avoidance or decreased prey detectability. On the other hand, studies on temperate zone bats could not show effects of moonlight on foraging activity (Leonard & Fenton 1983; Negraeff & Brigham 1995; Gaisler *et al.* 1998; Karlsson *et al.* 2006). However, although temperate zone bats might not decrease their overall flight activity, they may still adjust their vertical use of space, probably to increase foraging success (Hecker & Brigham 1999). This suggests that predation risk is only a minor driving force for temperate zone bats to alter their behaviour (cf. O'Shea *et al.* 2016) and can be outweighed by the potentially higher foraging success during moonlit nights. Indeed, temperate zone bats face relatively small numbers of airborne predators during the night, and most aerial predators hunt only opportunistically upon bats when bats emerge from roosts at dusk (Lesiński *et al.* 2009; Rosina & Shokhrin 2011; Lima & O'Keefe 2013). Especially fast-flying bats that are adapted to forage in the open space (Norberg & Rayner 1987) might be able to easily escape nocturnal birds of prey such as owls. This is probably also the reason why fast-flying species, like e.g. Pipi*strellus nathusii* or *Nyctalus noctula*, are the most light tolerant bats of the temperate zone (reviewed in Rowse *et al.* 2016). Open-space foraging insectivorous bats of the temperate zone may thus be perceived as top predators. This will result in a high selection pressure to increase foraging efficiency, but a minor pressure to avoid predators. Bats might thus be highly flexible in their use of habitats and altitudes, enabling them to feed opportunistically on patches of prey aggregations, such as swarming insects. Indeed, many insects that hatch synchronously adjust their emergence to the lunar cycle (Danthanarayana 1986; Nowinszky *et al.* 2010). Some studies suggest a decrease of aquatic insects near full moon (Anthony *et al.* 1981), whereas activity of terrestrial crop pests may increase with moonlight intensity (Bhagawati *et al.* 2015). These studies show that the timing of emergence is not consistent for all insect species, meaning that abundances of some insect prey species like specific moths may be low (Nowinszky *et al.* 2010; Nowinszky *et al.* 2012) while the abundance of other insect prey species, e.g. Trichoptera or Diptera, may be high during the full moon (Bidlingmayer 1964; Brack Jr. & Laval 1985; Bhagawati *et al.* 2015). Such species-specific responses towards the lunar cycle suggest temporal fluctuation of prey availability that is specific for the habitats that an affected prey species uses.

Here, we evaluate how the 3-dimensional use of space of common noctules (*Nyctalus noctula*) changes with moonlight intensity. *Nyctalus noctula* is a fast-flying species that forages in the open aerosphere (Schnitzler *et al.* 2003), and is known for its flexibility in exploiting temporarily occurring and patchily distributed insect swarms (e.g. Gloor *et al.* 1995, Vaughan 1997). Accordingly, if habitat specific insect abundances differ between moon phases, noctules should adjust their use of space to increase foraging efficiency. To test this hypothesis, we tracked common noctules with GPS loggers and related their habitat use and the use of forest strata derived from airborne laser scans (LiDAR) to the moon phase.

METHODS

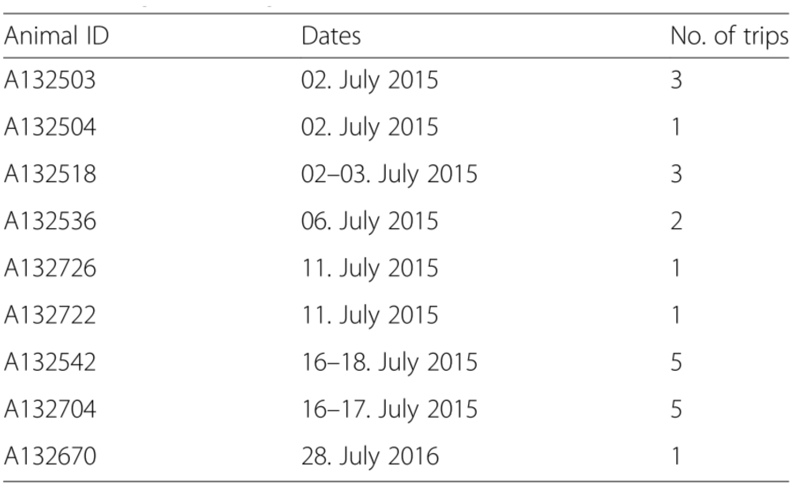
Study site and GPS tracking

In July 2015 and 2016, we equipped nine *Nyctalus noctula* (five post-lactating females and four males) with GPS loggers (Robin Cell Guide, Lucidlogix Technologies Ltd., Kfar Netter, Israel) to record 3-dimensional positions of flying bats. The study area in North-Eastern Germany consisted mostly of loose pine forest plantations interspersed by forest tracks (51%), but also included open fields (21 %), several larger water bodies (14 %), mixed or deciduous forest (8 %), and small villages (5 %) (Appendix 2.1). All tagged individuals roosted in artificial roost boxes in a pine stand, located about 50 km south of Berlin, Germany. During morning hours, we removed bats temporarily from their roosts and glued a GPS logger onto the dorsal fur of each bat using latex based surgical glue (Manfred Sauer, Lobbach, Germany). GPS loggers were placed into rubber balloons for protection against humidity. The whole unit weighed in total about 3.4 g, which corresponded to 10 to 13 % of the bats' body masses. Within a maximum of ten days after deployment of the GPS units, we relocated the tagged bats by using radio telemetry, recaptured them from their artificial roosting boxes or treeholes, and removed the GPS units. Similar to other studies (Cvikel *et al.* 2015; Roeleke *et al.* 2016), we did not notice any adverse effects of the relatively large weight of GPS units on the bats. All procedures were approved by the animal welfare and ethics committee of the Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg (permit: 2347-16-2015) and by the federal agency for nature conservation (permit: LUGV_N1-4743/103+5#283569/2015). All institutional and national guidelines for the care and use of animals were followed.

Data acquisition and processing

We programmed the GPS loggers to record GPS locations every 15 seconds from sunset to sunrise until batteries expired. In total, we recorded about 7,000 GPS locations from nine bats from which we retrieved GPS units. All bats started foraging trips around sunset, but only six bats performed additional trips within one night after times of inactivity. In these cases we divided the GPS locations of each bat into several continuous trips with regular GPS fix intervals, and deleted occasional GPS fixes when bats were not moving but remained in or close to their roosts. Further, we excluded flight times when - according to the three closest weather stations - more than 50 % of the sky was covered by clouds, resulting in 22 flight trips (Tab. 2.1 and Appendix 2.2, 4929 GPS locations, between one and five trips or one and three nights per bat). Since altitude estimates of GPS loggers do not have the same accuracy as locations in the 2-dimensional plane, about 16 % of locations yielded false negative flight altitudes at -4.3 m (median) below ground. Most of these localisations were recorded when bats started their flight trips, flew within the forest, or when bats hunted above water bodies (see points with altitude zero in Appendix 2.1). Since the majority of these measures were thus recorded in situations when low flight altitudes are most plausible, we decided to off-set these points to zero and still include them in the analysis. We think that excluding these points from the analysis may have led to a severe overestimation of flight altitudes. However, one must be aware that the offsetting of false altitude measures leads to an underestimation of flight altitudes of localisations that are close to the ground or close to the canopy. Altitude measures of localisations further away from the ground or habitat structures on the other hand are measured at higher accuracy since satellite detection is not hampered at higher altitudes.

Tab. 2.1 Nights during which we tracked individual bats



Animal ID	Dates	No. of trips
A132503	02. July 2015	3
A132504	02. July 2015	1
A132518	02–03. July 2015	3
A132536	06. July 2015	2
A132726	11. July 2015	1
A132722	11. July 2015	1
A132542	16–18. July 2015	5
A132704	16–17. July 2015	5
A132670	28. July 2016	1

Habitat use and movement behaviour

We assigned underlying land use types to the respective GPS locations using habitat maps derived from aerial infrared imagery (Land Brandenburg 2013) grouped into six categories: coniferous forest (i.e. mainly pine plantations), deciduous and mixed forest, open fields (incl. arable land, meadows, and grassland), urban areas, scrub or areas with successional growth, and water bodies or swamps. To evaluate the use of forest strata, we further assigned tree heights to the respective GPS locations when bats flew above the forest canopy. For this, we used aerial laser scan (LiDAR) data with a mean resolution of 2.9 points / m^2 and an accuracy of <20 cm, collected in 2009 by the federal office of the state of Brandenburg (https://www.geobasis-bb.de/geodaten/dgm-laserscanrohdaten.htm). Based on these raw data, we calculated a canopy height model (chm) for the forest areas, using the free version of the software LASTools (rapidlasso GmbH, Gilching, Germany) and following the tutorial by Isenburg (2014). A detailed description of the processing of the LiDAR data from raw 3-dimensional coordinates to the chm model is included in the supplement (Appendix 2.3). To assign the height of the uppermost canopy layer to the respective GPS points on a meaningful scale, we calculated the 95 % quantile of the canopy height values within a radius of 20 m from the GPS location. For each GPS location, we specified the moonlight intensity as either low (0 to 20 % of moon visible) or high (80 to 100 % of moon visible). If the bats performed foraging trips before moonrise, we defined the according moonlight intensity as low. This resulted in flight tracks for four bats during high moonlight intensity in early July 2015 (one female and three males), and tracks from seven bats during low moonlight intensity in early and mid July 2015 and late July 2016 (4 females and 3 males) (Appendix 2.2)

We used the function fitHMM from the R package moveHMM (Michelot *et al.* 2016) to assign two different movement behaviours (i.e. foraging with short step length and large turning angles, or commuting with larger step length and smaller turning angles) to single GPS fixes. Whenever the probability of correct classification was below 75%, we categorized the movement of a bat as undefined.

Statistics

We used Mann-Whitney-U-tests to compare the flight altitudes of *N. noctula* between nights with high and low moonlight intensities above different habitats. To evaluate preferences for certain habitat types, we applied an use-versus-availability approach (Manly *et al.* 2002). We defined available habitat for the respective tracks by five randomly rotated GPS tracks per recorded track (function NMs.randomShiftRotation, Calenge 2006) to keep the properties, such as the spatial autocorrelation structure, of the movement tracks (Martin *et al.* 2008). The centre of rotation was set to the starting point of the respective track. We then fitted a binomial generalized mixed model with the interaction of habitat class and moonlight intensity as fixed factors to explain the identity of locations (i.e. real bat or randomly rotated track). We used the respective trips nested within the individual bat as a random factor to account for dependency of locations within single trips and between different trips of the same individual. We further included the sex of the tracked individuals as a random factor to account for potential biases in the dataset. We also modelled the probability of bats flying above or below the forest canopy, using a similar mixed model with only moonlight intensity as a fixed factor. Full models were compared to reduced models using Aikaike Information Criteria corrected for small sample sizes. We calculated 95% confidence intervals and plotted the fixed effects using the R package effects (Fox 2003). We assume statistical significant preference / avoidance when 95% confidence intervals did not overlap with a probability value of 0.5. For statistical tests, we assumed a significance level of 0.05. Unless stated otherwise, all measurements are given as median ± median absolute deviation (mad). Throughout the text, ranges are given as 2.5% to 97.5% quantiles. Data processing and statistics were done with the software R (Version 3.3.2). GPS data are stored at the movebank data repository (Study ID 297041945 at https:\\movebank.org).

RESULTS

Moonlight and flight altitude

The median overall flight altitude of *N. noctula* equalled 13 ± 16 m (median ± median absolute deviation), but reached up to 71 m above the ground (97.5 % quantile). This corresponded to a maximum altitude of 63 m above the canopy level (97.5 % quantile) when noctules flew above forested areas In general, *N. noctula* flew at lower altitudes during high than during low moonlight intensities, except when flying above urban areas (Fig. 2.1, Tab. 2.1). N. noctula used forested areas less often during high than during low moonlight intensities (Tab. 2.2). When the bats used the forested areas during high moonlight intensities nonetheless, they flew mostly underneath the canopy level (Fig. 2.2).

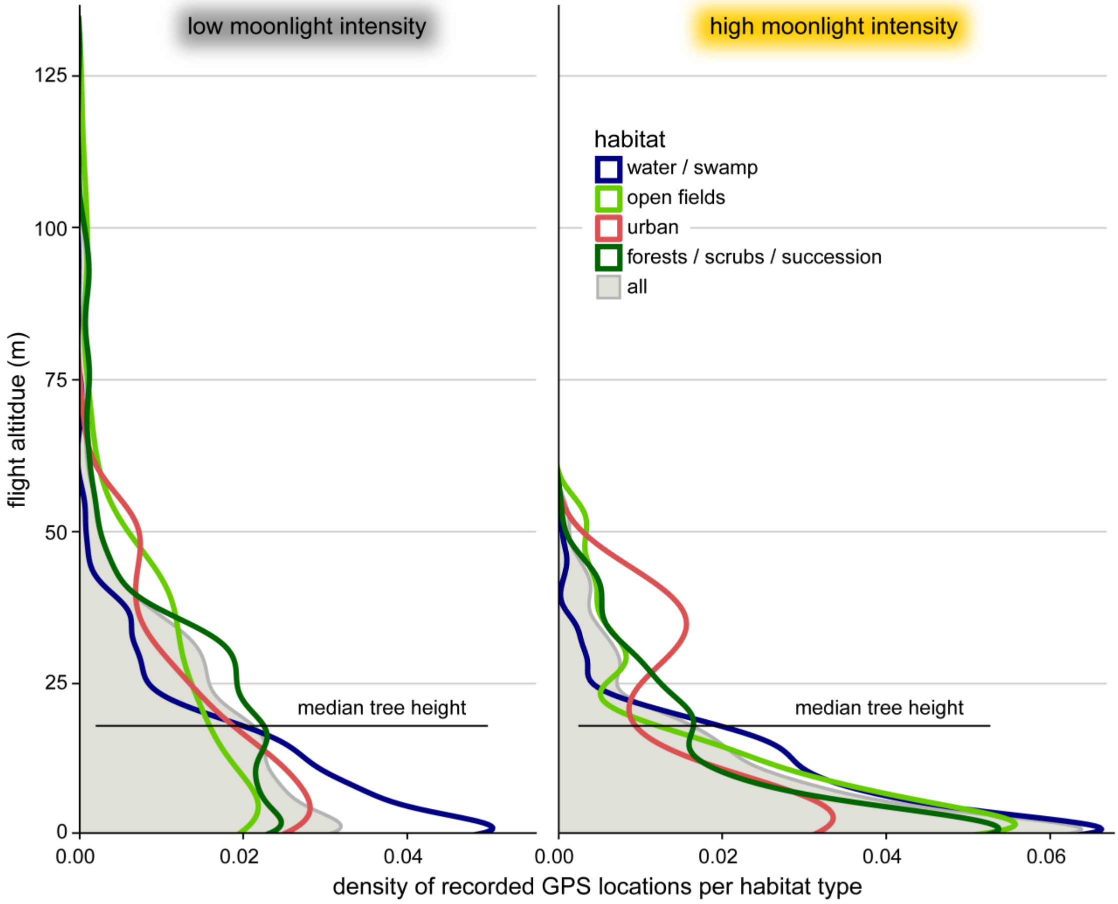
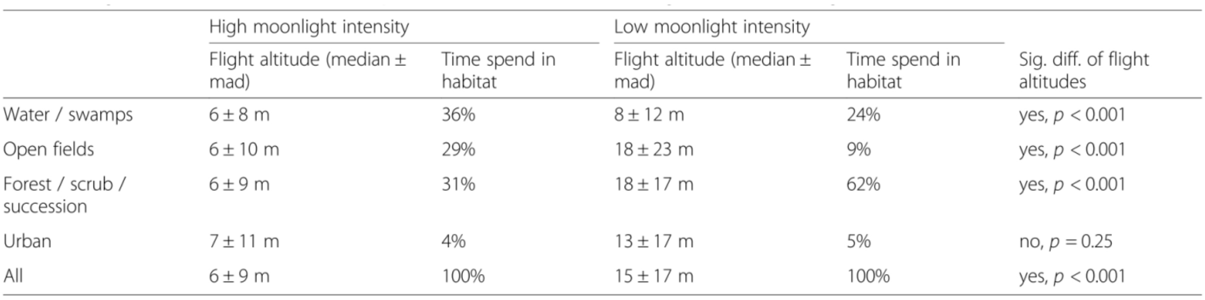


Fig. 2.1 Probability of *N. noctula* flying above the canopy level when using forested areas, depending on the moonlight intensity. Dots depict effect estimates from the underlying model, bars depict the corresponding 95% confidence intervals.

Tab. 2.2 Flight altitude and relative time spend in different habitats during different moonlight intensities



	High moonlight intensity		Low moonlight intensity		
	Flight altitude (median ± mad)	Time spend in habitat	Flight altitude (median ± mad)	Time spend in habitat	Sig. diff. of flight altitudes
Water / swamps	6 ± 8 m	36%	8 ± 12 m	24%	yes, $p < 0.001$
Open fields	6 ± 10 m	29%	18 ± 23 m	9%	yes, $p < 0.001$
Forest / scrub / succession	6 ± 9 m	31%	18 ± 17 m	62%	yes, $p < 0.001$
Urban	7 ± 11 m	4%	13 ± 17 m	5%	no, $p = 0.25$
All	6 ± 9 m	100%	15 ± 17 m	100%	yes, $p < 0.001$

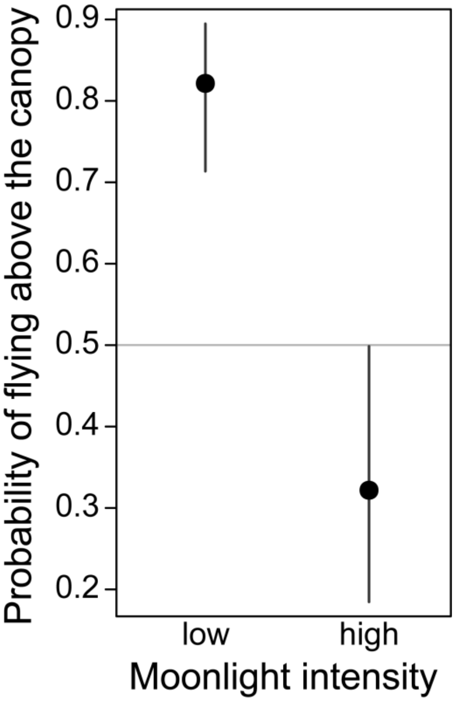


Fig. 2.2 Relative distribution of flight altitudes of *N. noctula* for different habitat types and for all recordings, recorded at different moonlight intensities. The horizontal black line shows the median tree height, derived from all bat locations in forested areas.

Moonlight and habitat use

Irrespective of the moonlight intensity, N. noctula consistently preferred water bodies (Fig. 2.3). The recorded movement behaviour suggests that bats used the water bodies mainly for foraging (Fig. 2.4, in total 67 % of the GPS locations over water were classified as foraging). At high moonlight intensities, noctules flew more often above open fields than at low moonlight intensities (Fig. 2.3). Their movement behaviour above open fields also suggests increased foraging activity under moonlit conditions (Fig. 2.4, 36 % of GPS locations defined as foraging during low moonlight intensities, but 70 % of GPS locations defined as foraging during high moonlight intensities).

N. noctula showed relative avoidance of coniferous forest at high moonlight intensities. Our model yielded also different significant effects of moonlight intensity on the use of urban areas, deciduous forest, and scrub or areas with successional growth (Fig. 2.3), as well as a significant decrease of movement behaviour associated with foraging activity in deciduous forest during high moonlight intensities (Fig. 2.4). However, these habitat types accounted only for a small fraction within the landscape, and since the GPS locations recorded in these habitat types only sum up to 12 % of the total number of locations, we refrain from further interpretation of these results.

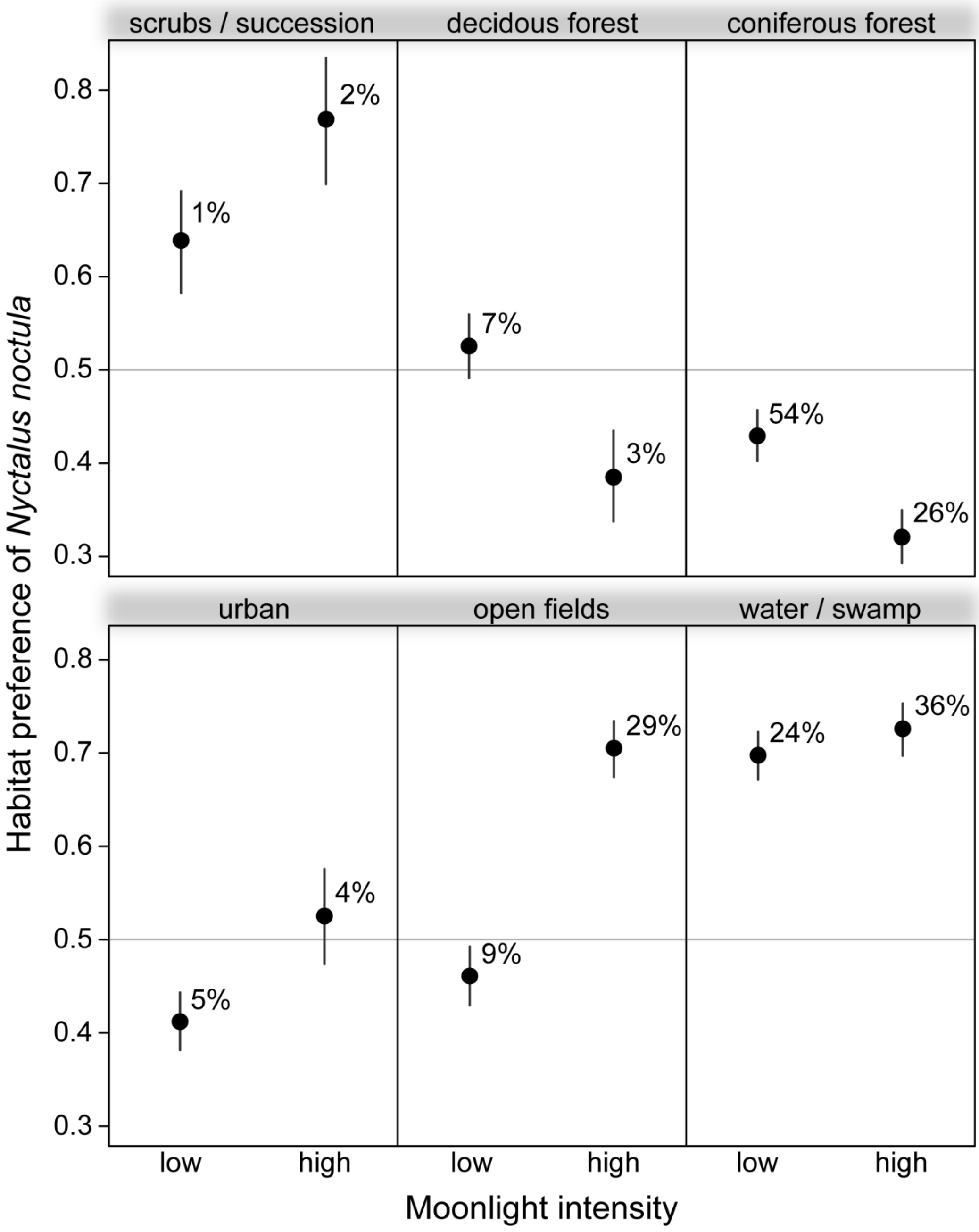


Fig. 2.3 Preference of *N. noctula* for different habitat classes, depending on the moonlight intensity. Values above 0.5 indicate that *N. noctula* used this habitat more frequently than expected from availability derived from randomly rotated tracks. Values smaller than 0.5 indicate relative avoidance of the respective habitat type. Dots depict effect estimates from the underlying model, bars depict the corresponding 95% confidence intervals. Percentages depict the relative number of GPS locations within each habitat type for the respective moonlight intensity.

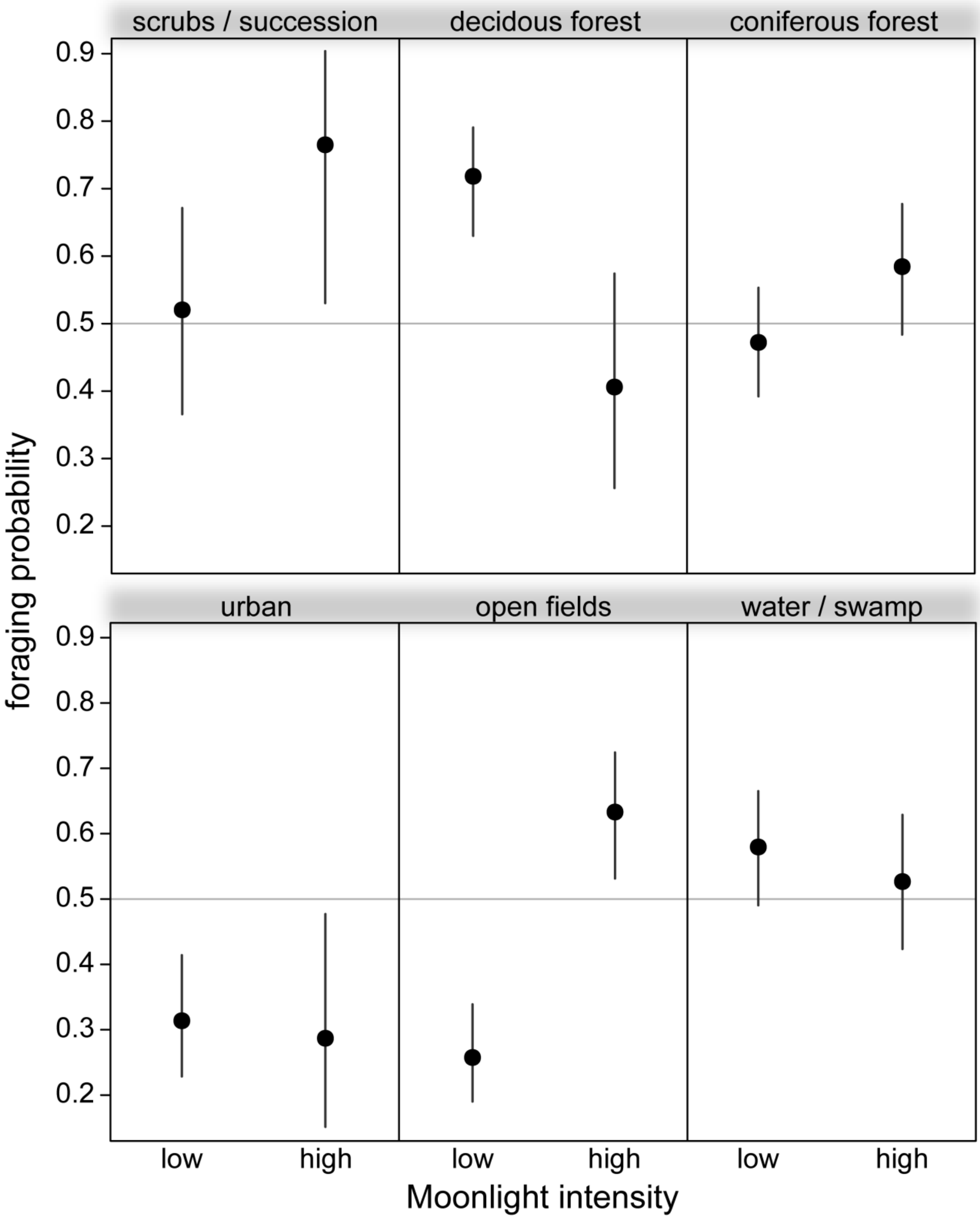


Fig. 2.4 Probability that *N. noctula* showed movement behaviour associated with foraging, shown for the different habitat types and depending on the moonlight intensity. Values higher than 0.5 indicate that *N. noctula* used the respective habitat primarily for foraging during the given moonlight intensity. Dots depict effect estimates from the underlying model, bars depict the corresponding 95% confidence intervals.

DISCUSSION

In early summer, we tracked nine common noctule bats (*Nyctalus noctula*) each for a period of several days in an area that was dominated by pine silviculture. Irrespective of the moonlight intensity, bats preferred water bodies for foraging, but also spent a considerable amount of time within or above the forest. However, during high moonlight intensities, bats used the forest less often but shifted their foraging activity towards open fields. When still using the forest during high moonlight intensities, bats tended to then fly under the shelter of the canopy level. *N. noctula* flew closer to the ground during high than during low moonlight intensities. It is intrinsic to the study setup that tracking during full moon and new moon cannot occur at the same time. However, we tracked all noctules (except one recorded in 2016) within two weeks in July 2015, a period of the year with constantly high insect abundance (Hallmann *et al.* 2017) and diversity (Heim *et al.* 2017), and without substantial changes in the annual life cycle of noctules (Racey 1974; Blohm 2003). Further, there were no significant differences between ambient temperatures during the flights recorded at different moon phases (high moonlight intensity: 20.6 ± 3.6 °C, low moonlight intensity: 19.6 ± 4.0 °C, mean ± standard deviation) which might have influenced insect abundances. We are thus confident that the observed space use patterns are indeed related to moonlight intensities, and not confounded by the different days during which we tracked bats.

Habitat use and the effect of moonlight

Waterbodies were the most preferred habitats for flight and foraging activity, followed by deciduous forests, and scrubland or successional areas. This is in accordance with a study by Froidevaux *et al.* (2016) which combined bat activity based on ultrasonic recordings with LiDAR data of forested area. In that study, long-range echolocating bats, such as *N. noctula*, were most active over rather heterogeneous areas, i.e. forest gaps and successional patches. However, since deciduous forests and successional areas were rare in our study area, the observed patterns for these habitats have to be interpreted with caution.

When noctules were foraging over waterbodies, they were least influenced by moonlight intensity. This is in concordance with former studies on habitat use of *N. noctula* (Kronwitter 1988; Roeleke *et al.* 2016) and several dietary studies showing that *N. noctula* regularly feeds on aquatic insects (Gloor *et al.* 1995; Rydell & Petersons 1998). Insects hatching from the water surface are probably the most predictable food source for noctules in midsummer, irrespective of moonlight intensities. However, *N. noctula* is also known for its high dietary flexibility (reviewed by Vaughan 1997), which explains the use of all available habitats within our study area.

We further found that the flight space above or within coniferous forests was overall used less often than expected from availability. The avoidance of coniferous forests was most pronounced during high moonlight intensities. When *N. noctula* nonetheless used the coniferous forest during high moonlight intensities, most GPS positions were recorded underneath the canopy level, and not above, as was the case when moonlight intensities were low. This is surprising since *N. noctula* is adapted to fly in uncluttered space at high forest strata (Norberg & Rayner 1987; Müller *et al.* 2013). The flights underneath the canopy layer during both high and low moonlight intensities were probably mainly associated with roost searching and not foraging behaviour. A possible explanation for the lack of flights above the canopy during high moonlight intensities could be that foraging above the canopy at high moonlight intensities may not be beneficial enough for *N. noctula* to compensate for increased predation pressure from occasional bat-hunting birds of prey which are associated with the edge space between forests and open fields (Redpath 1995). Alternatively, the lack of observations of noctules hunting above the forest canopy at high moonlight intensities might also simply be explained by the shift towards more profitable hunting areas, i.e. open fields.

However, one should be aware that altitude measures of bats that fly close to and especially underneath the canopy are suffering from reduced accuracy. Satellite signals blocked or reflected by vegetation or other structures and surfaces arrive with a delay and thus are more likely to result in falsely negative altitude estimates. Yet, the obvious breakpoint around the median canopy level height in the distribution of flight altitudes above forested areas makes us confident that the overall pattern of flight altitudes in relation to the canopy reflects the true behaviour of *N. noctula*.

Concurrent with decreased use of forest, activity of noctules above open fields and adjacent urban areas was highest during flight trips at high moonlight intensities. This finding is contradictory to the often proposed lunar phobic behaviour of bats (reviewed by Saldaña-Vázquez and Munguía-Rosas 2013) associated with predator avoidance.

Indeed, some authors suggest that responses of bats towards the moon phase may most likely be driven by prey availability (e.g. Lang *et al.* 2006). Hecker and Brigham (1999) found that under moonlit conditions, some bat species (mainly belonging to the genus *Myotis*) shifted their hunting grounds from lower strata of the forest to the canopy level. They conclude that prey availability rather than predator avoidance may be the driving factor. This is supported by Speakman *et al.* (Speakman *et al.* 2000), who found that bats continued their night activity patterns in the Nordic summer, despite bright conditions during the whole night and despite higher prey availability at daytime. They conclude that night activity of bats in temperate zones may have evolved to avoid competition with birds, but not to reduce predation pressure. This is supported by Voigt and Lewanzik (2011) who suggest that during daytime, flight costs for bats are considerably higher than for birds, and another study by Speakman and Webb (1993) showing that Nyctalus azoreum primarily forages at night time, although avian predators are not present in its habitat. Indeed, dietary studies on night active birds of prey such as owls indicate that bats comprise only a minor fraction of their prey (Lesiński *et al.* 2009; Rosina & Shokhrin 2011; Lima & O'Keefe 2013), but this might vary geographically (Garcia *et al.* 2005) and seasonally (Charter *et al.* 2012). Despite the low fraction of bats in the diet of predators, Speakman (1991) estimated that birds of prey may still account for 10 % of the mortality of bats in Britain. Based on that estimate, one would assume that also temperate bats are under strong selection pressure to avoid predators. Our results on the effect of moonlight on the activity of *N. noctula* appear inconsistent with lunar phobia being caused by predator avoidance. The tracked bats exhibited a behaviour which is better explained by the term lunar philia, since they shifted their use of space towards open fields under moonlit conditions. In this context, lunar philia has to be understood as an active habitat choice towards landscapes where bats are exposed to moonlight under bright conditions, without any a priori implications of the underlying reasons. Our findings suggest that predator avoidance is not causative for the observed pattern, probably because noctules are not as vulnerable to predation as slow flying bat species. On the other hand, when using the forest under moonlit conditions, noctules switched from flying above to flying underneath the canopy. Since noctules are not adapted to forage within dense forest, the reason might have been to avoid being spotted against the moonlit sky by predators ambushing from exposed tree branches. This may partially also explain the lower flight altitudes of *N. noctula* when foraging above open fields under moonlit conditions. Being an opportunistic forager (Vaughan 1997), *N. noctula* seems to be able to shift its habitat use in response to moonlight in such a manner that it optimizes the exploitation of cyclic appearing insects while minimizing predation risk by adjusting their flight altitude and avoiding habitats with temporarily high predation risk.

Such a temporal plasticity in habitat use is supported by the finding the *N. noctula* not only spend more time above open fields, but also increased the relative amount of foraging behaviour above open fields during high moonlight intensities. We thus speculate that prey availability above open fields increases under moonlit conditions, turning open fields regularly into valuable foraging habitats for open-space foraging bats, and compensating for potentially increased predation pressure, at least for fast-flying bats like *N. noctula*. Unfortunately, literature on the effect of moonlight on insect abundances is contradictory. Reduced insect activity under moonlit conditions was reported in the early literature and yet later contradicted by some authors (Williams & Singh 1951; Williams *et al.* 1956), but other studies support the idea of moonlight avoidance by insects (Anthony *et al.* 1981). Some authors on the other hand suggest that emergence of insects is synchronized by the moon phase, with the timing of emergence being species-specific but most often associated with near full moon (Danthanarayana 1986; Nowinszky *et al.* 2010). However, most studies on insect abundance so far used light-traps, a method that likely is biased during high moonlight intensities. Yela and Holyoak (1997) showed that light-traps were less efficient for catching noctuid moths in forests during high moonlight intensities, while catches from bait traps were not influenced by moonlight. Using light-traps, (Brack Jr. & Laval 1985)caught more Lepidoptera under dark conditions and more Hemiptera under bright conditions. When investigating the diet of *Myotis sodalis*, they found a higher portion of Diptera and aquatic insects, and a lower portion of Lepidoptera with increasing moonlight. It remains unclear whether this shift in the diet could be attributed to shifting insect availability or to a shift in habitat selection by bats. Contrary to that, a study by Nowinszky *et al.* (2012) showed that especially open-habitat associated moths as well as dipteran species may be most active during moonlit nights. Bidlingmayer (1964) found that abundance of different mosquito species increased with moonlight when sampling with funnel traps on roads near a beach. This indicates that mosquitoes may synchronize hatching close to full moon and then distribute over the landscape. Overall, evidence is accumulating that many insect taxa synchronize hatching to the moonphase, yet without a consistent pattern for the exact time. This species-specific timing must thus result in different insect densities at the respective habitats of the insects, leading to temporal heterogeneity in habitat suitability for insectivorous predators. Especially light tolerant species such as N. noctula and other open space foraging bats (Meineke 2015; Rowse *et al.* 2016) may be able to exploit such insect rich open habitats despite intense moonlight. Further, a study by Eklöf *et al.* (2002) showed that open space foraging bats use vision when hunting for moths in cluttered habitats, a fact they may have enhanced the foraging success of N. noctula when hunting at the edges of open fields during high moonlight intensities.

Yet, we must acknowledge that due to ethical and technical constraints, our study period was limited to the post breeding season. It might thus be that the observed responses towards moonlight levels may change throughout the season, e.g. when female bats are raising young and may thus be more risk sensitive towards potential predation.

Conclusions

This study confirms that predators such as insectivorous bats can be highly flexible in their use of space, probably in order to increase foraging efficiency by exploiting temporarily occurring prey accumulations. The shift of N. noctula from forested to open fields during high moonlight intensities argues against the notion that bats generally exhibit lunar phobia as a predator avoidance strategy and thus hide during moonlit nights. We speculate that some bat species actively chose open fields under moonlit conditions to exploit insects that are lured out of the vegetation when moonlight intensities are high. Yet, predator avoidance behaviour may explain decreases in bat activity in temporarily risky spaces, such as the space above the canopy of forested areas. Irrespective of the underlying reasons, the observed change in use of space highlights that habitat suitability is not static for bats and other nocturnal animals but may shift periodically in response to the lunar phase.

ACKNOWLEDGEMENTS

We thank Oliver Lindecke for discussions and Stephanie Kramer-Schadt for statistical advice. MR was funded by the Deutsche Forschungsgemeinschaft (DFG-GRK 2118/1 – BioMove). The publication of this article was funded by the Deutsche Forschungsgemeinschaft (DFG-GRK 2118/1 – BioMove) and the Open Access Fund of the Leibniz Association. The funding agencies had no influence on the content of this study.

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CHAPTER TWO - COMPETITION AT FORAGING PATCHES

Published in Frontiers in Ecology and Evolution 6, 2018

as

How bats escape the competitive exclusion principle - Seasonal shift from intraspecific to interspecific competition drives space use in a bat ensemble

by

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https://doi.org/10.3389/fevo.2018.00101

ABSTRACT

Predators that depend on patchily distributed prey face the problem of finding food patches where they can successfully compete for prey. While the competitive exclusion principle suggests that species can only coexist if their ecological niches show considerable differences, newer theory proposes that local coexistence can be facilitated by so-called stabilizing and equalizing mechanisms. A prerequisite to identify such mechanisms is the understanding of the strength and the nature of competition (i.e. interference or exploitation). We studied the interaction between two open-space foraging bats by testing if common noctule bats *Nyctalus noctula* shift their space use in response to simulated aggregations of conspecifics or heterospecific *Pipistrellus nathusii*.

When confronted with playbacks of heterospecifics, *N. noctula* increased their activity in early summer, but decreased activity in late summer. This pattern was accompanied by a decrease in the proportion of large insects in late summer, suggesting a more intense competition for food in late compared to early summer. When confronted with playbacks of conspecifics, *N. noctula* did not change their activity, irrespective of season.

Our results indicate that in early summer, intraspecific competition is more severe than interspecific competition for insectivorous bats. Likely, conspecifics engage in interference competition for flight space, and may suffer

from reduced prey detectability as echolocation calls of conspecifics interfere with each other. During insect rich times, interspecific competition on the other hand may be mediated by fine scale vertical partitioning and the use non-interfering echolocation frequencies.

In contrast, when food is scarce in late summer, bats may engage in exploitation competition. Our data suggests that *N. noctula* avoid aggregations of more agile bats like *P. nathusii*, probably due to impeded hunting success. Yet, as fast and efficient fliers, *N. noctula* may be able to escape this disadvantage by exploiting more distant foraging patches.

INTRODUCTION

All predators face the same problem of finding and catching prey. In large carnivores, the capture rate is commonly limited by the high failure rates (e.g. Eaton 1970; Holekamp *et al.* 1997) during energetically demanding capture attempts (e.g. Heglund *et al.* 1974; Gorman *et al.* 1998). In contrast, predators feeding on relatively small prey items like invertebrates, insects, or Krill and Zooplankton depend more strongly on the detection of prey aggregations and the abundance or energetic value of single prey items (Morse 1971; Lubin *et al.* 1977; Nowacek *et al.* 2011). Especially aerial hunting insectivores such as bats and birds often hunt on patchily distributed insects swarms which they may locate only over short distances. However, individuals may improve their search efficiency by using public information that is inadvertently provided by conspecifics or heterospecifics with similar food requirements (Danchin *et al.* 2004). While group foraging birds can increase their hunting success by visual observations of other birds (Greene 1987), aerial-hawking bats may do so by eavesdropping on the echolocation calls of other foraging bats (Balcombe & Fenton 1988; Gillam 2007; Dechmann *et al.* 2009; Dorado-Correa *et al.* 2013). Since bats use specialized calls, so called feeding buzzes (Kalko 1995), to capture their prey, conspecifics and heterospecifics can use such acoustic information to locate promising prey patches. Indeed, there is evidence that foraging bats of some species stay in an optimal eavesdropping distance to each other when they hunt in large groups, thus forming a sensory network that allows them to scan an area much larger than their individual detection range for insect prey (Cvikel *et al.* 2015). While two bats are flying within hearing range of each other during prey search, they may both profit from an increase in effective prey detection range, yet they would still compete when both are reaching the respective prey patch. Moreover, most insectivorous bat species hunt mainly during the first few hours after sunset (Kunz 1973), probably because the activity of airborne insects usually declines substantially afterwards (Taylor & O'Neill 1988; Meyer *et al.* 2004; Milne *et al.* 2005). This short period of prey availability limits the temporal partitioning of resources by competing species and thus increases interspecific competition for taxa that hunt on the same prey. Since competing bat species often also overlap in other aspects of their biology, e.g. roost and habitat preferences, competition may become even more exacerbated. The competitive exclusion principle suggests that species with an overly high niche overlap cannot coexist (Gause 1934; Hardin 1960; see also e.g. Levine and HilleRisLambers 2009). However, recent developments in coexistence theory suggest that equalizing or stabilizing mechanisms could promote the coexistence of ecologically similar taxa, next to those mechanisms purely driven by environmental niche differences (Chesson 2000). Within this framework, stabilizing mechanisms are a condition for coexistence; given that intraspecific competition is stronger than interspecific competition, a population's growth rate will increase at low abundances of that species. Equalizing mechanisms on the other hand support coexistence by reducing fitness disadvantages of the inferior of competing species. Movement behavior may act as such a mechanism, e.g. when competing species alter their movements and thus their space use in such a way that they avoid aggregations of strong competitors (Jeltsch *et al.* 2013; Schlaegel *et al.* in prep).

To explore the presence and extent of such mechanisms, one ideally should evaluate the nature and the strength of intra- and interspecific competition within the investigated species *ensemble* (*sensu* Fauth *et al.* 1996). For bats that hunt on ephemeral insects, it is often assumed that food resources within a patch of swarming insects are virtually unlimited (cf. Bell 1980; Anthony *et al.* 1981; Arlettaz 1999, see also Kalko 1995: maximum capture rate of swarming insects by medium sized pipistrelle bats is roughly 7 insects / min). Exploitation competition among insectivorous bats is thus unlikely during insect rich times. Yet, large groups of hunting bats may still engage in interference competition since they need a certain amount of flight space during aerial foraging. Large open-space foraging bats like *Nyctalus noctula* usually use an area of at least 1 ha during spatially concentrated hunting bouts over preferred foraging patches (Roeleke *et al.* 2016, Roeleke *et al.* in prep., Voigt *et al.* in prep). Indeed, Amichai *et al.* (2015) recently showed that large aggregations of bats are foraging less effective, since the respective individuals have to direct their attention more often towards conspecifics, and are thus not able to detect prey items at the same time. This is in concordance with some early studies showing that bats that are on collision course may use special calls described as honk calls when approaching conspecifics too closely (Suthers 1965; Fenton & Bell 1979). To date, it remains unclear whether these calls are just a warning to avoid collision, or could also be interpreted as aggressive vocalizations (Voigt-Heucke *et al.* 2010). Moreover, vocalizations emitted by several bats at the same time may also interfere with the detection of each other's specialized hunting calls. Indeed, Corcoran and Conner (2014) showed that *Tadarida brasiliensis*, a species that forms roosting communities of millions of individuals, uses specialized aggressive vocalizations during competition for prey. Through broadcasting of ultrasounds that jam the sound detection of their competitors, they make them unable to detect a prey item that was recognized before. Under such a framework of interference competition, we would assume that intraspecific competition within limited flight space is higher than interspecific competition, given that heterospecifics, but not necessarily conspecific bats might still be able to show fine-scale spatial segregation (Salsamendi *et al.* 2012, own observations at study site) , due to their respective wing morphologies and resulting flight and foraging modes (Norberg & Rayner 1987; Arlettaz 1999; Schnitzler & Kalko 2001; Voigt *et al.* 2010; Voigt & Holderied 2012).

However, seasonal as well as possibly anthropogenically driven changes in insect availability might violate our assumption of constant, unlimited food resources for aerial hawking bats. Recent studies show that in Central Europe insect abundance is decreasing towards late summer (Anthony *et al.* 1981; Hallmann *et al.* 2017; Heim *et al.* 2017), which coincides with the time when several bat species face a trade-off between spending their time for feeding, mating, and either finding a winter roost or migrating southwards. Given that foraging time as well as prey availability can be limited in late summer, competition might then change towards the exploitation of resources, which will bring an advantage to the smaller and more maneuverable fliers (Norberg & Rayner 1987) that might be more successful in catching a limited number of prey items within short time. Yet, the question remains whether larger and faster species can mitigate this increase in interspecific competition by exploiting more distant but possibly less rich and yet unoccupied prey patches to equalize this potential disadvantage.

Here we used playback experiments to examine the nature of competition between two co-occurring and potentially competing bat species by recording their reactions towards simulated aggregations of con- and heterospecifics during different life-history stages (i.e. early season during which breeding and molting occurs and late season during which mating, search for winter roost, and potentially migration occurs). Our playback approach makes use of the vocalization and hearing ability of aerial hawking insectivorous bats, which allows to measure spatial changes in activity in response to experimental acoustic treatments by quantifying bat activity through the number of ultrasonic calls that can be recorded within the experimental area. Our focal species was the common noctule bat *Nyctalus noctula* (Schreber 1774), a fast flying and partially migratory bat. At our study site in Germany, we exposed locally foraging *N. noctula* to playbacks of either hunting conspecifics, or hunting *Pipistrellus nathusii*. These two species have similar activity patterns (Heim *et al.* 2016) and a high niche overlap in terms of diet, habitat use, and roost preference (Eichstädt 1997; Vaughan 1997). Based on the above speculations on the nature of intra- and interspecific competition in aerial hawking bat ensembles, we hypothesized that the reaction of *N. noctula* towards the different playback types depends on the overall density of competitors within the area and the season, and that this reaction will be linked to different prey availability within the different seasons. In particular, we predicted that *N. noctula* will increase foraging activity during conspecific playbacks in the early season, when prey is plentiful, and that N. *noctula* will abandon hunting grounds during con- or heterospecifics playbacks in the late season, when prey is scarce.

MATERIAL AND METHODS

Study sites

In 2016, we conducted playback experiments directed towards *N. noctula* during the non-migratory breeding season (mid June to mid August, hereafter referred to as early season) and during its mating and potentially migratory season (beginning of September until beginning of October, hereafter referred to as late season). Playback experiments took place in Northeastern Germany, i.e. in northern parts of the federal country Brandenburg, called Uckermark. The Uckermark is dominated by agricultural fields, but includes many waterbodies, ranging from small kettle holes to relatively large lakes. We aimed at conducting playback experiments at the shores of 23 of these limnic habitats. Although there are only few forest remnants, and roosting opportunities in the area are thus expected to be scarce, we knew from previous GPS studies *(Roeleke et al. 2016, Roeleke et al.* unpublished data) that *N. noctula* colonies in the Uckermark preferentially forage above waterbodies within distances of at least 7 km from their roost. The 23 playback locations were distributed over an area of approximately 60,000 ha. During each experimental night, we conducted playback experiments at two sites simultaneously. Distance between the paired playback locations ranged from 1 to 5 km. Since we conducted the experiments roughly at the same time, it is unlikely that we broadcasted playbacks to the same individuals at the different sites during a given night. We further aimed at conducting playbacks twice at each site – once during the early and once during the late season (see section Playback experiments). However, due to spatial and temporal variation in bat activity, we could not always achieve this for all sites. To avoid pseudo-replication, we only visited each site once per season.

Playback preparation

At each site, we broadcasted three different playback types towards foraging *N. noctula*; feeding buzzes of *N. noctula*, feeding buzzes of *P. nathusii*, and a sine tone between 20 and 40 kHz as a control (Appendix 3.1). Feeding buzzes are specialized bat calls that are designed for the terminal phase of prey capture, and which are unambiguously identifiable. The single playback trials were three minutes long and consisted of three phases; i) one minute of silence (baseline), in order to record the acoustic baseline activity of *N. noctula* at the respective site, ii) one minute of broadcasting the respective playback (playback), and iii) one minute of silence again (post), in order to see potential post- playback effects (cf. Übernickel *et al.* 2013; Voigt-Heucke *et al.* 2016).

Playback experiments

We started the playback trials as soon as we observed foraging activity of one or more *N. noctula* via the recording setup. After each trial, we waited at least three minutes and checked again for acoustic foraging activity before we broadcasted the next playback. In most nights, we conducted the experiments shortly after sunset when the first *N. noctula* arrived. However, in case all bats left the area during the playbacks, we tried to conduct a second round of playback experiments later on when *N. noctula* activity over the area was more stable. At around midnight, *N. noctula* activity always declined to low levels. If we did not manage to conduct our experiment until midnight, we stopped the experiments to ensure that all bats within our study were confronted with playbacks in a similar situation, i.e. during their first foraging bout of the night. During some experimental trials, we also noticed *P. nathusii* foraging close to the shoreline and thus close to our experimental setup. However, since the natural *P. nathusii* activity was low compared to the broadcasted stimuli, we are certain that their potential effect was negligible. We did not evaluate potential effects of the playbacks on *P. nathusii* since the playbacks were not directed towards them, and we thus could not assure consistent baseline activity of *P. nathusii* before broadcasting.

We only performed experiments at wind speeds ≤ 3 m/s during nights without rainfall. Please see Appendix 3.1 for a detailed description of playback preparation and the experimental setup.

Acoustic analysis

We analyzed the acoustic records with SasLabPro (Avisoft Bioacoustics), using a hamming window spectrogram, with fast Fourier transformation of 1024, and 87.5 % time overlap. We identified and counted calls of *N. noctula* which had signal to noise ratio higher than 30 dB for each of the three phases of the respective playback trials, thereby accounting for the difference of approx. 30 dB between our playbacks and the assumed sound pressure levels foraging bats produce.

Insect trapping and analyses

At each playback site, we trapped flying insects with a custom built ultraviolet (UV) light trap (light source of about 365 nm wavelength). When insects were approaching the light, they collided with a smooth plastic surface in front of the lamp and subsequently slipped into a bottle filled with 95 % ethanol. We placed the traps at the shore of the respective waterbodies, approx. 5 m from the playback setup, at 3 m height. As soon as we noticed the first *N. noctula* with our recording setup, we switched on the UV light of the trap and attached the bottle with the ethanol for one hour. Thus, we ensured that insects were not attracted to the UV light before the onset of the playback experiment.

To derive the most important prey measurements from a bats point of view, we sorted and counted insects by para-taxonomic groups reflecting a combination of order and size (Tab. 3.1). We dried the sorted samples for 72 hours at 50°C and measured dry mass with an electronic balance (ME5, Sartorius, Germany, 0.001 mg resolution).

Data management and statistical analysis

Our acoustic analysis showed that sometimes bat activity stopped for a longer time during any of the three phases of our experiment (i.e. baseline, playback, post). We excluded these trials from further analysis since we could not be sure if the focus animals were really foraging in such cases. Please see Appendix 3.2 for a detailed description of the estimation of the experimental area and the subsequent data cleaning.

To evaluate the relative difference of *N. noctula* activity between the pre phase and the playback phase, we calculated the relative difference between pre and playback phase as:

$$\frac{calls\ playback\ phase - calls\ pre\ phase}{(calls\ playback\ phase + calls\ pre\ phase)/2}$$

We then modeled the relative difference with a linear mixed effect model (R package lme4, Bates *et al.* 2015). As predictor variables we used the three-fold interaction of playback type (i.e. conspecifics, heterospecifics, control), baseline activity (number of *N. noctula* calls during the pre-phase), and season. As random effect we included experimental trial nested within site. To test whether the effects of the playback would last longer than the broadcasting of the playback itself, we ran a similar model with the relative difference between pre- and post- phase as dependent variable. We ensured normal distribution of modeled residuals by visually checking quantile plots of the models. We calculated pseudo-R-squared values with the R package MuMIn (Barton 2014) and effect sizes of the predictor variables with the R package effects (Fox 2003). We assumed statistical significant effects of predictor variables when the 95 % confidence intervals did not span 0. After confirming with Kolmogorov-Smirnov-Tests that numbers and masses from the different insect groups were not normally distributed, we used paired Mann-Whitney-U-Tests to test whether there was an effect of season on mass or number of caught insects, or on the relative number of the different size classes within each sample. We used all samples for this test, including those from location and season combinations were we did not obtain data from the playback experiments. All data handling and analyses were done with R 3.3.2 (R Core Team 2016). Review and approval of the experiments was not required by national guidelines, since no animals were caught, handled, or physically manipulated.

RESULTS

Bat activity at waterbodies

We sampled 30 different waterbodies in the study area for *N. noctula* activity. More waterbodies were used by foraging *N. noctula* in the early than in the late season (Chi²-Test, $Chi^2 = 4.65$, $N = 30$, $p = 0.03$). At sites where *N. noctula* was present in both seasons, the level of *N. noctula* activity did not differ between seasons (Mann-Whitney-U-Test, $W = 124$, $N = 28$, $p = 0.21$) (Tab. 3.1).

Insect trapping

Most caught insects were of rather small size. Number and dry mass of caught insects varied largely between the sampled sites (Tab. 3.1). Although there seemed to be a slight shift from large (body length >9 mm) to small insects (body length < 6 mm) from the early to the late season, we did not detect any significant differences for number and mass of the different insect size classes (paired Mann-Whitney-U-tests, $N = 46$, Fig. 3.1). Yet, paired Mann-Whitney-U-tests ($N = 46$) showed that the relative number of large insects was significantly higher in the early season ($V = 132$, $p = 0.045$), while the relative number of small insects was higher in the late season ($V = 57$, $p = 0.025$). Please see Appendix 3.3 for a site specific presentation of abundances and masses of the different insect classes.

Tab. 3.1 Presence and continuous foraging activity of *N. noctula* and total number and mass of insects at sampled sites

	Early season				Late season			
Site	***N. noctula* present**	**Continuous foraging**	**No. of insects**	**Mass of insects (mg)**	***N. noctula* present**	**Continuous foraging**	**No. of insects**	**Mass of insects (mg)**
1-1	yes	yes	23.0	4.6	no	no	260.0	82.1
1-2	yes	yes	56.0	19.2	yes	yes	252.0	129.7
2-1	no	no	39.0	11.6	no	no	10.0	0.9
2-2	no	no	NA	NA	no	no	NA	NA
3-1	no	no	NA	NA	no	no	NA	NA
3-2	no	no	NA	NA	no	no	NA	NA
4-1	yes	yes	2095.0	546.5	no	no	63.0	8.8
4-2	no	no	144.0	86.4	no	no	40.0	3.9
5-1	yes	yes	743.0	272.3	yes	yes	1091.0	595.2
5-2	no	no	5518.0	4201.9	yes	yes	7073.0	3914.8
6-1	no	no	8.0	372.2	no	no	5.0	0.4
6-2	yes	no	NA	NA	no	no	NA	NA
7-1	yes	yes	20.0	41.4	no	no	232.0	134.5
7-2	yes	yes	45.0	58.2	yes	yes	292.0	114.0
8-1	yes	yes	136.0	79.7	yes	yes	42.0	27.7
8-2	yes	yes	25.0	73.4	yes	yes	36.0	53.9
9-1	no	no	NA	NA	no	no	NA	NA
9-2	yes	no	NA	NA	no	no	NA	NA
10-1	yes	yes	794.0	941.2	no	no	723.0	117.8
11-1	yes	yes	177.0	337.7	no	no	381.0	102.7
12-1	yes	no	29.0	120.4	yes	yes	97.0	65.0
13-1	yes	no	29.0	10.4	yes	yes	67.0	84.0
14-1	yes	yes	18.0	8.4	yes	no	314.0	64.2
14-2	yes	yes	197.0	116.1	yes	no	90.0	34.0
15-1	yes	yes	5.0	1.0	yes	yes	646.0	110.1
15-2	yes	yes	177.0	53.0	no	no	461.0	301.8
16-1	yes	yes	66.0	7.9	yes	yes	13.0	2.3
16-2	yes	yes	1.0	0.3	yes	yes	11.0	1.6
17-1	no	no	NA	NA	no	no	NA	NA
17-2	yes	no	27.0	3.0	yes	yes	72.0	11.0
sum	21	16	10372.0	7366.4	14	12	12271.3	5960.3

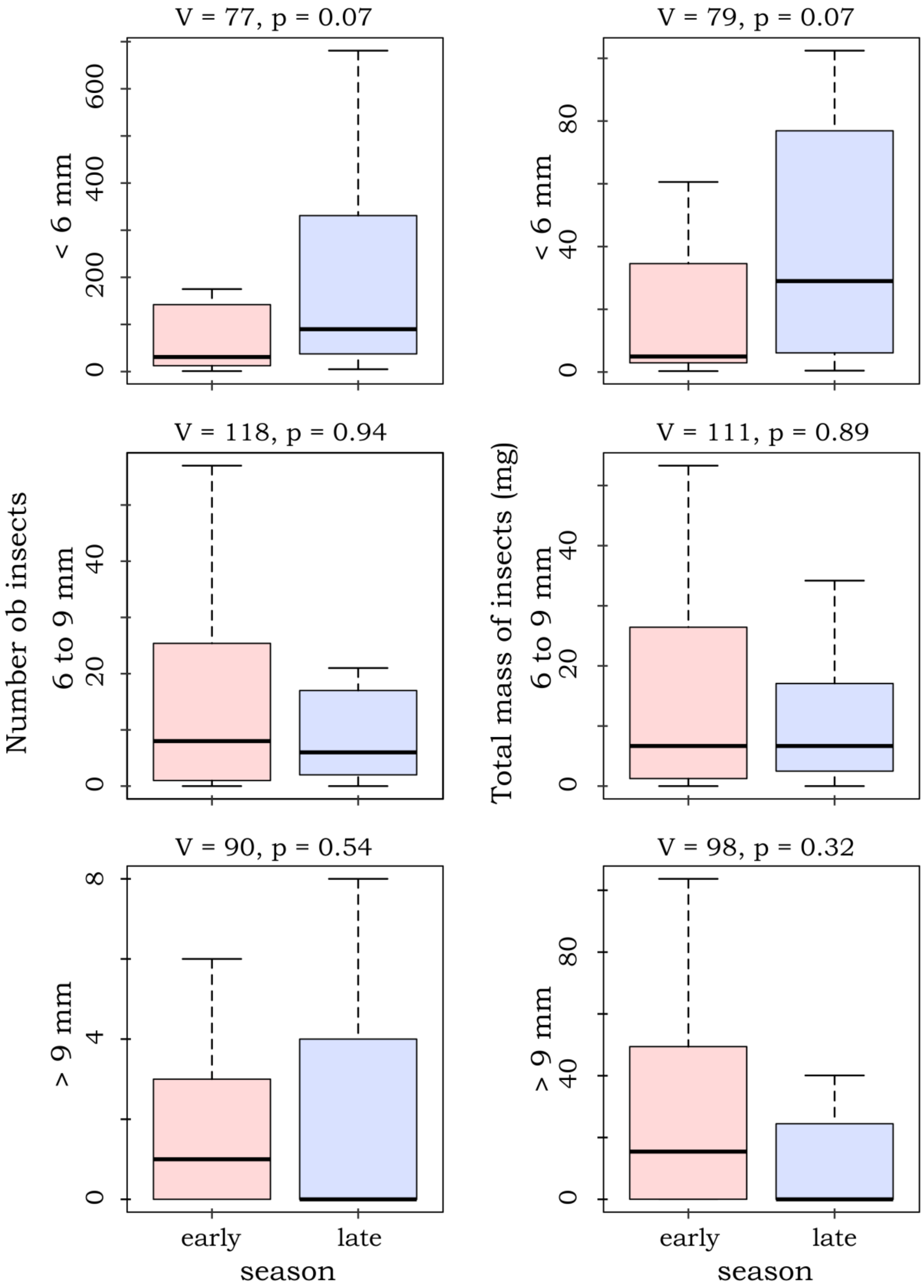

Fig. 3.1 Boxplots and test statistics for number of insects and dry mass for the different seasons, sorted by different size classes of insects. Whiskers depict at maximum 1.5 times the inter-quartile range. For graphical reasons outliers are not shown. Please see Tab. 3.1 for total numbers at the sampled sites.

Playback experiments

Nyctalus noctula did not change their activity when confronted with our control treatment, a sine tone between 20 and 40 kHz. In general, *N. noctula* showed less shifts in activity when their initial density (i.e. number of calls recorded during the pre-phase) was comparably high. However, when including activity during the pre-phase not as an interaction term but only as a main effect in the model, it turned out that *N. noctula* generally responded negatively towards playbacks when the initial density of conspecifics was high (i.e. around 500 calls per minute during the pre-phase). Our full model with the three-fold interaction between initial density, season, and playback type had a pseudo R^2-value of 0.42. This model revealed that *N. noctula* did not react towards the hunting calls of heterospecific *P. nathusii*. Further, there was only a slight positive response towards hunting calls of conspecifics at rather low initial densities (Fig. 3.2A). However, this turned into a clear avoidance of conspecifics in the late season when the initial density was low to medium. At the same time, at least at low initial densities, *N. noctula* activity increased when we broadcasted heterospecific playbacks in the late season. Only at high initial densities, *N. noctula* started to avoid the experimental area during the *P. nathusii* playbacks (Fig. 3.2B).

Irrespective of playback type and season, the number of calls during the pre-phase and the post-phase of the playback did not differ significantly, i.e. the relative difference was fluctuating around 0 (Fig. 3.2C and 3.2D).

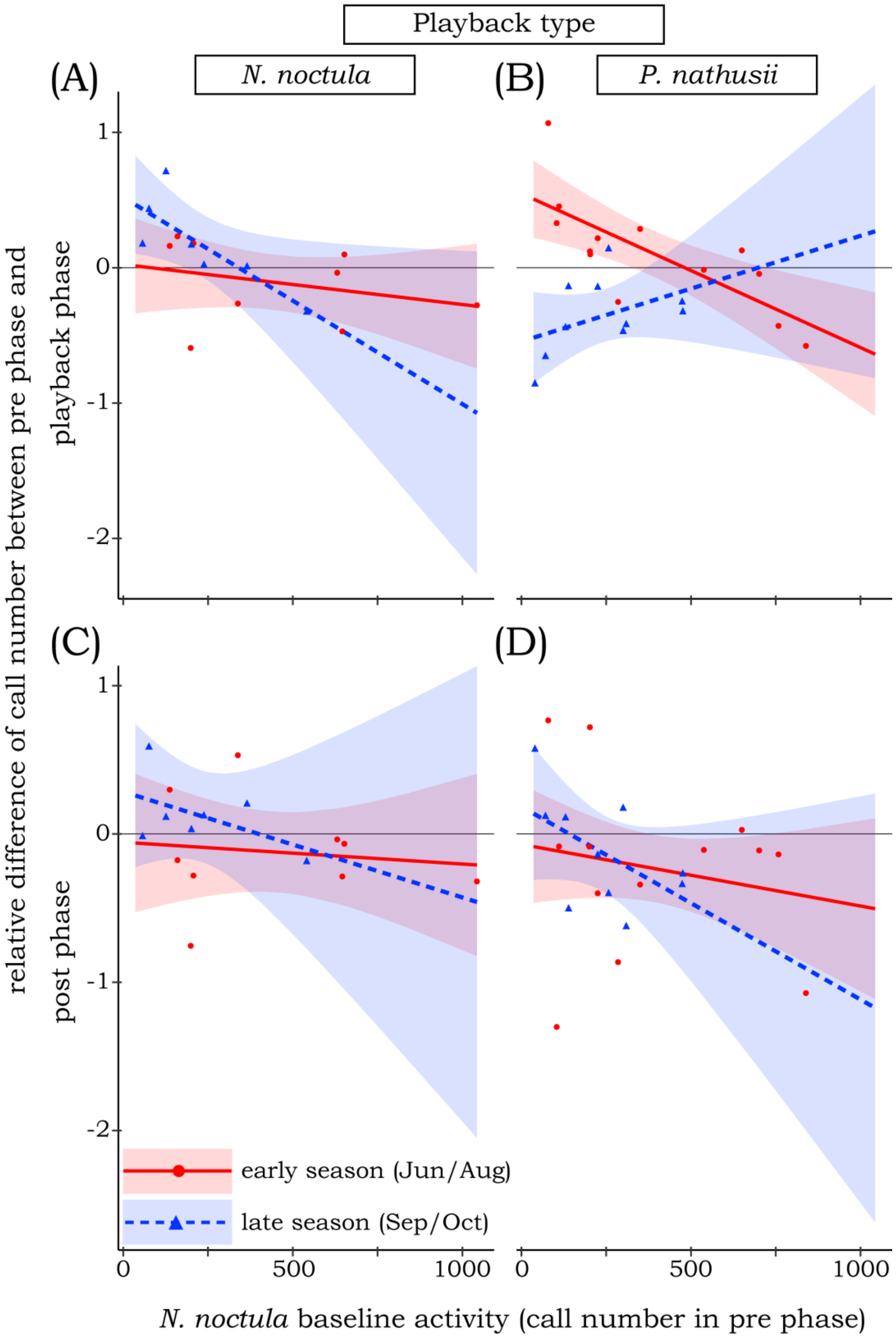

Fig. 3.2 Relative difference of *N. noctula* activity between pre-phase and playback phase (A and B) or the pre-phase and post phase (C and D) of the experiment, depending on *N. noctula* activity during the pre -phase, the different playback types, and the season. Raw data is depicted by circles and triangles. Lines show the estimated effect, shaded areas show the corresponding 95% confidence intervals. Solid red line and red circles: early season. Dashed blue line and blue triangles: late season. For simplicity, insignificant effects towards the control treatment (sine tone) are not shown.

DISCUSSION

Insectivorous bat species can co-occur despite high overlaps in their ecological niches (e.g. Bell 1980; Fenton 1990; Salsamendi *et al.* 2012). Yet, the mechanisms that prevent ensembles of competing bats from competitive exclusion are not fully resolved. The aim of this study was to better understand the nature and relative strength of intraspecific and interspecific competition, and to reveal seasonal changes in competition. Therefore, we directed playbacks of foraging conspecifics and heterospecifics towards foraging *N. noctula* during two different seasons, i.e. early and late summer. *Nyctalus noctula* responded only marginally towards playbacks of conspecifics. The response of *N. noctula* towards playbacks of competing heterospecifics, on the other hand, turned from an increase of activity in the early season to a decrease of activity in the late season. We conclude that the studied insectivorous bats experienced stronger intraspecific than interspecific competition during the early season, whereas the opposite was true during the late season.

Seasonal shifts of habitat use

During late summer, foraging *N. noctula* used fewer waterbodies in our study area than during the early summer. This seems to be counter-intuitive at first glance, since one would expect higher abundances of foraging bats during the late season, due to the by then weaned offspring. Further, migrating bats from northern and north-eastern countries are arriving around late August to late October in Central Europe, including our study area (Ahlén *et al.* 2009; Furmankiewicz & Kucharska 2009; Ciechanowski *et al.* 2010). The influx of migrating *N. noctula* is probably the reasons why Heim *et al.* (2016b) found an increase of *N. noctula* activity above agricultural fields in the study area in late summer. We suggest that the observed decrease in use of our sampled waterbodies was not due to an overall reduced activity in the area, but rather due to a shift of habitat use from limnic to terrestrial foraging grounds. This is in concordance with isotopic analyses by Voigt *et al.* (2016) who found that *N. noctula* feeds less on aquatic insect during late summer than during early summer. The shift in habitat use may partially result from the need to mate in the late season. Male bats have to establish and defend solitary roosts, while females search for these so-called mating roost. Thus, males may have to feed nearby their roost, and females may save time when feeding opportunistically during their search for mating roosts rather than at designated foraging areas such as waterbodies. A recent tracking study suggests such a strategy, at least for females, by showing that female *N. noctula* cover large areas and focus less on single waterbodies for foraging in late summer (Roeleke *et al.* 2016).

Seasonal shifts of prey availability

Contrary to our expectations and past studies (Black 1974; Janzen and Pond 2009; Hallmann *et al.* 2017; Heim *et al.* 2017, but see Hails 1982), we could not detect differences in number or biomass of flying nocturnal insects between the early and the late season. Yet, in the late season, there seemed to be a tendency that fewer big insects (i.e. body length > 9 mm) were present at the sampled waterbodies (cf. Gloor *et al.* 1995), and we detected a significant decrease of the proportion of large insects compared to the early season. While there are many dietary studies that show that *N. noctula* is an opportunistic feeder, most studies agree that relatively large insects are important components of its diet (reviewed in Vaughan 1997). A decrease of relatively large insects at the sampled waterbodies may thus have increased competition for prey items. This provides a further explanation why fewer waterbodies were used by foraging *N. noctula*, since a decrease in feasible prey items may have forced *N. noctula* to forage in habitats with less competitors. Such a temporarily insect rich surrogate foraging habitat could have been agricultural land. Heim *et al.* (2016) speculate that harvesting activity during September could temporarily increase insect availability in the area (*cf.* Pluciński *et al.* 2015). Voigt *et al.* (2015) found that *Eptesicus serotinus*, an open space foraging bat with a similar wing morphology as *N. noctula* (Norberg & Rayner 1987), feeds on terrestrial and aquatic insects alike, which suggests flexibility in the habitat use of feeding open space foragers.

However, we must acknowledge that by using UV light traps, our sampling method was selective towards light sensitive insects. Further, we were limited to place the traps at the shores of the waterbodies at about 4 m height, whereas *N. noctula* were mostly foraging at altitudes of about 8 to 12 m above the water surfaces. Therefore, our insect sampling provides most likely only a proxy for general insect activity, but does not necessarily reflect actual prey availability for *N. noctula*.

Playback experiments – post effect and density dependent response

We did not detect any significant effects of the experimental treatment in the post playback phase, i.e. the bat activity almost instantly went back to the baseline activity level after the broadcasting of playbacks. This shows that *N. noctula* conceives new competitive situations very quickly, and adjusts its space use likewise quickly and dynamically.

Nyctalus noctula only reacted towards our playbacks when the baseline activity was low to medium (i.e. less than 500 calls per minute). Possibly, *N. noctula* perceived acoustic information from actual present conspecifics more reliable than our playback. However, feeding buzzes are naturally fainter than search calls (Holderied *et al.* 2005), and high acoustic search call activity may hinder the acoustic detection of feeding con- or heterospecifics in experimental as well as natural situations. However, it may also be that the space that could be efficiently used for foraging was already saturated with individuals. Using densely occupied foraging patches can be ineffective (Amichai *et al.* 2015), which may result in an individual partitioning of foraging space (*cf.* Beauchamp and Fernández-Juricic 2005).

Playback experiments – seasonal changes of competition

It was only during late summer that *N. noctula* showed a moderate positive response towards the playbacks of conspecifics. On the other hand, *N. noctula* was clearly attracted towards the playbacks of foraging *P. nathusii* in early summer, yet this turned into a clear avoidance during late summer. As mentioned above, all these responses held true for low to medium baseline activity of *N. noctula* (i.e. < 500 calls per minute), but vanished or even reversed when large aggregations of individuals were present. We suggest that the seasonally different responses towards our playbacks were driven by changes in the strength of intra- and interspecific competition.

In particular, the increased activity during playbacks of heterospecifics during early summer indicates that eavesdropping on foraging heterospecifics is an advantageous strategy for bats that hunt for patchily distributed prey in this season. Yet, it appears surprising that *N. noctula* did not show such a positive response towards playbacks of foraging conspecifics, since conspecifics theoretically should have the highest overlap of dietary requirements, and should thus be the most reliable indicator for availability of preferred insect prey. The observed lack of response towards foraging conspecifics, coupled with the positive response towards foraging heterospecifics, suggests a strong intraspecific competition, and at the same time, a negligible interspecific competition during early summer. As a consequence, we propose that bats are not competing for prey items, but rather for flight space and “soundspace” in early summer. By soundspace, we mean a multidimensional entity that is defined by a 3-dimensional spatial component, time, and the range of ultrasonic frequencies that bats use to echolocate. Echolocating bats need this space to broadcast their ultrasonic calls, and to receive the reflected echoes of their calls, in order to locate prey and obstacles. Nearby conspecifics use the same flight space and soundspace, and may thus interfere with each other during flight and during acoustic detection of prey, respectively. In contrast to that, heterospecifics individuals may partition foraging space vertically and overlap less in their soundspace due to the use of different echolocation frequencies. Fine scale vertical segregation has been shown for a variety of competing taxa that make excessive use of 3-dimensional foraging space (e.g. Saiful *et al.* 2001; Kiszka *et al.* 2011; Navarro *et al.* 2013; Humphries *et al.* 2016; Mansor and Ramli 2017). Although investigating fine scale vertical segregation of aerial hawkers is technically challenging, recent recordings of flight altitude of open space bats suggest vertical segregation, yet without clear evidence for foraging activity (Roemer *et al.* 2017). At our sample sites, we frequently observed that *P. nathusii* generally foraged at altitudes of approx. 4 to 8 m, while *N. noctula* often used altitudes of 8 to 15 m.

As mentioned above, heterospecific bats also show partitioning of their echolocation frequencies (approx. peak frequencies for *N. noctula* 20 kHz and for *P. nathusii* 40 kHz, Skiba 2003). Since the auditory system of bats is finely tuned to their own frequency range (reviewed by Hiryu *et al.* 2016; Pollak 2016), acoustic interference across these two species should be negligible. Given that prey is not limited, vertical partitioning of foraging space and call frequency partitioning should thus allow an ensemble of these two species to efficiently forage at higher densities than it would be possible for an aggregation of any of these two species alone.

Contrary to the pattern observed in early summer, *N. noctula* showed decreased activity when exposed to playbacks of foraging heterospecifics during late summer. At the same time, there was an, admittedly very moderate, positive response towards playbacks of foraging conspecifics during low baseline activities (i.e. < 250 calls per minute). We conclude that the strength of interspecific competition must have drastically changed from early to late summer. In particular, *N. noctula* seemed to expect strong interspecific competition when we broadcasted feeding buzzes of *P. nathusii*, which forced them to abandon the respective foraging areas during the playback. Given that interference of heterospecifics is probably negligible, we conclude that the observed negative response was driven by increased exploitation competition, due to low prey availability. Since large insects were relatively scarce during late summer, open space foragers like *N. noctula* might not have been able to forage efficiently at patches already occupied by *P. nathusii*. Probably *P. nathusii* can catch prey quicker than *N. noctula* in such a situation, due to its higher maneuverability (Norberg & Rayner 1987). Further, its lower flight altitude suggests that *P. nathusii* may catch ascending insects before these reach the spheres of higher foraging bats like *N. noctula*. Marggraf *et al.* (in review) found that *P. nathusii* decreased activity in response to playbacks of foraging conspecifics, but did not react towards playbacks of foraging *N. noctula*, which indicates that interspecific competition is not symmetric in these two species. Thus, especially during times of prey scarcity, it would be crucial for *N. noctula* to locate patches of prey that are not exploited by superior foragers like *P. nathusii*. Therefore, we suggest that eavesdropping on hunting conspecifics is the most promising strategy when prey is limited, as long as density of conspecifics is not too high for efficient foraging.

Conclusions

We found that the aerial hawking open space foraging bat *N. noctula* actively seeks heterospecific *P. nathusii* during foraging bouts in early summer, but avoids patches occupied by foraging heterospecifics in late summer. *Nyctalus noctula* did not respond to foraging conspecifics in early summer, but showed a slight positive response to conspecifics in late summer. We conclude that the number of aerial hawking open space foragers at a food patch is limited by intraspecific interference competition for flight space and soundspace in early summer, but that interspecific exploitation competition for insect prey is limiting the number of bats in late summer. High intraspecific competition may thus act stabilizing on insectivorous bat ensembles when food resources are plentiful. During probably lower prey availability in late summer, aerial hawkers that are specialized for fast flight in uncluttered habitats may suffer from inferior capture rate compared to more maneuverable bats like *P. nathusii*. Water bodies were used less during this time. We speculate that fast flying aerial hawkers can use farther away or less rich hunting grounds, since their specialized wing morphology allows them to fly large distances at low energetic costs (Winter & von Helversen 1998). This adaption to fast yet cheap flight may equalize fitness disadvantages towards superior foragers. One could even speculate that habitats which are suboptimal from a foraging perspective may support the diversity of bats by offering refuges from interspecific competition.

ACKNOWLEDGEMENTS

We are grateful to Maris Pärn for help with sorting insect samples. We thank Olga Heim, Silke Voigt-Heucke, and Lara Marggraf for providing bat call records and help with preparing the playback files. Viktoriia Radchuk for statistical advice. The Leibniz Centre for Agricultural Landscape Research and Gernot Verch for providing facilities during the fieldwork. Niels Blaum, Florian Jeltsch, and members from the RTG BioMove for discussion of the manuscript. This work was supported by Deutsche Forschungsgemeinschaft in the framework of the BioMove Training Group (DFG-GRK 2118/1).

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CHAPTER THREE - FORAGING STRATEGIES IN DIFFERENT LANDSCAPES

First submitted 23.01.2019

as

Flexibility of social foraging behaviour in an insectivorous bat

by

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ABSTRACT

Predators are confronted with altered spatial distribution and abundance of prey in anthropogenic landscapes.

We asked if common noctule bats *Nyctalus noctula* vary in levels of social foraging in two contrasting anthropogenic landscapes.

Above farmland, bats mostly started to hunt in small patches after encountering conspecifics. In a forested landscape, bats started to hunt during straight flight and in small patches alike, irrespective of conspecific presence. Bats in a forested landscape had lower feeding rates and encountered more conspecifics than bats in farmland.

We suggest that heterogeneous prey distribution above farmland restricted bats to hunt in small patches. Bats improved prey search by eavesdropping on conspecifics. In forested landscape, higher competitor density impaired hunting success in small patches. Yet, homogeneous prey distribution enabled hunting outside of small patches. Low resource abundance combined with heterogeneous resource distribution may promote social foraging and thus impact sociality in aerial insectivorous bat.

INTRODUCTION

Humans influence ecological processes worldwide (Ellis 2011) and in consequence also global biodiversity patterns (Boivin *et al.* 2016). A particular strong driver of changes in biodiversity patterns is habitat degradation through human land-use regimes (Barnes *et al.* 2014). In 2015, agricultural land and managed forest plantations covered 56% of the land surface in the European Union (FAO 2017). Agricultural land and forest plantations are particularly dynamic landscapes because of the temporal patterns of seeding and harvesting. Yet, temporal fluctuations vary between these two landscapes owing to differences in harvest cycles. Whereas biomass fluctuations are rapid in agricultural landscapes, they are slow in forested landscapes. Besides increased temporal dynamics, human land-use 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 habitats such as forests or wetlands are patchily distributed, animals have to commute longer distances between foraging patches, which ultimately leads to larger home ranges (Ullmann *et al.* 2018). This effect will be strongest in monotonous landscapes such as cropland, where resource rich habitats and ecotones are rare and patchily distributed, thus leading to a heterogeneous distribution of resources on the landscape level. In more diverse landscapes such as forest which includes clearings and water bodies, resources will be distributed more homogenously. Consequently, the abundance of wild animals and plants is commonly reduced in agricultural landscapes, but not necessarily in forested landscapes (Newbold *et al.* 2015).

Nevertheless, animals 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 top predators such as aerial insectivores may compensate for human-induced changes in prey abundance and distribution through their high mobility (Kniowski & Gehrt 2014), and thus may be able to exploit a multitude of landscapes. Yet, since aerial insectivores often depend on ephemeral, patchily distributed prey, they may suffer from difficulties in locating profitable foraging grounds in structurally poor landscapes such as farmland. There, insect prey is often associated with relatively rare structures such as hedgerows or forest edges (Grüebler *et al.*

2008; Froidevaux *et al.* 2019), water bodies or other areas with relative low human impacts (Wickramasinghe *et al.* 2003; de Araújo *et al.* 2015; Treitler *et al.* 2016; Froidevaux *et al.* 2017). Consequently, structurally richer landscapes such as forests will provide more homogeneous prey distribution, thus making the localisation of prey easier.

Bats are the most abundant aerial insectivores at night. Several studies have shown that they can reduce pest insects in agricultural landscapes, and thereby provide ecosystem services also monetarily valuable to humankind (Boyles *et al.* 2011; Ghanem & Voigt 2012; Maine & Boyles 2015). However, the range at which bats can detect prey items with ultrasonic echolocation calls is usually shorter than ten meters (Holderied & von Helversen 2003; Stilz 2004; Jones & 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) proposed that aerial hunting bats may improve the detection of prey patches by flying in an optimal eavesdropping distance to each other, thus acting as a sensory network. Similar behaviour has already been described for swallows which depend on likewise ephemeral prey (Brown 1988). However, such social foraging strategy will only pay off if resources are relatively scarce and patchily distributed (Ryer & Olla 1995; Egert-Berg *et al.* 2018) because the aggregation of hunting bats at distinct prey patches will also result in increased competition, either for a limited number of prey items or for undisturbed hunting space (Voigt-Heucke *et al.* 2010; Corcoran & Conner 2014; Roeleke *et al.* 2018a). Thus, bats face a trade-off between finding prey patches and avoiding competition when depending on patchily distributed food sources. Consequently, the benefit of social foraging will differ between individuals that live in landscapes that offer different resource abundance and distribution.

Here, we asked how flight paths, hunting activity, and conspecific density of an aerial hunting insectivorous bat, the common noctule, *Nyctalus noctula* (Schreber, 1774), will differ between the most prominent anthropogenic landscapes in Western Europe, i.e. agricultural and silvicultural landscapes. The common noctule is a highly mobile species adapted to rapid pursuit of insects flying in the open space (Norberg & Rayner 1987; Jones 1995; Schnitzler & 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 & Petersons 1998). Consequently, the common noctule can be categorised as food and habitat generalist that hunts opportunistically over water bodies (Roeleke *et al.* 2016), open fields (Mackie & Racey 2007; Roeleke *et al.* 2018b), forest edges (Rachwald 1992; Kaňuch *et al.* 2008; Heim *et al.* 2018) or even urban areas (Kronwitter 1988; Gaisler *et al.* 1998).

We hypothesised that hunting strategies of common noctules will depend on the underlying landscape (cf. Nakano *et al.* 1999). We predicted that common noctules will primarily feed during area restricted movements within small areas (Fig. 4.1a) in structurally poor agricultural landscapes (Fig. 4.1c). To locate hunting grounds, bats will use social information by eavesdropping on conspecifics hunting calls (Fig. 4.1b). Consequently, the onset of area restricted movement will be triggered by encounters with conspecifics. In contrast, we predicted that common noctules in the more diverse forested landscape (Fig. 4.1f) will forage more often during commuting (Fig. 4.1d), thereby mitigating intraspecific competition. They will not depend on eavesdropping on conspecifics during foraging (Fig. 4.1e).

Our study investigated factors that promote different foraging strategies in individuals of the same species. It elucidates the potential role of flexible foraging strategies for persistence of species across different anthropogenic landscapes.

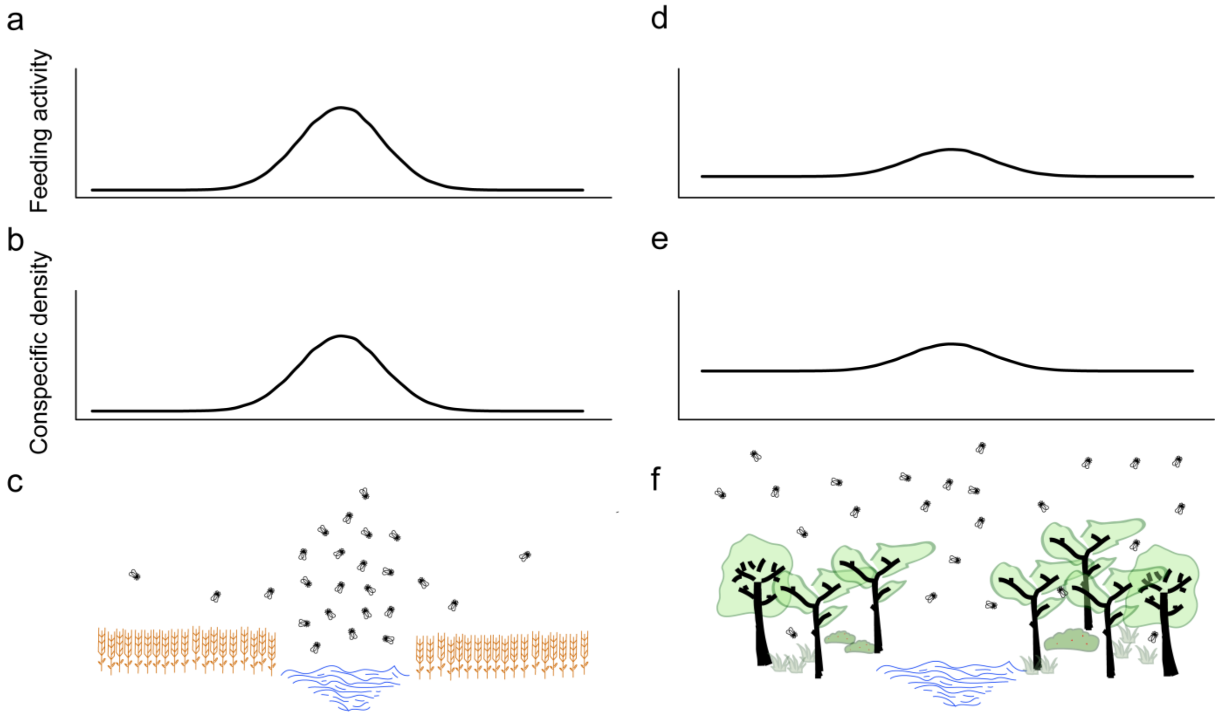


Fig. 4.1 Graphical presentation of hypotheses and underlying assumptions. Above farmland (left), feeding activity (a) and conspecific density (b) will be concentrated in certain small areas, driven by heterogeneous insect distribution (c). In the forested landscape (right), high insect abundance and the homogeneous distribution of insects (f) will lead to a more even spatial distribution of feeding activity (d) and conspecifics (e).

MATERIAL AND METHODS

Animal tracking

In mid-summer (July) 2016 to 2018, we equipped 27 common noctule bats (*Nyctalus noctula*) with combined GPS and ultrasound loggers (Vesper, A.S.D, Karmiel, Israel). This period coincides with the onset of independent foraging by subadult noctule bats. In the early morning, we removed subadult noctule bats from artificial bat boxes and used latex-based surgical skin glue (Sauer Hautkleber, Manfred Sauer, Lobbach, Germany) to attach loggers for a few days to their dorsal fur. The procedure of tag deployment took about 30 minutes, after which bats were returned to their roosting boxes. Loggers were packed in latex balloons together with VHF transmitters (V1, Telemetrie Service Dessau, Dessau, Germany) to facilitate retrieval. From sunset to sunrise, loggers recorded 3-dimensional GPS positions every 31 s. Loggers included an ultrasonic microphone (SPU0410LR5H-QB, Knowles Electronics, Itasca, U.S.A.) which recorded ultrasonic bat calls for an duration of 1.5 s every 10 s (i.e. duty cycle of 15%), at a sampling rate of 160 kHz. We used the young of the year in this study to ensure that the choice of foraging strategy was merely based on the current information on prey availability and conspecific density, but not on knowledge from previous years.

All involved procedures were approved by the federal agency for nature conservation Brandenburg (permit 2347-16-2015 and 2347-15-2016) and the animal and welfare committee of Brandenburg (permit LfU_N1-4743/123+14#134057/2016 and LFU-N1-4743/128+19#235924/2018, LUGV_N1-4743/103+5#283569/2016).

Study sites

We compared movement and foraging behaviour of bats in 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 Northern Germany, about 100 km north from Berlin. This area was mainly used for cropping of wheat and corn, leading to a low structural heterogeneity. The area provided only few semi-natural structures like small forest remnants and shallow bodies of water (Appendix 4.1). Hereafter, we refer to this study site as farmland.

We further tracked 12 subadult *Nyctalus noctula* (nine males and three females) that roosted in a pine stand about 125 km south of the previously mentioned study site. The surrounding area was dominated by a river and lake system and pine silviculture, interspersed by smaller agricultural areas (Supplementary Figure 1). Hereafter, we refer to this study site as forested landscape.

Analysis of ultrasound recordings

We used the software Avisoft-SASLab Pro (Version 5.2.09, Avisoft Bioacoustics, Glienicke, Germany) to display the ultrasonic recordings as spectrograms (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). 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.

Analysis of movement and foraging behaviour

Unless otherwise stated, we conducted all following analytic steps separately for each site. The following workflow is summarised in Fig. 4.2.

Since all bats performed their longest consecutive flight during the first half of the night, we analysed only 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 con- and heterospecific bats recorded in one of the past three recording intervals, and the underlying land-use class (open fields such as meadows or crops, forest or wood plantation, water, urban areas) extracted from aerial infrared images (Land Brandenburg 2013). We used a hidden Markov model (R package moveHMM, Michelot *et al.* 2016) to identify two different movement states derived from step lengths and turning angles of subsequent GPS locations. We define the movement state characterised by short step lengths and uniformly distributed turning angles as area restricted movement (ARM), and the movement state 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 utilization (R package adehabitatHR, Calenge 2006). We used the area enclosed by the 90% isopleth of these utilization distributions to create what we hereafter call ARM patches (Fig 4.2a).

We then used a binomial generalised mixed model (R package lme4, Bates *et al.* 2015) to explain the identity of a given GPS point as ARM or DM by the number of conspecifics and feeding buzzes, whereas the individual bat was the random factor (Fig 4.2b). Since the models yielded significant correlations, we reiterated the hidden Markov model with conspecifics and feeding buzzes as covariates to examine their influence on the switching probability between movement states (Fig 4.2c). Although these covariates had only minor influence on the state sequence of the movement model, we rebuilt the kernels to obtain refined ARM patches for the analysis of habitat use during ARM.

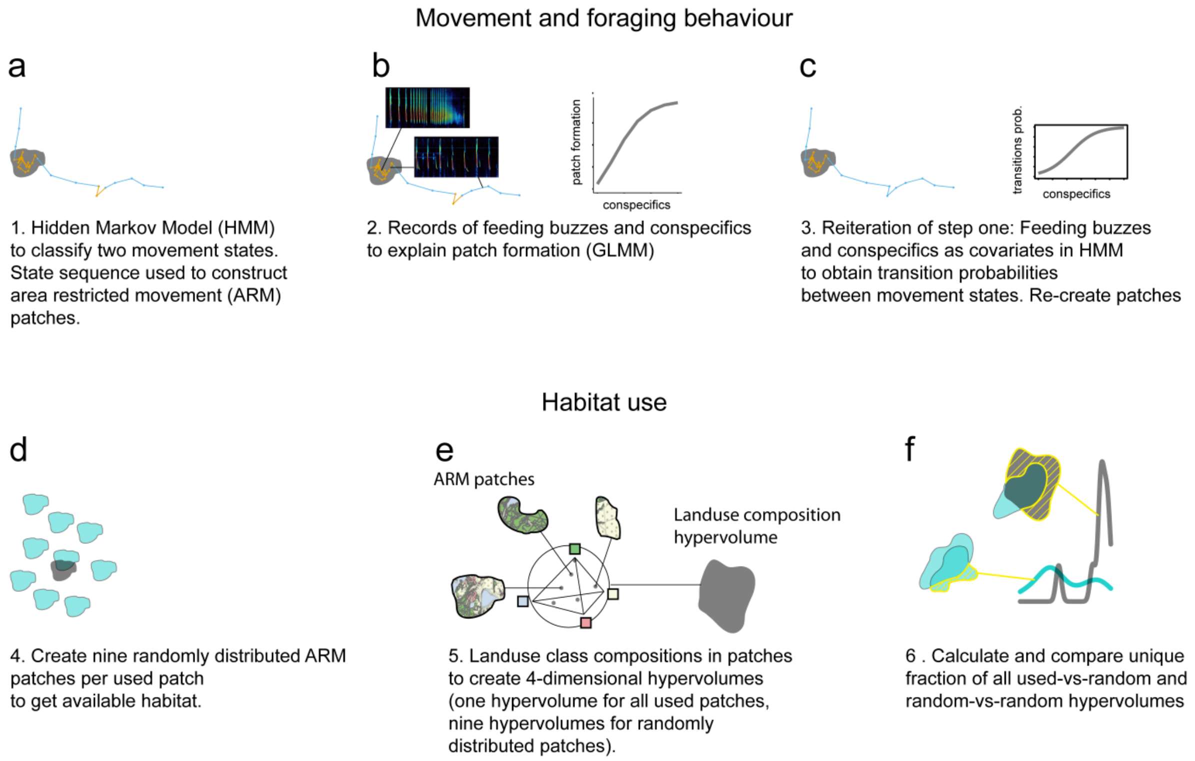
We ran another binomial generalised mixed model to examine whether the probability to meet conspecifics differed between study sites.

Analysis of habitat use in ARM patches

To test whether bats chose ARM patches with non-random habitat compositions, we defined the available habitat composition based on nine random patches per used patch. Random patches had the same shape as used patches and were sampled within the landscape using uniformly distributed angles and the empirical distribution of the actual distances between used patches. This resulted in a total of 66 used and 594 (9 * 66) available patches, with 32 used ARM patches stemming from bats in farmland, and 34 used ARM patches stemming from bats in the forested landscape (Fig 4.2d). We used the fractions of the four land-use classes within available patches (pooled per landscape) to calculate Simpson diversity of farmland and forested landscape. We compared the diversity of the two landscapes with a Mann-Whitney-U test.

For each used and available ARM patch, we calculated the relative proportion of the four land-use classes open, forest, water, and urban (Fig 4.2e). Within each of the two study sites, we calculated ten 4-dimensional hypervolumes from the proportions of the land-use classes (R package hypervolume, Blonder & Harris 2018). The first volume depicted the composition of the four land-use classes that stemmed from the used ARM patches, whereas the other nine volumes used the nine instances of the available patches. To compare the habitat composition of the used and the available hypervolumes, we calculated the amount by which the 4-dimensional hypervolumes overlapped. For this, we overlaid each of the nine available hypervolumes with the used hypervolume and calculated the proportion of the non-overlapping part, hereafter called unique fraction. This unique fraction measures how much patches that underlie the hypervolumes vary in their habitat composition, a high unique fraction indicating large differences in habitat composition. The unique fraction of the available hypervolumes when overlaid with each other can be thought of as a baseline that reflects the spatial distribution of habitat classes in the respective landscape. The unique fraction of the used hypervolumes when overlaid with the available hypervolumes should be higher than the baseline unique fraction when bats showed preferences for certain habitat compositions. To test potential differences in the unique fractions, we built probability density functions from the calculated unique fractions and compared them with Kolmogorov-Smirnov tests (Fig. 4.2f).

All statistical tests were performed two-tailed. We assumed significant differences for an alpha threshold below 0.05. For the generalised mixed models, we assume significant differences if 95 % confidence intervals did not overlap across effects of factor levels.



1. Hidden Markov Model (HMM) to classify two movement states. State sequence used to construct area restricted movement (ARM) patches.

2. Records of feeding buzzes and conspecifics to explain patch formation (GLMM)

3. Reiteration of step one: Feeding buzzes and conspecifics as covariates in HMM to obtain transition probabilities between movement states. Re-create patches

4. Create nine randomly distributed ARM patches per used patch to get available habitat.

5. Landuse class compositions in patches to create 4-dimensional hypervolumes (one hypervolume for all used patches, nine hypervolumes for randomly distributed patches).

6 . Calculate and compare unique fraction of all used-vs-random and random-vs-random hypervolumes

Fig. 4.2 Analytic workflow

RESULTS

Movement and foraging behaviour

Flight time of bats averaged 135 ± 49 min (mean ± standard deviation) above the forested landscape and 103 ± 55 min above farmland per flight trip. We recorded on average 57 ± 38 hunting events (feeding buzzes) for bats above farmland, and 39 ± 16 feeding buzzes for bats above forested landscape. Feeding activity per minute flight time was higher in the agricultural landscape (0.50 ± 0.22 recorded feeding buzzes per min flight, median ± median absolute deviation 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). Please note that 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 1,758 (2.5 % to 97.5 % quantile) per flight trip. Bats in the forested landscape were more likely to meet conspecifics than bats in the agricultural 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 (generalised linear mixed model, Appendix 4.2).

The time bats spent within spatially well-defined foraging patches (ARM patches) did not differ between sites and equalled 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 farmland (Mann-Whitney-U tests, N = 66; ARM patch size: forested landscape = 1.4 ± 1.6 ha, farmland = 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).

Above farmland, feeding activity of tagged bats occurred mostly in ARM patches, whereas no significant relation was observed between feeding activity and flight within ARM patches in the forested area (Fig. 4.3a). For both areas, we found a strong positive correlation between ARM patch use and the number of adjacent conspecifics (Fig. 4.3b), i.e. the more conspecifics we recorded, the more likely it was that bat activity was restricted to small areas.

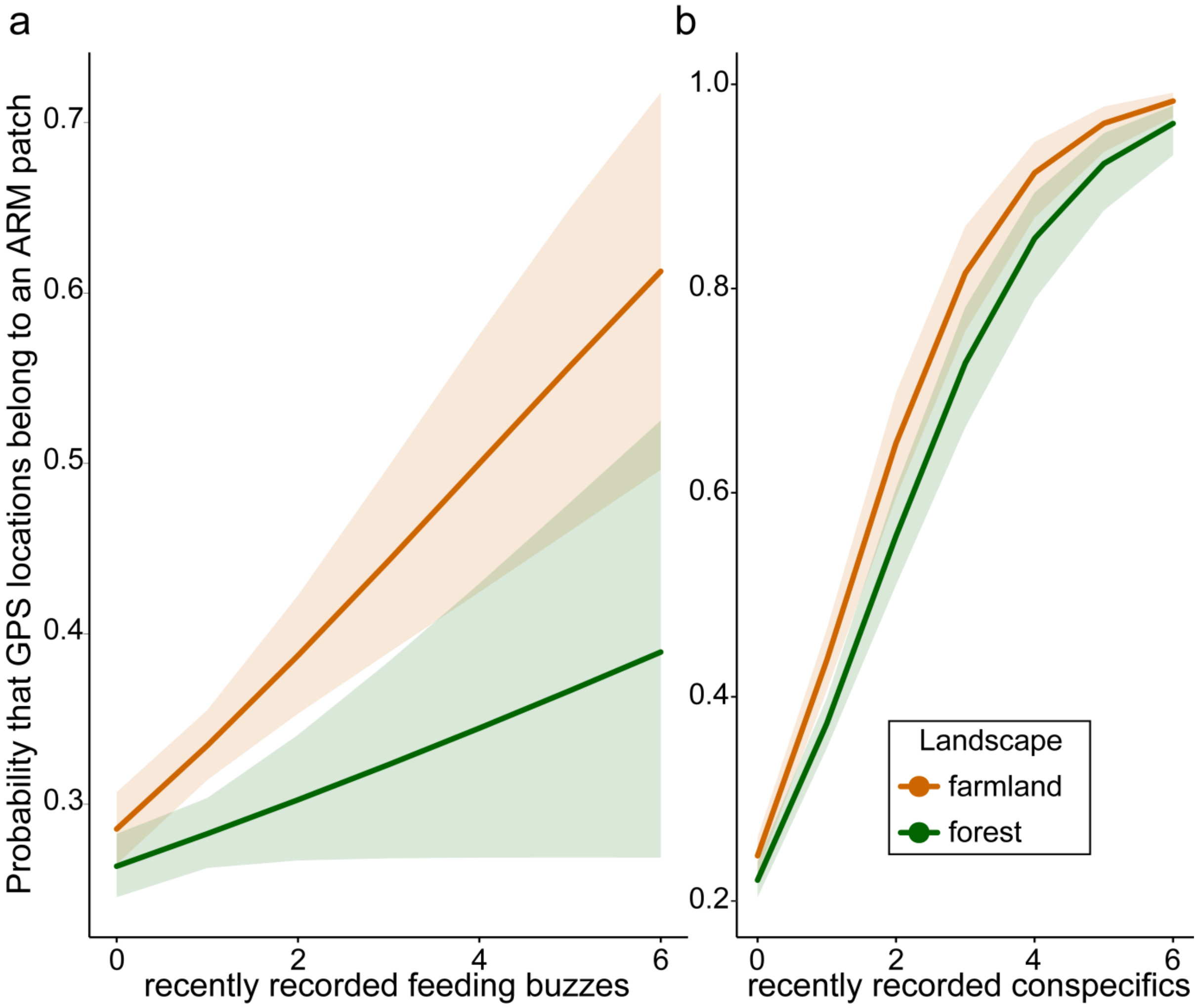


Fig. 4.3 Probability that GPS locations belonged to an ARM patch in relation to recently recorded feeding buzzes of tagged bats (a) and number of adjacent conspecifics (b), based on a binomial generalised mixed model. The probability of a GPS location belonging to an ARM patch was obtained from a hidden Markov model that distinguished the two movement states area-restricted movement (ARM) and directed movement (DM).Lines depict the effect estimates, shading depicts the 95 % confidence intervals of the effect estimates.

The likelihood to switch from directed movement (DM) to ARM increased strongly with the number of conspecifics encountered recently (i.e. during the last 30 s) for bats above farmland. In the forested landscape, the switching probability from DM to ARM increased only slightly with the number of recent conspecific encounters (Fig. 4.4a). The probability to switch back from ARM to DM was not influenced by the number of conspecifics in either of the two studied landscapes (Fig. 4.4b).

For bats above farmland, we observed a slight rise in the probability to switch from DM to ARM with increase of recent own feeding activity. In the forested landscape, we did not observe an effect of recent feeding activity on the switching probability between movement states (Fig. 4.4c). The probability to switch back from ARM to DM was not influenced by recent feeding activity in any of the two studied landscapes (Fig. 4.4d).

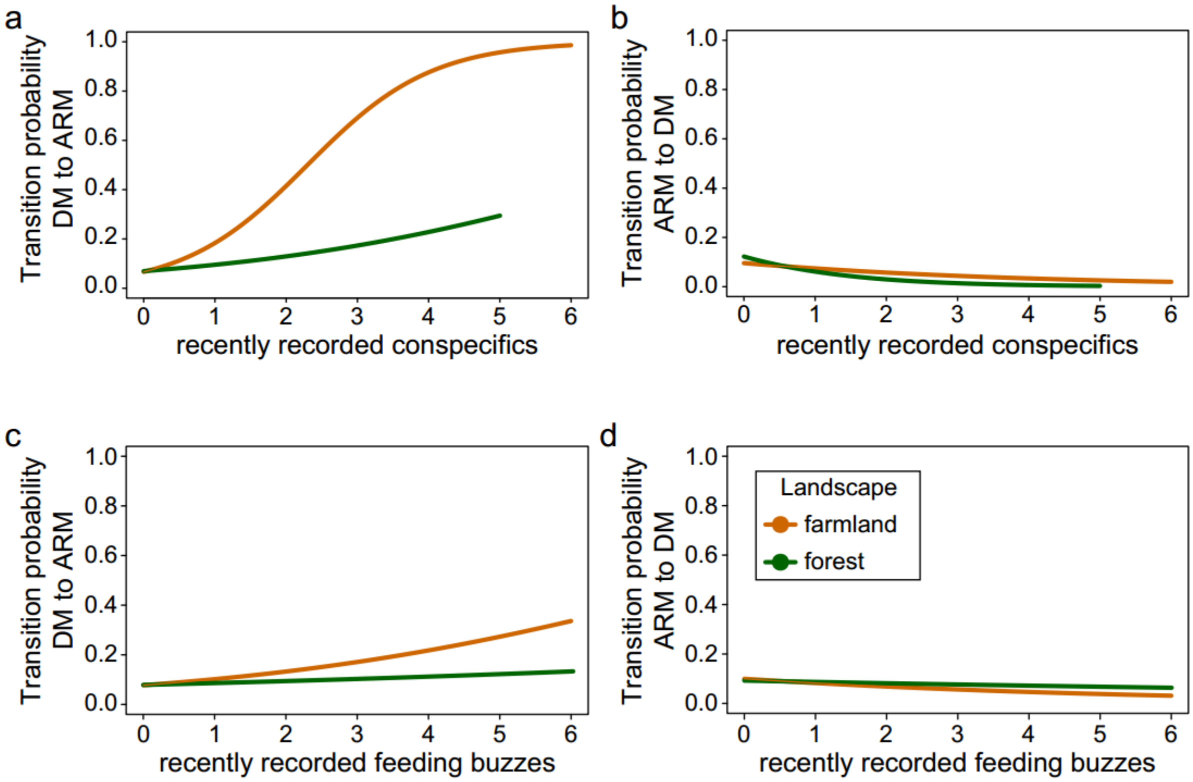


Fig. 4.4 Effect of adjacent conspecifics (a and b) and recent feeding activity (c and d) on the probability to switch between two movement states (area-restricted movement, ARM; directed movement, DM) in the two studied landscapes.

Habitat use

Diversity of land-use classes derived from available patches was higher in the forested landscape than in farmland (Mann-Whitney-U test, N = 288 and 306, U = 28447, $p < 0.001$). Bats used habitats for ARM in the two landscapes non-randomly. Above farmland, ARM patches seemed to include more open habitat than expected from random. Above the forested landscape, surprisingly few ARM patches included water (Fig. 4.5).

When comparing habitat composition of available and actually used patches, the unique fraction of the used habitat composition (water, urban, forest, open) was higher than when comparing habitat composition of available patches with each other (Fig. 4.6, Kolmogorov-Smirnov tests, N = 9 and 36, agricultural landscape: D = 0.639, p = 0.003; forested landscape: D = 0.694, p = 0.001).

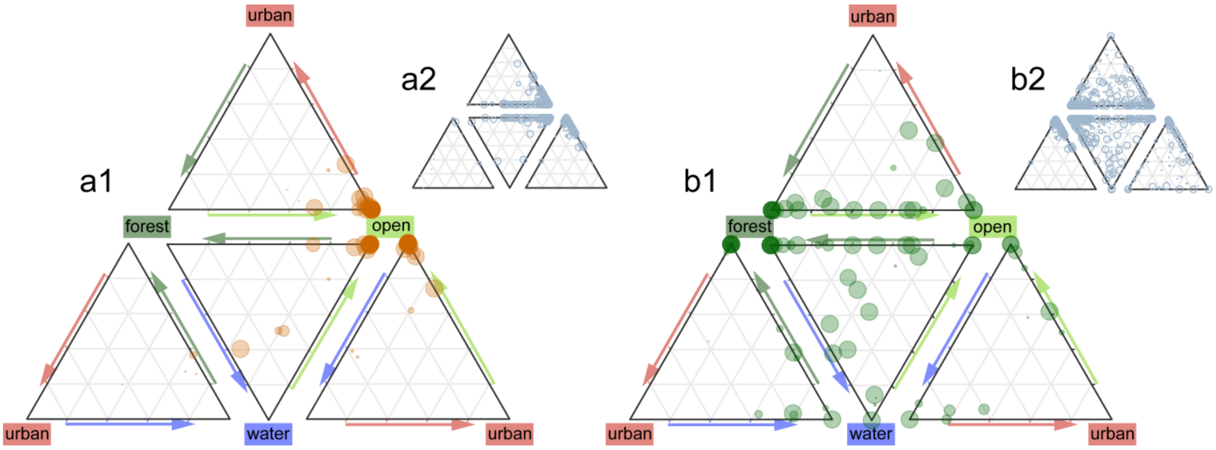


Fig. 4.5 Comparison of habitat composition in used (large triangles, a1 and b1) and available (small triangles, a2 and b2) ARM patches in agricultural (a) and forested (b) landscape. Every point represents the habitat composition of an ARM patch: The position of a point reflects the 3-dimensional composition of the patch with respect to the three land-use classes indicated at the corners of an interior triangle, whereas the size of the point represents the total fraction of the three respectively shown land-use classes. Small (or missing) points thus indicate that the respective patch constituted mainly (or completely) of the fourth land-use class not included in a particular triangle. Coloured arrows show which axis depicts the respective land-use class.

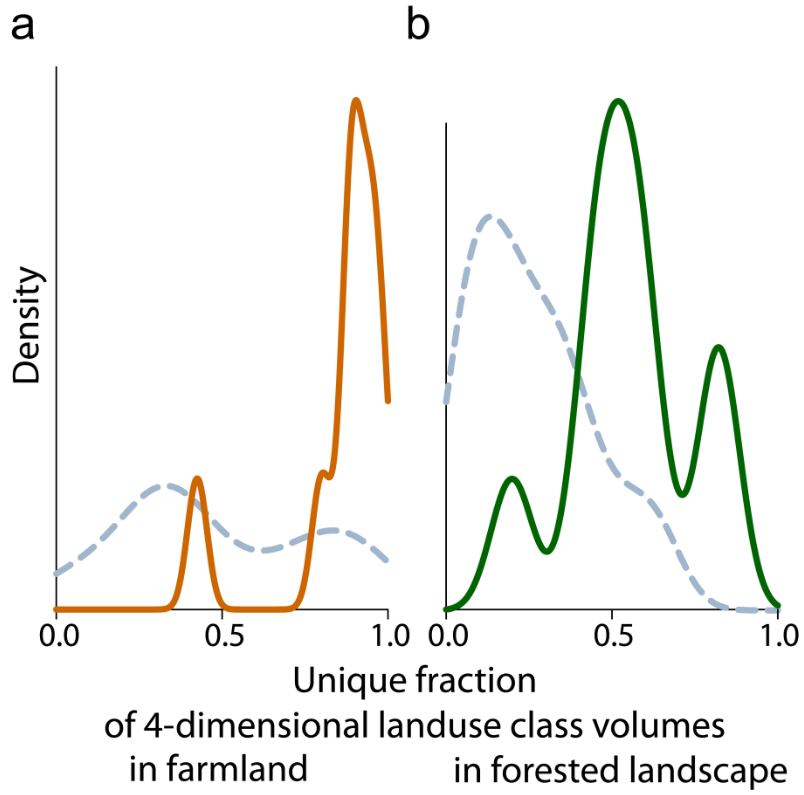


Fig. 4.6 Distributions of the unique fraction of land-use class hypervolumes in agricultural (A) and forested (B) landscape. Coloured lines depict the unique fraction from used ARM patches compared to available ARM patches. Dotted, light grey lines depict the unique fraction of available ARM patches compared to each other. Distributions differed significantly from each other (Kolmogorov-Smirnov tests, N = 9 and 36, agricultural landscape: D = 0.639, p = 0.003; forested landscape: D = 0.694, p = 0.001)

DISCUSSION

We equipped common noctule bats with miniaturised GPS loggers carrying an additional ultrasonic microphone to record movement and hunting behaviour, and the presence of adjacent conspecifics. In particular, we used the combined information on movement and hunting activity to compare habitat use and foraging strategies of bats in two contrasting anthropogenic landscapes: farmland and forested landscape. To our knowledge, similar delineation of movement patterns during prey search and actual hunting events has rarely been achieved (but see Weimerskirch *et al.* 2007; Watanabe *et al.* 2014). Particularly, we lacked information how social foraging of aerial insectivores varies with land-use regimes. Recently, Egert-Berg *et al.* (2018) demonstrated the power of combining GPS data with acoustic records of conspecifics to compare social foraging behaviour across five bat species. They showed that social foraging is only common in species which hunt on ephemeral and patchily distributed food resources. Noctule bats hunt on ephemeral prey, yet prey distribution may depend on the underlying landscape. Here we asked if common noctules are flexible in their foraging behaviour by adjusting social foraging to the local conditions of the environment in which they forage.

Movement and foraging behaviour

Noctule bats emitted less feeding buzzes per time in the forested landscape than above farmland. Foraging trips in the forested landscape thus seemed to be less efficient than above farmland. Since we observed about as many ARM patches in the forested landscape as above farmland, yet without an increase of feeding activity, we argue that foraging efficiency of noctule bats in the forested landscape might have been impaired by intraspecific competition. Indeed, the higher rate of encounters with conspecifics above forested landscape than above farmland suggests that the overall density of noctule bats was higher in the forested landscape, probably due to a larger number of roosting opportunities. In combination with the comparably low feeding activity, this suggests that noctule bats in the forest mainly compete for prey, while bats in agricultural landscapes are limited by scarce roosting opportunities and the search for scarce food patches, but not by the competition for single food items within such insect rich patches.

We found strong support for our hypothesis that bats use different foraging strategies above farmland and forested landscape, probably driven by differences in prey distribution and the competitive environment. 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 1974b, a; Kronwitter 1988; Weimerskirch *et al.* 2007; Watanabe *et al.* 2014). However, only above farmland did we observe a strong correlation between ARM and number of feeding buzzes. This suggests that hunting success in the forested landscape was similar during DM and ARM. The high hunting activity during DM in the forested landscape might have been a reaction to high intraspecific competition at ARM patches. Indeed, insectivorous bats seem to escape competition by avoiding dense aggregations of conspecifics (Cvikel *et al.* 2015; Roeleke *et al.* 2018a). Further, insects might have been distributed more homogeneously in the forested landscape than in farmland (cf. Ferguson *et al.* 2003). Bats above farmland were thus probably not able to meet their energetic demands through foraging during DM above the predominant crop fields. Heterogeneous distribution of prey may also explain why travel distance between roost and ARM patches was larger in farmland than in the forested landscape. Indeed, insect distribution (Brack Jr. & Laval 1985; Tscharntke *et al.* 2005; Grüebler *et al.* 2008) and in consequence foraging activity of bats (Frey-Ehrenbold *et al.* 2013; Heim *et al.* 2015, 2018; Roeleke *et al.* 2016; Froidevaux *et al.* 2017) often seem to be boosted by certain landscape elements in farmland, thus leading to a patchy distribution of foraging grounds.

We further found support for our prediction that only noctule bats above farmland eavesdrop on conspecifics to locate prey aggregations. Bats encountered conspecifics mainly during foraging in ARM patches above farmland. Local enhancement of foraging bats has often been documented with playback experiments (Gillam 2007; Dechmann *et al.* 2009; Übernickel *et al.* 2013). However, in our case, conspecifics density could have also been a mere correlation driven by high prey availability. Yet, our findings that bats were also more likely to start ARM, i.e. to switch from DM to ARM, after recent encounters with conspecifics suggests that this change in movement behaviour was indeed driven by the presence of conspecifics. Since the effect of conspecifics on movement behaviour was more pronounced than the effect of own recent feeding activity, we suggest that the presence of conspecifics is a better indicator of plentiful prey patches than own detection of single prey items. 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 when prey patches are hard to find, e.g. if prey occurs only temporarily and unpredictably.

Foraging behaviour of common noctules contrasted between our two study areas. 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 social foraging in the forested landscape. We propose two reasons for the different reactions towards conspecifics above farmland and in the forested landscape; first, the overall higher bat density in the forested landscape increased the probability to encounter conspecifics during commuting flights, thus making an encounter not necessarily a good predictor for food availability. Second, a spatially homogenous distribution of prey insects, paired with an overall high intraspecific competition, made social foraging non beneficial (Ryer & 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 dense aggregations of conspecifics (Roeleke *et al.* 2018a) or even engage in agonistic behaviour when competing for prey (Voigt-Heucke *et al.* 2010; Corcoran & Conner 2014). Interestingly, also a bat's recent own 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.

Habitat use

Noctule bats in the agricultural landscape chose ARM patches with non-random habitat compositions. Yet, habitat compositions of ARM patches were similar to each other. ARM patches contained mostly open habitat such as crop fields and grasslands. This was surprising to us since earlier studies in the study area documented a preference for water bodies during foraging (Eichstädt 1995; Roeleke *et al.* 2016) earlier in summer, and comparably low hunting activity above open fields (Heim *et al.* 2016). Our findings show that habitat use of insectivores that depend on ephemeral insects is hard to predict without detailed knowledge about the distribution of insect prey in space and time. In the future, it will be especially useful to understand whether prey distribution in open habitats is stable across seasons, and whether it is driven by factors related to land-use management or stochastic effects such as air currents and temperature gradients.

Also bats in the forested landscape chose ARM patches with non-random habitat compositions. Yet, habitat compositions of ARM patches in the forested landscape differed less from random but varied more among each other than in farmland. We conclude that the choice of habitat composition in forested landscapes was of minor importance, probably because prey was distributed more homogeneously and hence avoidance of competitors and proximity of ARM patches to the roost were more important. However, we found it surprising that bats included high proportions of forest in their ARM patches, and did not use the nearby water bodies more often, as was the case in one of our earlier studies in the same area (Roeleke *et al.* 2018b).

Possible shortcomings

We studied the foraging strategy of subadult noctule bats to ensure that animals were naive about the location of foraging grounds, i.e. that they could not rely on experiences from previous years. A recent study indicates that noctule bats probably learn about foraging grounds through local enhancement when occasionally encountering conspecifics (Ripperger *et al.* 2018). Although more experienced bats might depend less on social foraging, spatio-temporal unpredictability of prey aggregations above farmland - as it was supported by the observed lack of correlation between ARM and distinct habitat features - will make social foraging also beneficial for more experienced bats.

Although the observed patterns of conspecific encounters and feeding activity during the use of ARM patches substantiated convincingly our hypotheses, we must acknowledge that these patterns constitute correlations. At this point, it is not possible to disentangle if the high conspecific density during foraging in ARM patches was driven by active attraction between conspecifics or by local enhancement at insect rich patches. However, increased switching probability towards ARM after encountering conspecifics indicates that bats above farmland indeed based their decisions on social information.

Our secondary interest focused on the composition of habitats bats chose during foraging in ARM patches. We propose that habitat composition can be more important than the presence of single land-use classes, especially since insect prey is known to be most abundant at ecotones (Brack Jr. & Laval 1985; Tscharntke *et al.* 2005; Grüebler *et al.* 2008). Yet, effects of multi-dimensional habitat composition are hard to assess in detail. For statistical purposes, we had to break down the multi-dimensional composition into a one-dimensional measure (cf. Bevanda *et al.* 2015 for a slightly different method), and thus lost information on the importance of single land-use classes. The role of the relative amount of single land-use classes within ARM patches (as depicted in Fig. 4.5) is thus purely descriptive and has to be interpreted cautiously. Further, the reported habitat use represents just a temporal snapshot, and might change with seasonal mass occurrences of insects.

Conclusion

For many predators, especially those that hunt on ephemeral prey, we are currently not able to quantify or even identify single hunting events directly. However, recent ongoing technical developments have made it possible to track the movements of many predators. In these movement tracks, we often see ARM which is typically associated with foraging events (Smith 1974b, a; Weimerskirch *et al.* 2007; Watanabe *et al.* 2014). Such events are commonly named area restricted search. While the term area restricted search implies a combination of an animal's behaviour and intention, it is meanwhile often used to describe the mere movement of animals. Our results substantiate the importance to distinguish between movement behaviour and foraging activity. Here we demonstrated that feeding activity during ARM is not necessarily higher than during DM. Foraging behaviour of noctule bats differed between landscapes; while noctule bats above farmland seemed to be attracted by conspecifics and foraged primarily within well-defined patches, noctule bats in the forested landscape were less attracted by conspecifics and foraged likewise successfully within and without ARM patches. We propose that different foraging strategies were driven by higher intraspecific competition during flight, paired with homogeneous prey distribution, in the forested landscape. Our study complements and expands recent findings on social foraging in bat species (Egert-Berg *et al.* 2018). We showed that social foraging by bats is not only species-specific, but that the degree to which social foraging is used can be flexibly adjusted to different resource landscapes and competitive environments. In particular, we demonstrated that social foraging was the preferred strategy of open-space foraging bats that needed to find prey in a structurally poor agricultural landscape. Indeed, 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 habitat deterioration. Flexibility of foraging strategies might be a prerequisite for the persistence of highly mobile predators exploiting different landscapes in general.

DATA AVAILABILITY

GPS tracking data is stored in the movebank tracking data repository (https://www.movebank.com) under the study ID 622521340.

ACKNOWLEDGEMENTS

We are grateful to Cedric Scherer, Oliver Lindecke, Viktoria Radchuk, and members from the Biomove research training group for discussions. We thank Anja Fritz, members from the IZW batlab, Gernot Verch, and the Leibniz Centre for Agricultural Research for their support during fieldwork. MR and UES were funded by the DFG (GRK 2118 – Biomove).

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.

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GENERAL DISCUSSION

In the presented work, I measured movements of Common noctule bats *Nyctalus noctula*, either directly via GPS loggers or indirectly via activity derived from recordings of ultrasonic bat calls. The aim of this work was to infer the flexibility of foraging strategies of aerial hawking insectivores. Similar flexibility of foraging strategies might hold true for other foragers that hunt on patchily distributed prey as well. On longer, evolutionary meaningful timescales, adjustments of foraging strategies to competitive environment and abiotic external factors may support species coexistence. The ultimate goal of this work was thus to identify potential stabilizing and equalizing mechanisms (*sensu* Chesson 2000) promoted by context dependent foraging strategies.

In chapter one I focused on the influence of an abiotic environmental effect (moonlight) on habitat use of foraging *N. noctula*. In chapter two I investigated how fine scale space use of *N. noctula* was affected by social interactions, which I simulated by broadcasting calls of hunting conspecifics and heterospecifics. In chapter three, I finally investigated the interplay between environmental effects and social interactions by comparing flexibility of foraging strategies across ecosystems.

Accordingly, I focused on the movement behaviour of *N. noctula* during foraging flights in all three studies. I assumed that bats sought to optimize their net energy gain during their flights, which is strongly linked to the rate at which bats catch and consume flying insects. Consequently, it appears most reasonable to interpret the observed differences in foraging strategies as adjustments to the ability of individuals to catch insects in different situations. Yet, I acknowledge that the experimental setups allowed only simultaneous insect sampling during the playback study (chapter two). Therefore, the proposed link between foraging movements and insect distribution in chapter one remains speculative. However, although I could not sample insect availability directly in chapter three, the quantification of feeding events of the focal bats, as recorded by telemetry devices, should have been a good proxy for the food items that were available to individual bats. Following, I will shortly discuss each of the three studies separately, before I deduce general patterns arising from the combination of the results.

ABIOTIC FACTORS INFLUENCE USE OF FORAGING HABITATS (CHAPTER ONE)

N. noctula adjusted habitat use to external factors which probably influenced the distribution of insect prey. Experienced individuals might be able to predict the distribution and resource richness of prey patches if the influence of environmental factors is systematic (e.g. humidity or temperature, Anthony *et al.* 1981; Erickson & West 2002; Ciechanowski *et al.* 2007). The same may be true for aerial-hawking insectivores birds who can infer prey availability from weather conditions (Troy & Baccus 2009), but also for terrestrial insectivores (Vickery & Rivest 1992). Prey availability may also fluctuate periodically, and may then be easy to predict by predators. Examples reach from sub-daily fluctuations driven by the tide (Irons 1998) to yearly fluctuations driven by mass migration of prey (Darimont *et al.* 2008). The ability to adjust the choice of hunting grounds to changes in prey distribution, and possibly also to partially predict such changes, seems to be not surprising but rather a prerequisite for the survival of animals that depend on patchily distributed ephemeral prey. In chapter one I showed that the moonlight intensity influenced not only which habitats *N. noctula* used, but also to which extent distinct habitats were used for area restricted foraging. Probably, foraging in open habitats was most profitable during high moonlight intensities because insects were lured out of the ground vegetation by the moonlight and aggregated in the open airspace. However, the use of open fields during moonlit nights may also result in an increased predation pressure from visual oriented predators such as owls. Yet, the particular fast movements of *N. noctula* might make them hard to catch by predatory birds. Their movement characteristics may allow *N. noctula* to exploit insect aggregations that frequently appear under moonlit conditions. Such aggregations might be inaccessible to slower flying and light-averse competitors. The exclusive ability to exploit such temporary but frequently occurring resource may potentially act equalizing on bat assemblages, given that competitors of *N. noctula* have an advantage during hunting in dark places, e.g. because they can hunt more efficiently thanks to their higher manoeuvrability.

SOCIALITY DURING FORAGING DEPENDS ON PREY AVAILABILITY (CHAPTER TWO)

N. noctula adjusted local activity within foraging patches to the density of feeding heterospecifics, as simulated by playbacks of hunting calls. The reaction towards heterospecifics changed across seasons and was accompanied by seasonal changes in prey composition. Local *N. noctula* activity at foraging grounds increased during times of plentiful prey when I simulated aggregations of hunting heterospecific *Pipistrellus nathusii*, but not when I simulated aggregations of hunting conspecifics. In contrast, during times of prey scarcity, *N. noctula* activity decreased when I simulated aggregations of hunting *P. nathusii*. The results indicate that *N. noctula* use social foraging via eavesdropping on specialized foraging calls of other hunting bats. However, the fact that *N. noctula* showed only strong positive reactions towards heterospecifics but not towards conspecifics hints at a trade-off that arises during social foraging. Hunting with conspecifics may aid detection of food patches, but also increases competition. In the case of insectivorous bats individuals of the same species probably compete for open flight space and the ability to receive undisturbed acoustic information during echolocating insect prey. In contrast, competition with heterospecifics seems to be less pronounced, probably due to fine-scale vertical segregation and separation of frequencies used to echolocate prey. Higher intraspecific than interspecific competition acts stabilizing in species assemblages, and is in this case probably partially related to space use arising from slight differences in movement characteristics. During insect scarce times on the other hand, competition between heterospecifics seemed to be more intense than competition between conspecifics. I ascribe that to the higher flight agility of *P. nathusii*, which probably made *N. noctula* inferior during competition for single, scarce prey items.

The presented work depicts the trade-off between competition and improved prey detection that comes with a social foraging strategy (Clark & Mangel 1984). The adaptive value of social foraging requires not only patchy food distribution, but also a minimum abundance of food, so that all individuals in a foraging group get some share of the resource (cf. di Bitetti & Janson 2001). If the costs of social foraging become too high, e.g. through competition for a limited resource like prey insects in our study, individuals should forage solitary (Ekman & Rosander 1987), which might lead to the avoidance of con- or heterospecific competitors. In this study, it is most remarkable that the studied *N. noctula* were extremely flexible in their foraging strategy, i.e. they adjusted the extent to which they foraged within the simulated groups both to the seasonally changing prey composition and to the identity of the simulated groups.

SOCIAL FORAGING IS CONTEXT DEPENDENT (CHAPTER THREE)

N. noctula adjusted its foraging strategy to conspecific density and prey availability that differed between landscapes. In an agricultural landscape, *N. noctula* foraged mainly during area restricted movements. These movements led to the formation of foraging patches in small areas where prey seemed to be available in large numbers. However, the onset of such area restricted movements seemed to be mainly triggered by the presence of conspecifics, and only to a lesser extent by previous own feeding activity. In contrast, in a forested landscape dominated by pine stands and a river-lake-system, *N. noctula* foraged to the same amount during directed and area restricted movements. The effect of conspecific presence on the formation of foraging patches was much smaller in the forested than in the agricultural landscape. Own feeding activity had no effect on formation of foraging patches. However, in both landscapes, conspecific density was highest when focal individuals were hunting within foraging patches, which supports the notion that bats followed an ideal free distribution (Fretwell 1972). Yet, the different influence of conspecific presence on the onset of area restricted movements showed that bats in the agricultural landscape used a social foraging strategy to locate prey patches, while bats in the silvicultural landscape followed a solitary foraging strategy to locate hunting grounds. I propose two complementing reasons for this difference:

a) In silvicultural landscapes, prey is distributed evenly, whereas prey is distributed patchily in agricultural landscapes. Bats thus use social foraging to locate ephemeral prey patches in the latter case, i.e. they eavesdrop on the specialised hunting calls of conspecifics, thereby forming a sensory network that can sample an area far larger than the area a single individual could sample (Cvikel *et al.* 2015). In contrast, in the silvicultural landscape, prey is omnipresent and thus easy to find. Given such even resource distribution, social foraging does not improve hunting success (e.g. Ryer & Olla 1995; Cortés-Avizanda *et al.* 2011; Egert-Berg *et al.* 2018, see also Ekman & Rosander 1987).

b) According to the ultrasonic recordings, the density of conspecifics in the forested landscape was almost twice as high as in the agricultural landscape.

This might have led to strong intraspecific competition in the forested landscape, e.g. through interference during flight or acoustic jamming, as proposed in chapter two. Further, an overall higher population density makes the mere presence of conspecifics less informative, i.e. it is more likely to meet conspecifics just by chance while they are themselves searching for food. However, several playback studies have shown that eavesdropping bats indeed discriminate between search calls and specialized feeding calls of conspecifics (Balcombe & Fenton 1988; Gillam 2007; Übernickel *et al.* 2013), suggesting that bats not only use social cues like conspecific presence, but also public information (*sensu* Valone 1989, see also Danchin *et al.* 2004; Coolen *et al.* 2005) like foraging activity of conspecifics.

CONCLUSION

The studies presented here investigated the effects of external factors (chapter one: moonlight, chapter two: prey availability, chapter three: landscape structure) on navigation capacity and resulting movement paths (Nathan *et al.* 2008), and integrated feedbacks between navigation capacity and intra- and interspecific interactions (cf. Jeltsch *et al.* 2013, chapter two and chapter three: competition and social foraging, Fig. 5.1). Insectivorous bats are particular suitable to study such movement mediated feedbacks because a) they are highly mobile, b) their behaviour and competitive environment can be recorded with acoustic telemetry devices, and c) they live in complex competitive environments resulting from high niche overlaps of coexisting species (Willig *et al.* 1993; Eichstädt 1995; Razgour *et al.* 2011; Salsamendi *et al.* 2012).

The observed attraction of *N. noctula* towards hunting heterospecifics but not towards conspecifics during times of high prey availability supposes that negligible interspecific competition may act stabilizing on communities. In contrast, the avoidance of heterospecifics during times of prey scarcity argues for strong interspecific competition in certain situations. However, the proposed ability of *N. noctula* to move towards alternative foraging patches may act equalizing during times of increased interspecific competition. Flexibility of foraging strategies indicates context dependent trade-offs between intraspecific competition and resource detection. At relatively low densities, individual *N. noctula* probably improved detection of patchily distributed and ephemeral prey through social foraging. Insectivores that hunt on ephemeral insects in mid air might have a fitness disadvantage towards competitors that can exploit insects that are associated with vegetation structures and thus occur more predictably. However, social foraging might enable *N. noctula* to find ephemeral food patches more quickly and might thereby equalize fitness disadvantages towards foragers that can rely on more predicable food patches. In accordance with that interpretation, at comparably high densities, individual *N. noctula* did not make use of social foraging to hunt on probably evenly distributed prey. The relative avoidance of conspecifics in this situation supposes that intraspecific competition was comparably high in this environment. Intraspecific competition might act stabilizing on predator communities that prey on evenly distributed and thus predictable resources.

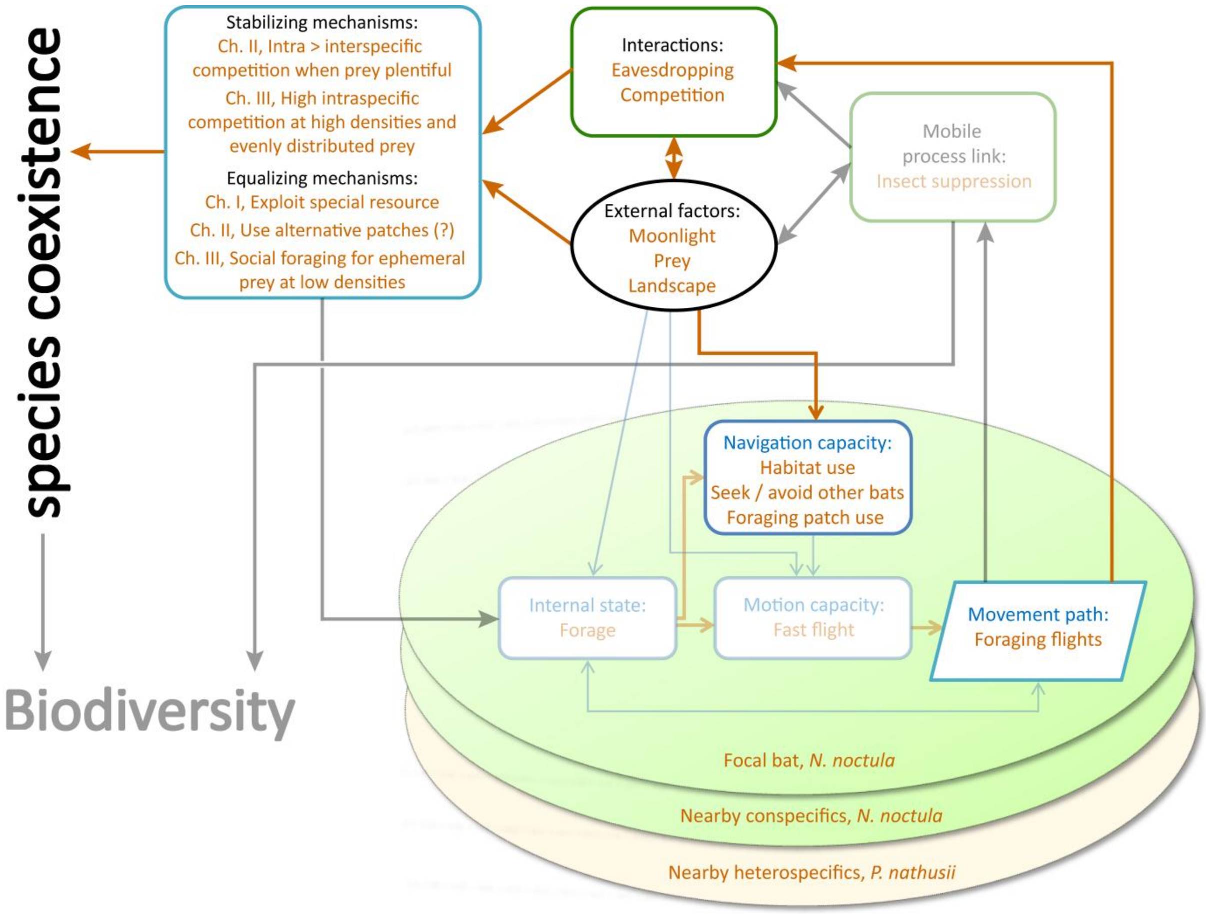

Fig. 5.1 Positioning of the entities studied in this thesis within the biodiversity-movement framework by Jeltsch *et al.* (2013, figure modified). Orange lettering specifies the given entities as presented in this thesis. Semi-transparent entities and connections were not explicitly examined in this thesis, although they might probably play a role in the studied system.

All three studies showed that *N. noctula* are highly flexible in their foraging behaviour. *N. noctula* can adjust the use of foraging habitats to external factors which may act on prey distribution. Possibly, they are able to predict the influence of external factors on the spatial distribution of prey. They further can adjust their space use to changing competitive situations and prey availability by interpreting public information provided by conspecifics and heterospecifics. Furthermore, *N. noctula* are able to integrate external factors with competitive pressure and public information to pursue appropriate foraging strategies flexibly and context dependent. *N. noctula* realized this flexibility by adjusting movement behaviour and space use. Although effects on species coexistence cannot be evaluated at the investigated timescale, the observed adjustments to external factors and competitive environment suggest fitness consequences of foraging movements. On the one hand, I propose that differences in flight characteristics of different bat species lead to higher intraspecific than interspecific competition. Different flight characteristics may thus stabilize bat communities. On the other hand, fast and energy efficient flight and the use of social foraging seem to be prerequisites to find ephemeral food patches. The ability to exploit such ephemeral patches may equalize fitness disadvantages towards competitors that can rely on predictable food resources or profit from superior hunting efficiency promoted by higher manoeuvrability.

The complexity and multitude of information that individual *N. noctula* integrated when deciding for a foraging strategy substantiates that focusing only on the single forager and the current distribution of food is insufficient to understand foraging behaviour. In fact, foragers have to trade competition against benefits from social foraging, integrate current food availability, anticipate food distribution beyond their perception range, and estimate how external factors will influence food distribution over the course of their foraging trips. The importance of successful foraging for an individual’s survival argues for a high flexibility of foraging strategies of animals that live in dynamic environments. Consequently, it is likely that not only bats but also other highly mobile predators that face similar problems regarding prey distribution and competition exhibit similar flexibility in foraging movements.

Especially spatial tracking of individual foragers at high spatio-temporal resolution can be a powerful tool to study foraging movements and the role of individual interactions in foraging ecology. The presented studies substantiate the significance of movement ecology for biodiversity research (Fig. 5.1) and for understanding intra- and interspecific interactions in particular. The assessment of changing competitive environments through recording individual movement and foraging behaviour can help to identify stabilizing and equalizing mechanisms that may facilitate the coexistence of mobile foragers (Chesson 2000; Jeltsch *et al.* 2013). The investigation of movement is thus more than merely a tool to study ecological processes. Movement behaviour shapes biodiversity patterns through dynamic interactions with external factors and individuals.

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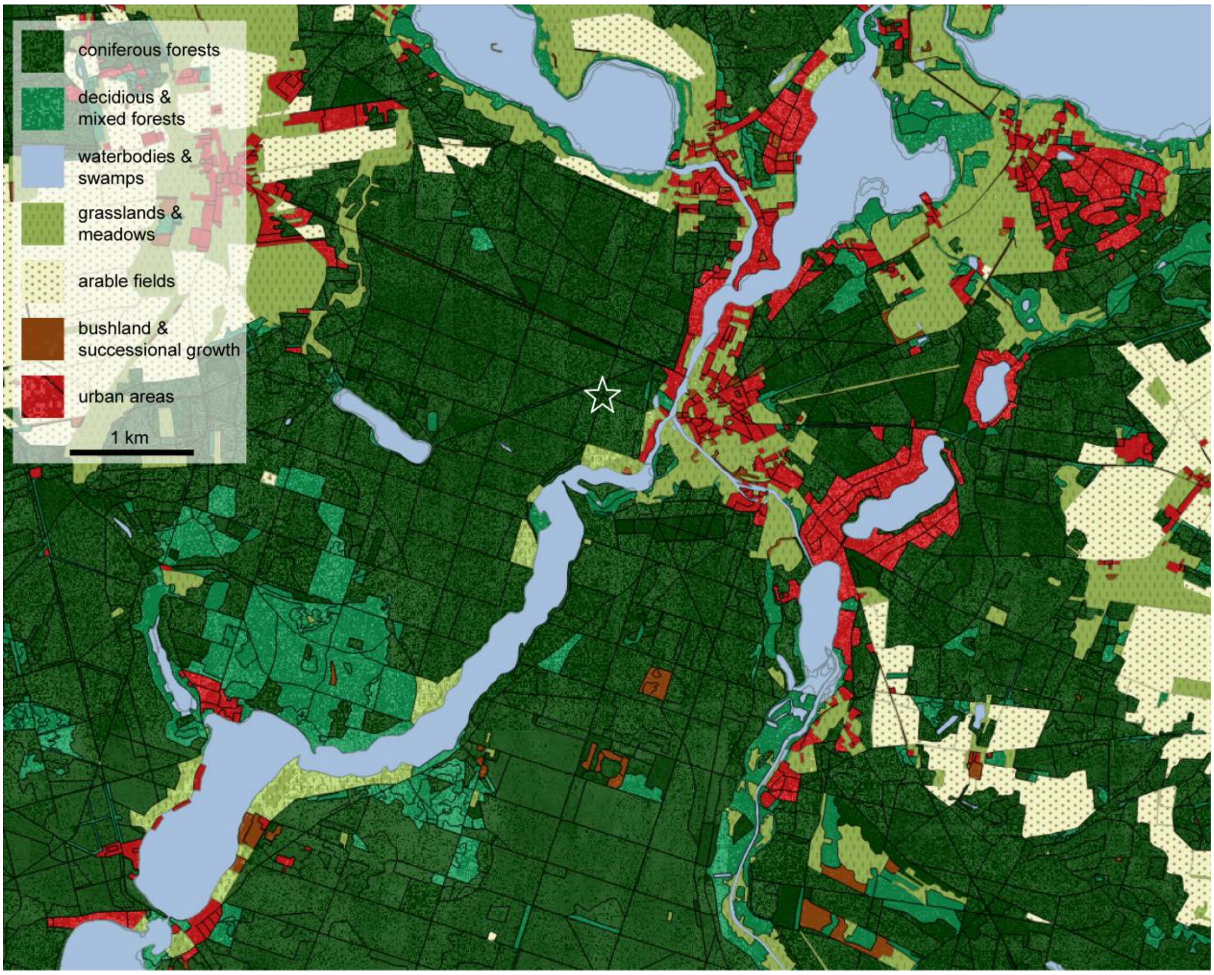
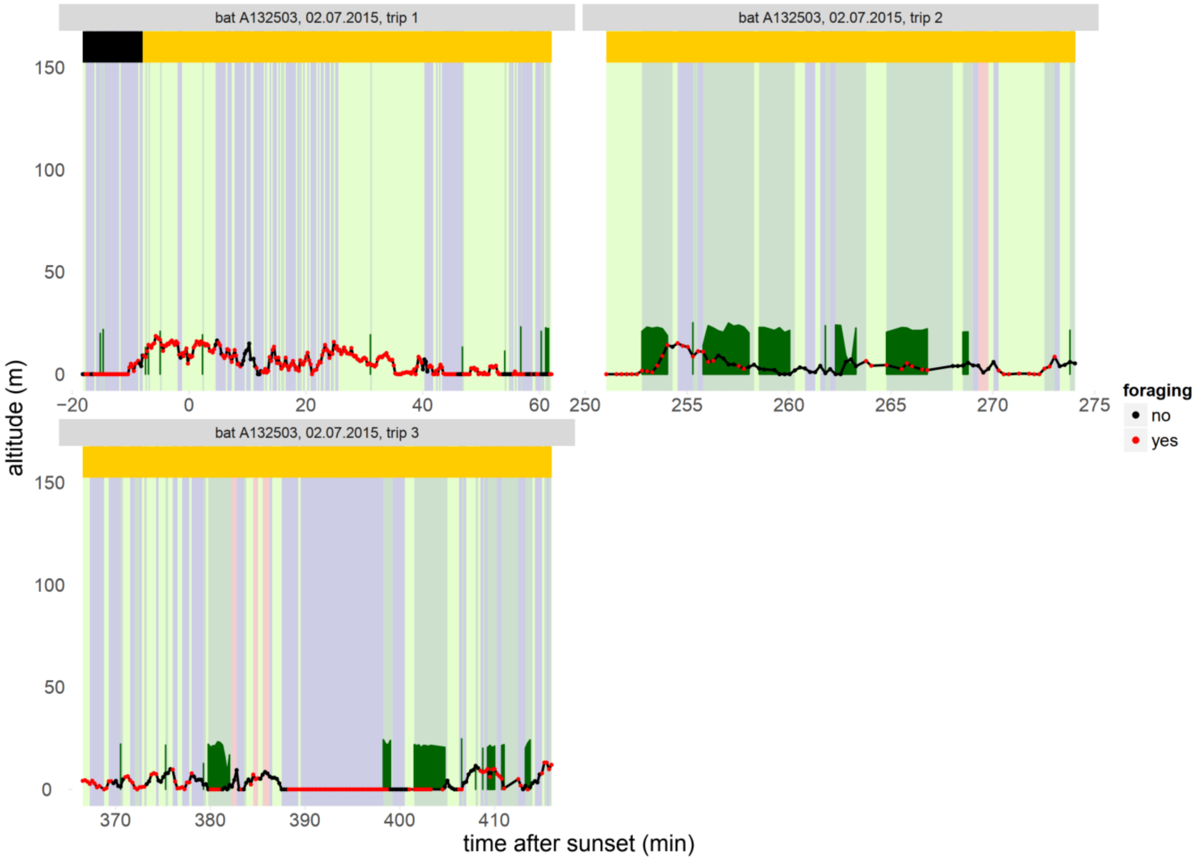
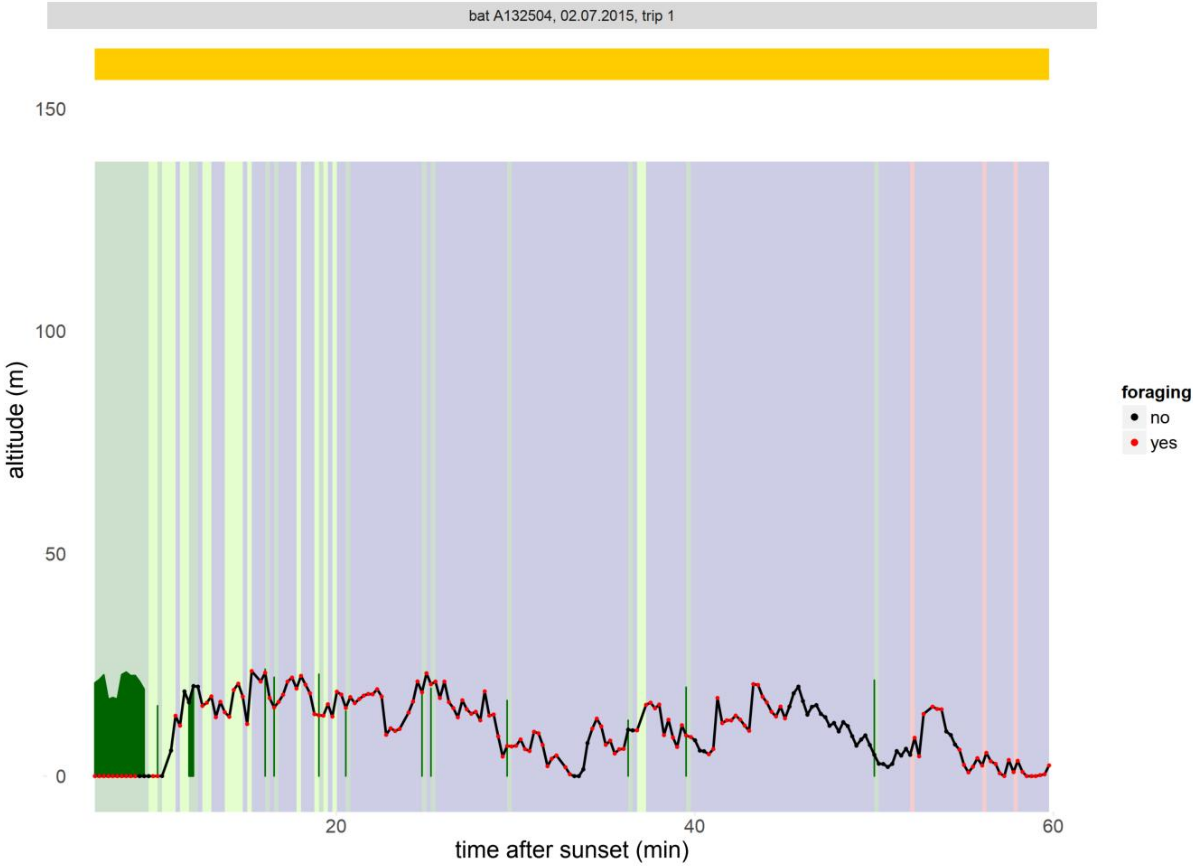
APPENDICES

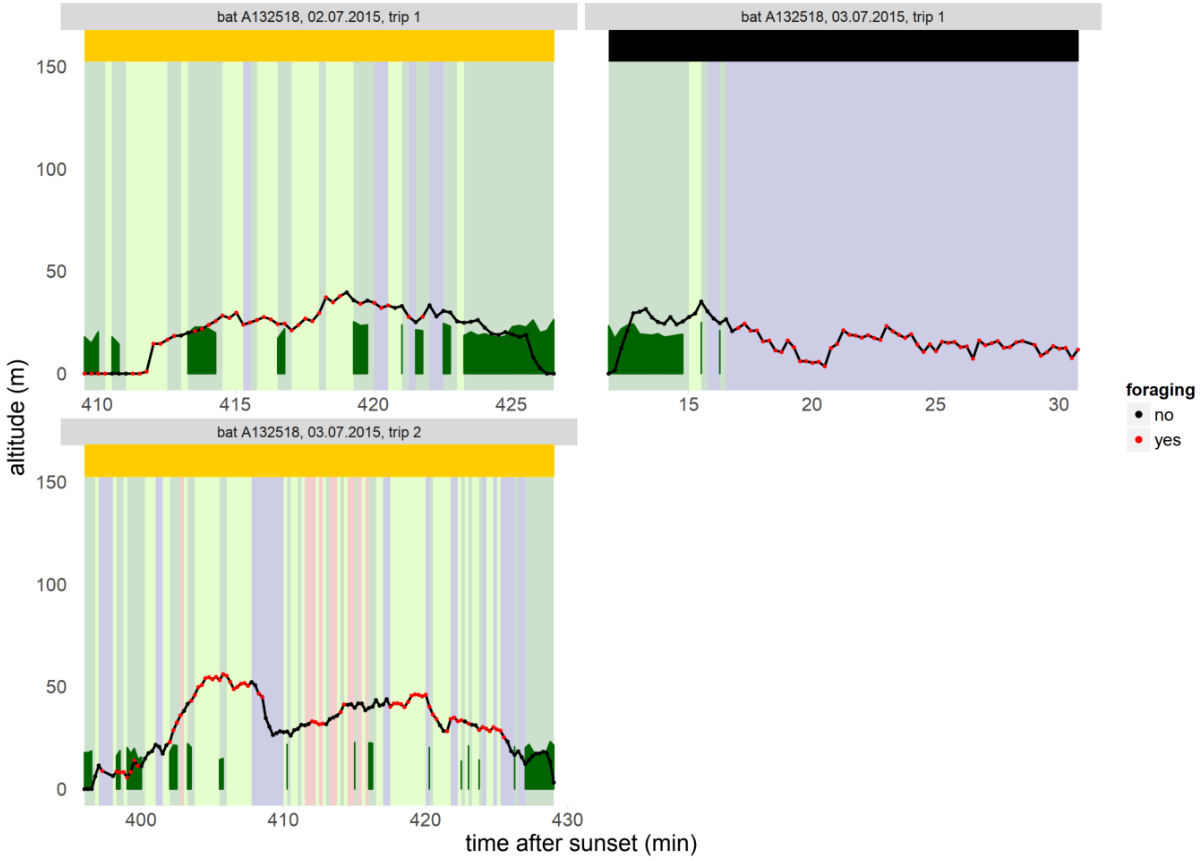
APPENDIX CHAPTER ONE

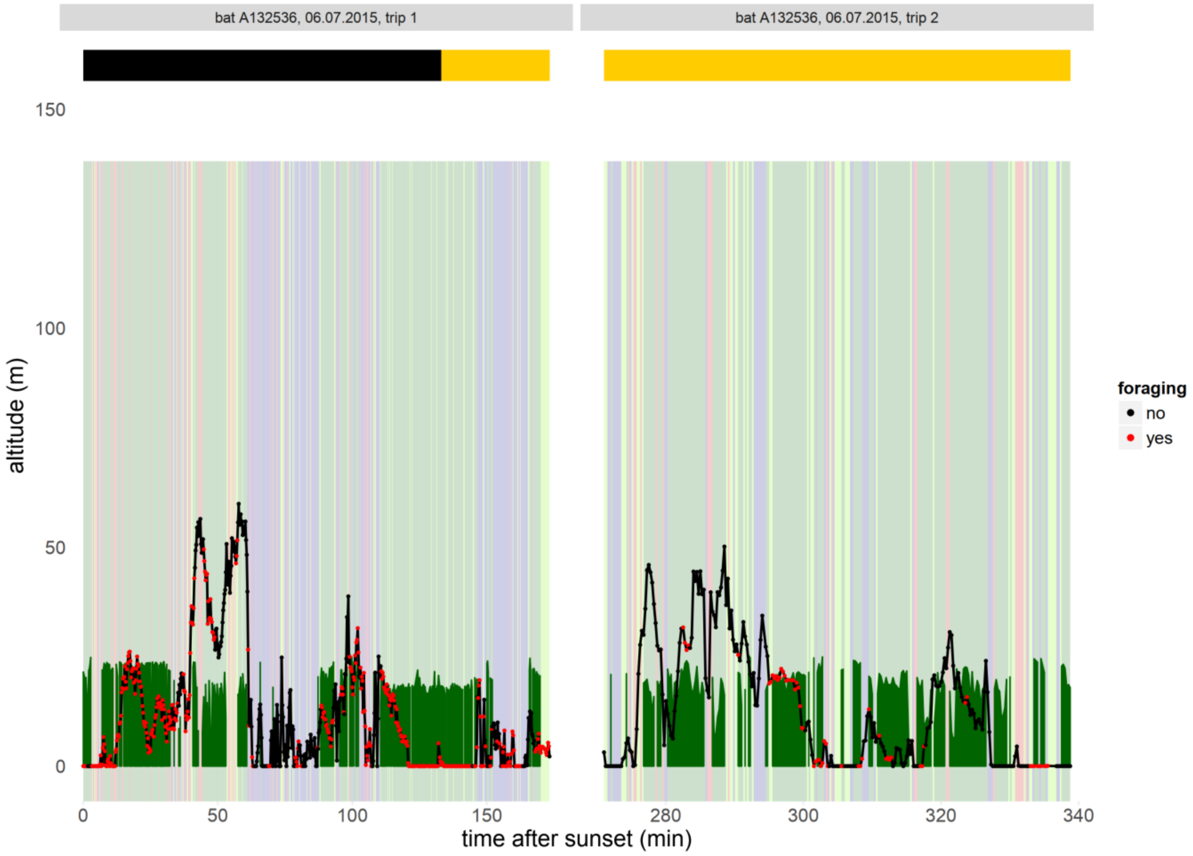


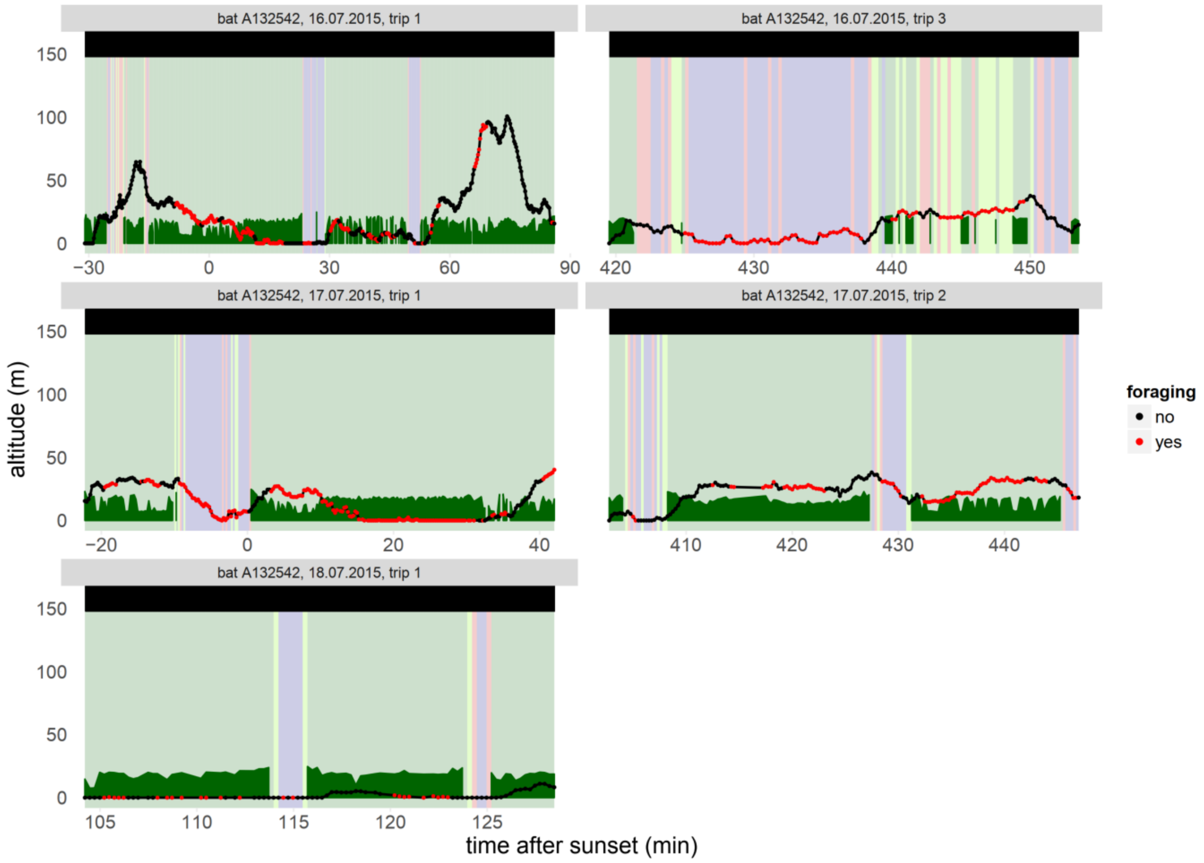
Appendix 2.1 Habitat types within the study area. The location of the artificial roosts is indicated by the white star.

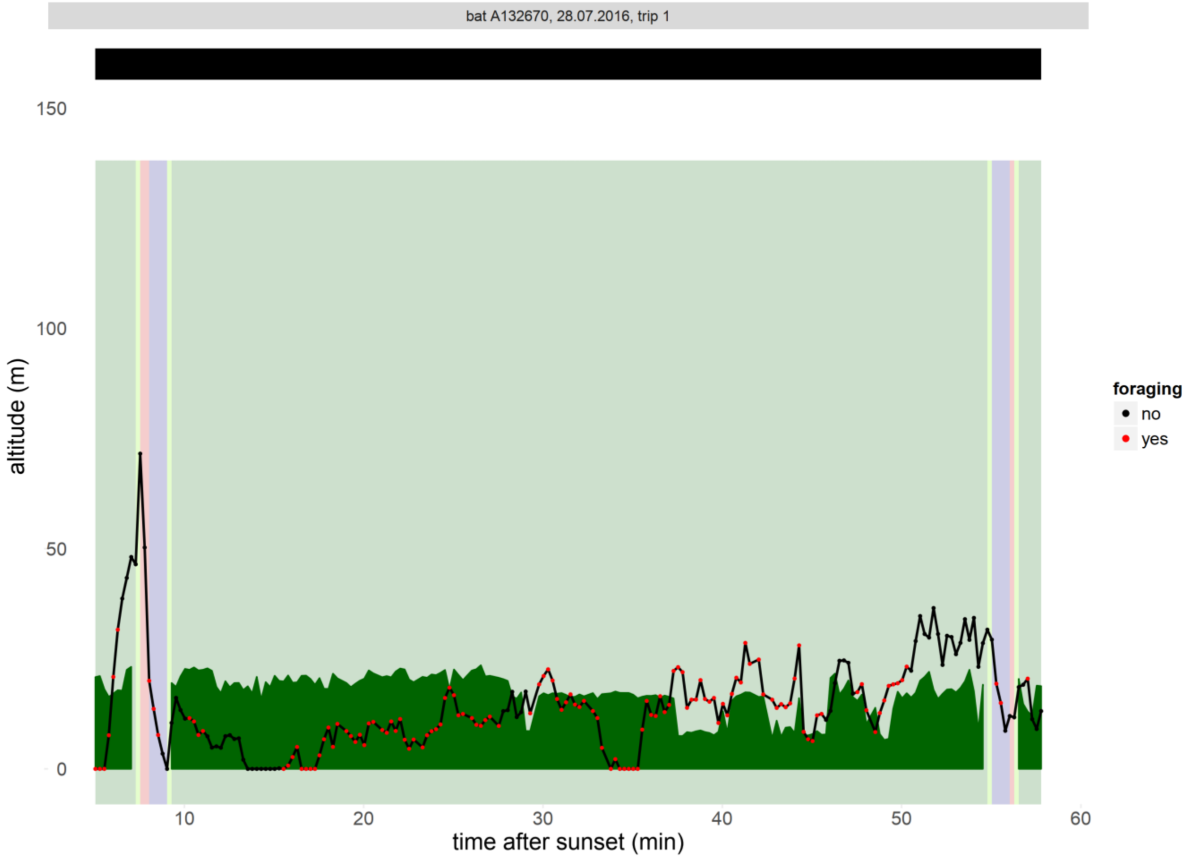

bat A132503, 02.07.2015, trip 1
bat A132503, 02.07.2015, trip 2
bat A132503, 02.07.2015, trip 3
altitude (m)
150
100
50
0
−20
0
20
40
60
250
255
260
265
270
275
370
380
390
400
410
time after sunset (min)
foraging
● no
● yes


bat A132504, 02.07.2015, trip 1
altitude (m)
150
100
50
0
20
40
60
time after sunset (min)
foraging
● no
● yes


bat A132518, 02.07.2015, trip 1
bat A132518, 03.07.2015, trip 1
bat A132518, 03.07.2015, trip 2
altitude (m)
150
100
50
0
410
415
420
425
15
20
25
30
400
410
420
430
time after sunset (min)
foraging
no
yes


bat A132536, 06.07.2015, trip 1
bat A132536, 06.07.2015, trip 2
altitude (m)
150
100
50
0
0
50
100
150
280
300
320
340
time after sunset (min)
foraging
no
yes


bat A132542, 16.07.2015, trip 1
bat A132542, 16.07.2015, trip 3
bat A132542, 17.07.2015, trip 1
bat A132542, 17.07.2015, trip 2
bat A132542, 18.07.2015, trip 1
altitude (m)
150
100
50
0
−30
0
30
60
90
420
430
440
450
−20
0
20
40
410
420
430
440
105
110
115
120
125
time after sunset (min)
foraging
no
yes


bat A132670, 28.07.2016, trip 1
altitude (m)
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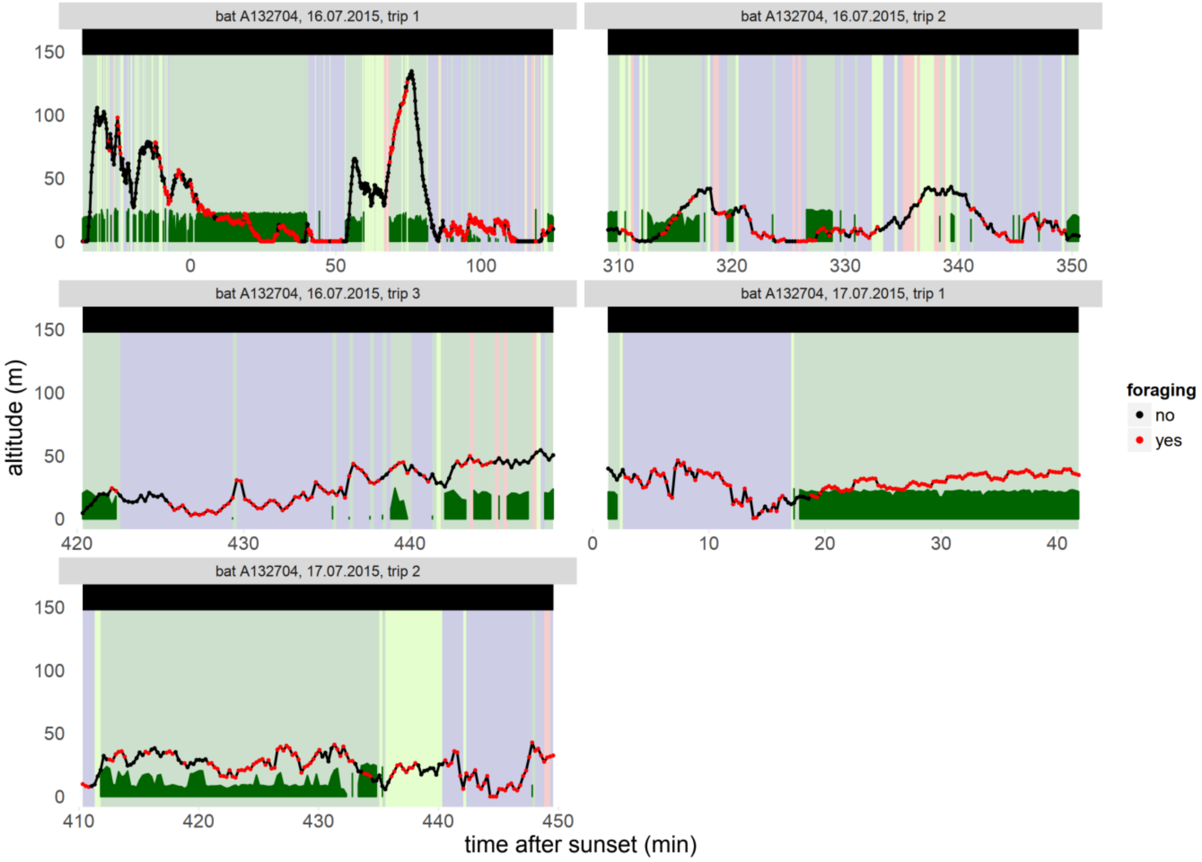
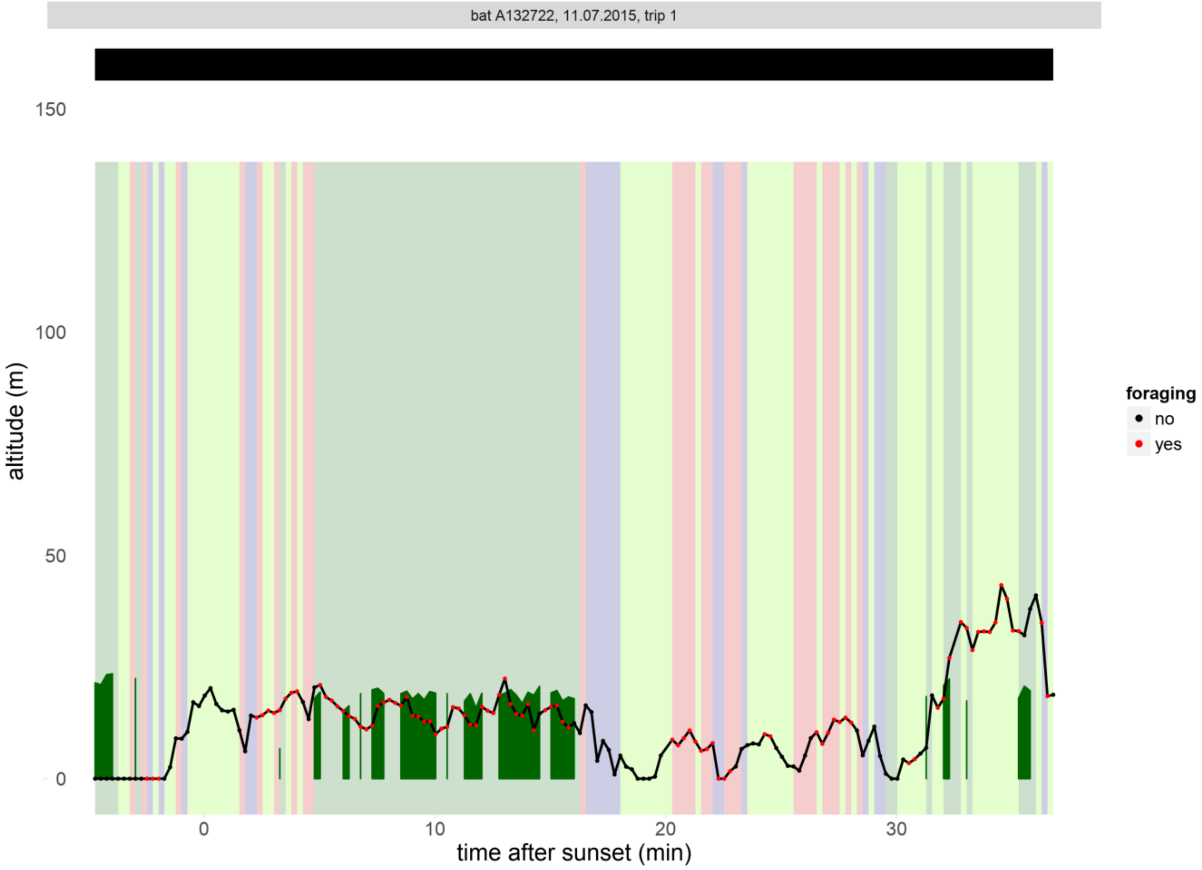
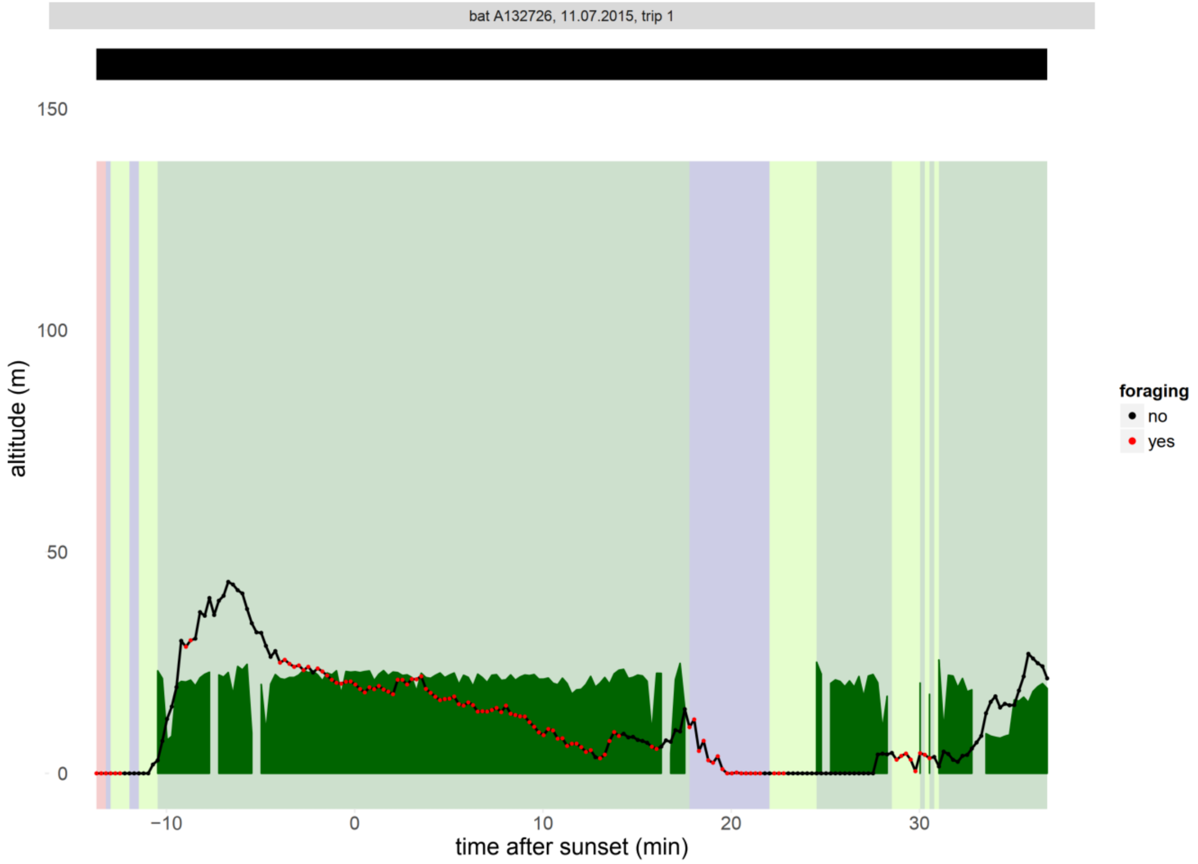
100
50
0
10
20
30
40
50
60
time after sunset (min)
foraging
no
yes


bat A132704, 16.07.2015, trip 1
bat A132704, 16.07.2015, trip 2
bat A132704, 16.07.2015, trip 3
bat A132704, 17.07.2015, trip 1
bat A132704, 17.07.2015, trip 2
altitude (m)
150
100
50
0
0
50
100
310
320
330
340
350
420
430
440
0
10
20
30
40
410
420
430
440
450
time after sunset (min)
foraging
● no
● yes


bat A132722, 11.07.2015, trip 1
altitude (m)
150
100
50
0
0
10
20
30
time after sunset (min)
foraging
● no
● yes



Appendix 2.2 Flight altitude for all recorded tracks. Each dot represents one GPS location, whereas colour depicts whether the observed movement behaviour was associated with foraging. Green ribbons depict the underlying canopy height in forested areas. Background colours depict the different habitat types; blue = water /swamp, red = urban, light-green = open fields, dark-green = forests and bushland / successional growth. The colour of the horizontal bar on top of each trip depicts the moonlight intensity; black = low, yellow = high

Appendix 2.3 Additional file 3. Workflow to create the canopy height model by using the lastool software

LiDAR processing with LAStools software

Normalize height, classify points:

txt2las: create laz-files from xyz files for the single pulse return layers

lastile: cut the floor pulses into smaller pieces to set class to ground (as proposed by data provider)

las2las: classify all points from the floor tiles as ground (-set_classification 2)

las2las: set number of return to "first" or 3 or 5 (first return, last return unclassified, last pulse ground) for later dsm calculation (-set_return_number first, 3, 5)

lasmerge: merge the classified floor tiles again

lasmerge: merge the laz-layers to one single file with all pulses

lastile: cut the all-layers-file into 2000 small tiles (200x200m, less than 1million points each). buffersize 15m to facilitate classifications later.

lasheight: define height above ground for all non-ground points. drop points below 0m and above 50m. Tick "replace-z", i.e. take the calculated height as z-coordinate. store z in user data

lasclassify: classify building and vegetation automatically. "include gutters" and "no tiny buildings". search area size 2, building planarity 0.08, forest ruggedness 0.35, ground offset 2.

Merge tiles:

lastile: remove buffer

lasmerge: merge tiles without buffer

Metrics:

lasinfo: first pulse density 1.98/m², spacing 0.71m

lasinfo: all points density 2.88/m², spacing 0.59m

lasinfo: only vegetation density 2.64/m², spacing 0.62m

Create Canopy Height Model (Raster) following Martin Isenburgs Tutorial at https://rapidlasso.com/category/tutorials/page/2/ :

las2dem: tiles without buffer, -drop_z_above 0.1 (only ground points, real dem) -step 0.62 (spacing of vegetation points to be used throughout workflow)

lasthin: tiles without buffer, -subcircle 0.2 -highest -step 0.31 (use highest point within half point spacing and draw a circle with radius 0.2m around). output as laz file, will be used for the further chm-strata

las2dem: thinned laz, -step 0.62 -kill 1 (all strata) output as .bil

las2dem: thinned laz, -step 0.62 -kill 1 -drop_z_below 2...5...10...15...20...25...30...35 output as .bil (chm for different strata)

lasgrid: input all .bil files created before -i .../*.bil -merged (merge all the files!) -highest (always take highest point) -step 0.62 -false -set_min_max 0 50 (use false coloring, set color range according to min-max values of recorded heights)

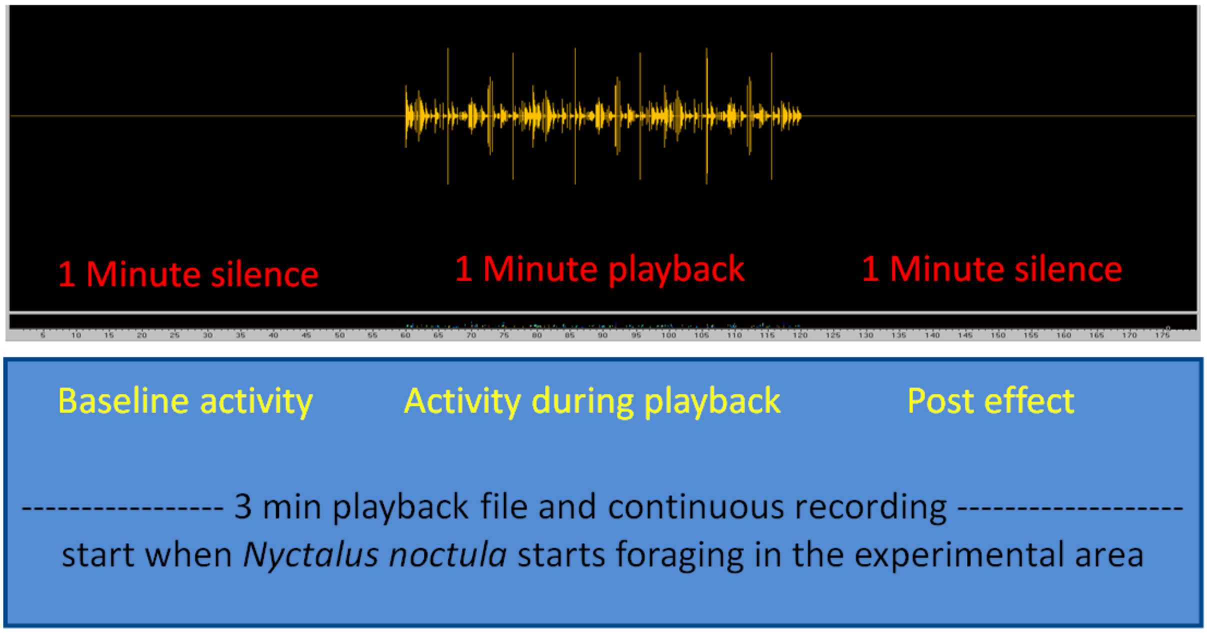
APPENDIX CHAPTER TWO

Appendix 3.1 Playback specifications

Playback files consisted of three phases: i) one minute of silence during which we recorded the baseline activity, ii) one minute of broadcasting the respective playback files to record potential responses of Nyctalus noctula in terms of changes in activity, iii) one minute of silence to record potential post effects of the playback (Fig. A3.1.1). The one minute playback phases with simulated hunting activity consisted of several feeding buzzes of either *N. noctula* or *P. nathusii*, starting with a few search phase calls. The calls for the playbacks were recorded at different locations in the study area in 2014 by Heim and colleagues (2017), and at known hunting grounds in and around Berlin in 2016 by ourselves. We constructed sound files of 20 s length by merging single feeding buzzes with a good signal to noise ratio and looped these files three times to reach a total playback length of 60 s. Feeding buzz rate was roughly around 1 Hz. We then applied mid-pass filters around the respective frequencies of the different playback types and normalized the records such that the loudest calls reached 35% of the maximum amplitude.

For the early season, we used unique files for each night. In the second season, we used the same files as in the first season when recording at the same site again. We created all sound files with the software SasLabPro (Avisoft Bioacoustics, Berlin).

During the experiment, we recorded acoustic bat activity with an omnidirectional ultrasonic microphone (FG Electret, Knowles inc. USA / Philadelphia) that was connected to a laptop computer via an USG 416Hb recording device (Avisoft Bioacoustics, Berlin, Germany). Recordings had a sampling rate of 250 kHz and a depth of 16 bit. For broadcasting of playbacks, we used an ultrasonic speaker with integrated signal converter and amplifier (USG Player BL Light, Avisoft Bioacoustics) connected to the same laptop. Both, recording and playback were operated with the software Recorder USGH (Avisoft Bioacoustics). At each site, we aimed to broadcast three different playback types in random order. These were i) recordings of foraging conspecifics (*N. noctula*), ii) recordings of foraging heterospecifics (*P. nathusii*), iii) a control sound in form of a sine tone undulating between the main frequencies of the both aforementioned species (20 to 40 kHz). Both, microphone and speaker were mounted on 3 m poles and directed towards the open water. The speaker was located directly at the shoreline of the waterbody and set to a maximum output level without clipping (sound pressure level approx. 102 dB at 10 cm distance). We placed the microphone a few centimetres behind the speaker to avoid overload of the sound recordings (Fig. A3.1.2)



---------------- 3 min playback file and continuous recording ------------------
start when *Nyctalus noctula* starts foraging in the experimental area

Fig A3.1.1 Scheme of the experimental treatment

Fig. A3.1.2 Photograph of the experimental setup. The microphone was mounted on the right pole, the speaker was placed a few centimetres in front of the microphone (middle pole). The insect trap was about five metres apart from microphone and speaker, on the left pole.

Appendix 3.2 – Estimation of experimental area and subsequent data cleaning

Our acoustic analysis sometimes revealed a steep drop in bat activity, indicating that bats had left the area during the playback trials during any of the three phases (i.e. pre-phase, playback, post-phase). We excluded these trials from the analysis since in these cases we could not proof unambiguously that focus animals were foraging. Therefore, we determined the radius around our speaker at which sound pressure of the playbacks dropped to 0 dB. For 40 kHz which is the main frequency of the highest used calls from *P. nathusii*, a source level of 100 dB at 10 cm distance, medium temperature of 16 °C, and medium relative air humidity of 69%, this radius equals roughly 45 m (for calculation see Stilz 2004). Given that bats would roughly fly with a speed of 5 m/s during foraging, they could cross this area within 18 s. To be sure that bats were continuously in the vicinity of the experimental area, we applied a moving window of 19 s to the timeline of our recordings. Subsequently, we excluded recordings from our analyses which did not have *N. noctula* calls within the moving window continuously. This resulted in the analyses of 57 out of 95 playback trials. This relatively large number of excluded files comes from the fact that bats often used the smaller waterbodies only for rather short foraging bouts before they continued their flight to probably more promising hunting grounds. Subsequently, we have several sites where we could not broadcast or analyse all three playback types.

Appendix 3.3 Numbers and masses of parataxonomic insect groups for the respective recording sites and seasons.

misc = Insects other than Coleoptera, Lepidoptera, or Trichoptera. These were mainly Diptera, especially Chironomidae and Mosquito-like insects

col = Coleoptera

lepi = Lepidoptera

trich = Trichoptera

Numbers in column names depict the different size classes:

3 = body length < 3 mm

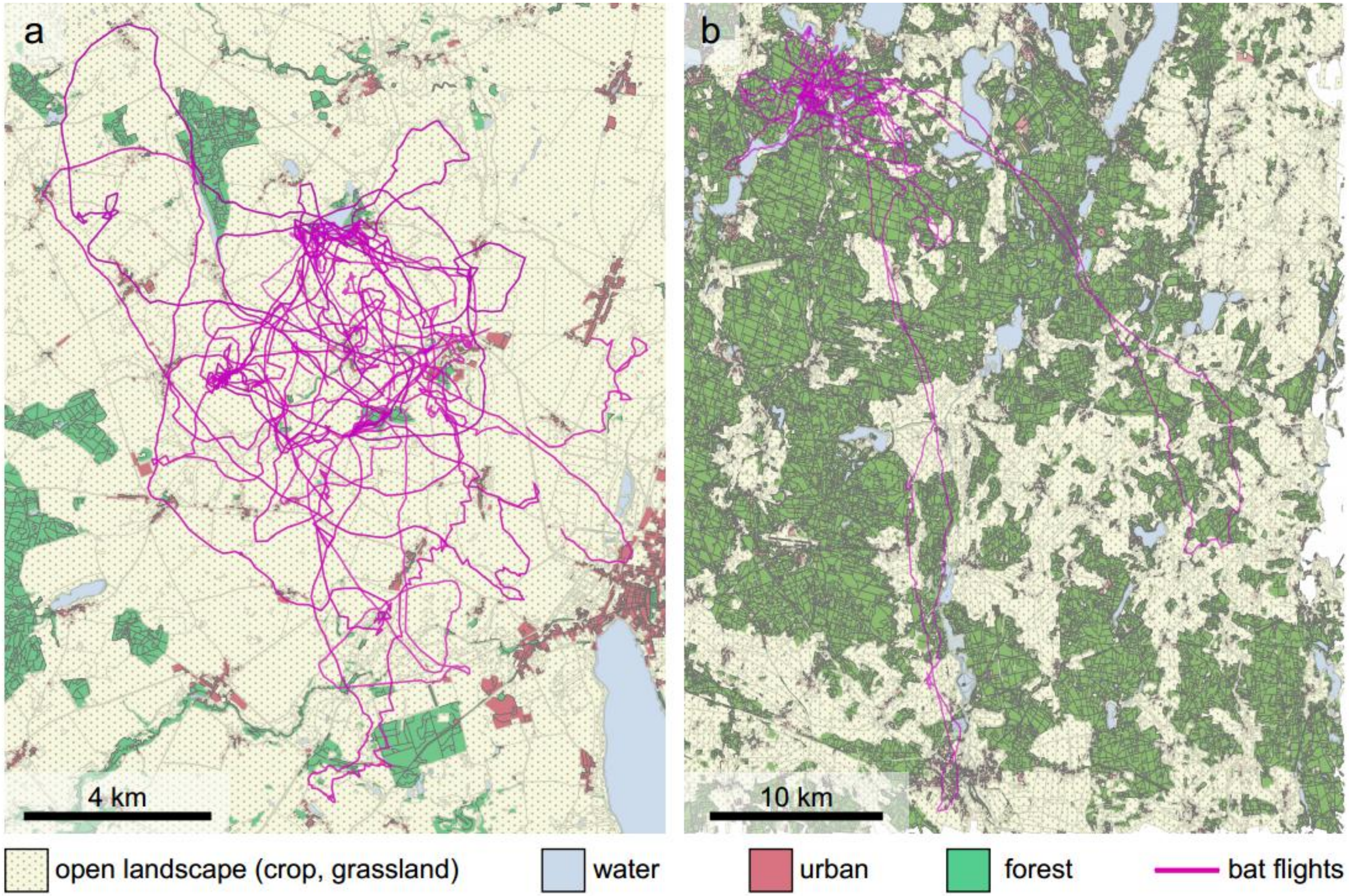
6 = body length between 3 and 6 mm

9 = body length between 6 and 9 mm

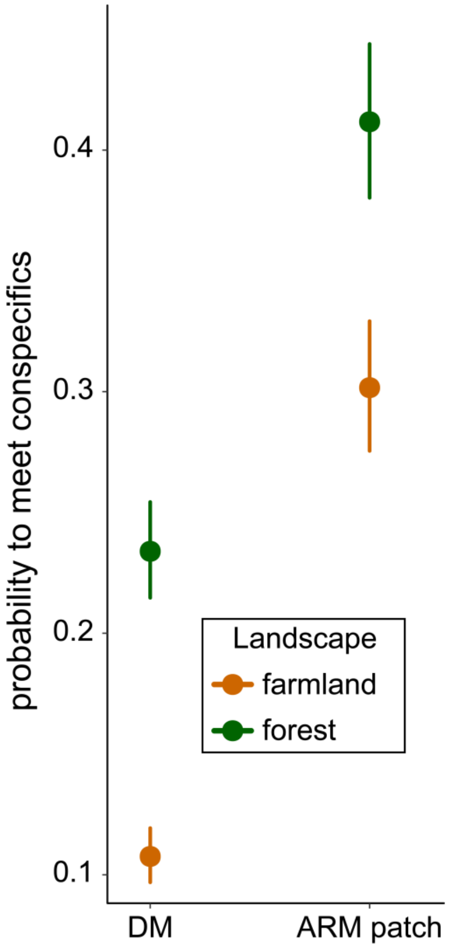
12 = body length > 9 mm

date	**location**	**season**	**misc12**	**misc9**	**misc6**	**misc3**	**col12**	**col9**	**col6**	**col3**	**lepi**	**trich**	**sum no**	**misc12 mass**	**misc9 mass**	**misc6 mass**	**misc3 mass**	**col12 mass**	**col9 mass**	**col6 mass**	**col3 mass**	**lepi mass**	**trich mass**	**sum mass**
6/12/2016	1-2	early	1	12	15	28	0	0	0	0	0	0	56	2.4	10.0	4.4	2.5	0.0	0.0	0.0	0.0	0.0	0.0	19.2
6/12/2016	1-1	early	0	0	13	10	0	0	0	0	0	0	23	0.0	0.0	3.8	0.9	0.0	0.0	0.0	0.0	0.0	0.0	4.6
6/20/2016	2-1	early	0	8	11	20	0	0	0	0	0	0	39	0.0	6.7	3.2	1.8	0.0	0.0	0.0	0.0	0.0	0.0	11.6
6/22/2016	4-2	early	0	55	22	22	0	2	25	18	0	0	144	0.0	45.9	6.4	1.9	0.0	7.5	19.9	4.9	0.0	0.0	86.4
6/22/2016	4-1	early	0	48	132	1395	0	7	345	168	0	0	2095	0.0	40.0	38.2	121.8	0.0	26.1	274.5	45.8	0.0	0.0	546.5
6/23/2016	5-1	early	1	18	102	295	1	3	167	156	0	0	743	2.4	15.0	29.6	25.8	13.1	11.2	132.9	42.5	0.0	0.0	272.3
6/23/2016	5-2	early	3	449	1205	500	3	367	2205	786	0	0	5518	7.2	280.4	351.4	50.5	39.2	1196.3	2115.0	161.9	0.0	0.0	4201.9
7/12/2016	6-1	early	0	0	4	1	0	0	1	0	2	0	8	0.0	0.0	1.2	0.1	0.0	0.0	0.8	0.0	370.2	0.0	372.2
7/14/2016	7-2	early	2	32	3	7	0	0	0	0	1	0	45	4.8	26.7	0.9	0.6	0.0	0.0	0.0	0.0	25.2	0.0	58.2
7/14/2016	7-1	early	3	4	9	3	0	0	0	0	1	0	20	7.2	3.3	2.6	0.3	0.0	0.0	0.0	0.0	28.0	0.0	41.4
7/15/2016	8-2	early	1	14	1	7	0	0	0	0	2	0	25	2.4	11.7	0.3	0.6	0.0	0.0	0.0	0.0	58.4	0.0	73.4
7/15/2016	8-1	early	20	6	82	27	0	0	1	0	0	0	136	47.8	5.0	23.8	2.4	0.0	0.0	0.8	0.0	0.0	0.0	79.7
7/27/2016	10-1	early	338	30	35	74	0	0	308	10	0	0	795	613.6	14.2	9.6	6.6	0.0	0.0	294.8	2.4	0.0	0.0	941.2
7/28/2016	11-1	early	11	48	20	16	0	2	63	12	5	0	177	26.3	40.0	5.8	1.4	0.0	7.5	50.1	3.3	203.4	0.0	337.7
8/3/2016	12-1	early	0	15	8	3	0	0	2	0	1	0	29	0.0	12.5	2.3	0.3	0.0	0.0	1.6	0.0	103.7	0.0	120.4
8/4/2016	13-1	early	1	4	8	11	0	0	0	5	0	0	29	2.4	3.3	2.3	1.0	0.0	0.0	0.0	1.4	0.0	0.0	10.4
8/8/2016	14-2	early	2	17	77	87	0	4	7	2	1	0	197	4.8	14.2	22.3	7.6	0.0	14.9	5.6	0.6	46.2	0.0	116.1
8/8/2016	14-1	early	0	0	12	4	0	1	1	0	0	0	18	0.0	0.0	3.5	0.4	0.0	3.7	0.8	0.0	0.0	0.0	8.4
8/9/2016	15-2	early	0	1	20	155	0	0	0	0	1	0	177	0.0	0.8	5.8	13.5	0.0	0.0	0.0	0.0	32.8	0.0	53.0
8/9/2016	15-1	early	0	0	3	2	0	0	0	0	0	0	5	0.0	0.0	0.9	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.0
8/10/2016	16-2	early	0	0	1	0	0	0	0	0	0	0	1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
8/10/2016	16-1	early	0	2	3	61	0	0	0	0	0	0	66	0.0	1.7	0.9	5.3	0.0	0.0	0.0	0.0	0.0	0.0	7.9
8/11/2016	17-2	early	0	0	3	24	0	0	0	0	0	0	27	0.0	0.0	0.9	2.1	0.0	0.0	0.0	0.0	0.0	0.0	3.0
sum	all	early	383	763	1789	2752	4	386	3125	1157	14	0	10373	721.0	531.3	520.1	247.3	52.2	1267.2	2896.7	262.7	867.9	0.0	7366.4

date	**location**	**season**	**misc12**	**misc9**	**misc6**	**misc3**	**col12**	**col9**	**col6**	**col3**	**lepi**	**trich**	**sum no**	**misc12 mass**	**misc9 mass**	**misc6_mass**	**misc3 mass**	**col12 mass**	**col9 mass**	**col6 mass**	**col3 mass**	**lepi mass**	**trich mass**	**sum mass**
8/29/2016	15-2	late	0	12	27	385	1	0	31	2	2	1	461	0.0	10.0	7.8	33.6	13.1	0.0	24.7	0.6	182.4	29.8	301.8
8/29/2016	15-1	late	0	1	51	571	0	3	11	8	1	0	646	0.0	0.8	14.8	49.9	0.0	11.2	8.8	2.2	22.5	0.0	110.1
8/30/2016	1-2	late	0	119	53	67	0	0	11	2	0	0	252	0.0	99.2	15.4	5.9	0.0	0.0	8.8	0.6	0.0	0.0	129.7
8/30/2016	1-1	late	7	21	40	190	0	0	1	0	1	0	260	16.7	17.5	11.6	16.6	0.0	0.0	0.8	0.0	18.9	0.0	82.1
8/31/2016	12-1	late	3	3	10	31	0	0	35	14	1	0	97	7.2	2.5	2.9	2.7	0.0	0.0	27.8	3.8	18.0	0.0	65.0
8/31/2016	13-1	late	1	8	7	45	0	0	2	0	3	1	67	2.4	6.7	2.0	3.9	0.0	0.0	1.6	0.0	55.1	12.3	84.0
9/1/2016	7-2	late	0	10	51	130	0	1	48	51	1	0	292	0.0	8.3	14.8	11.4	0.0	3.7	38.2	13.9	23.7	0.0	114.0
9/1/2016	7-1	late	1	11	17	53	1	2	101	46	0	0	232	2.4	9.2	4.9	4.6	13.1	7.5	80.4	12.5	0.0	0.0	134.5
9/5/2016	4-2	late	0	0	1	38	0	0	0	1	0	0	40	0.0	0.0	0.3	3.3	0.0	0.0	0.0	0.3	0.0	0.0	3.9
9/5/2016	4-1	late	0	3	5	55	0	0	0	0	0	0	63	0.0	2.5	1.5	4.8	0.0	0.0	0.0	0.0	0.0	0.0	8.8
9/6/2016	8-2	late	1	0	11	12	0	1	7	1	1	2	36	2.4	0.0	3.2	1.1	0.0	3.7	5.6	0.3	16.3	21.4	53.9
9/6/2016	8-1	late	3	2	3	15	0	1	10	7	1	0	42	7.2	1.7	0.9	1.3	0.0	3.7	8.0	1.9	3.1	0.0	27.7
9/7/2016	14-2	late	0	6	9	47	0	0	28	0	0	0	90	0.0	5.0	2.6	4.1	0.0	0.0	22.3	0.0	0.0	0.0	34.0
9/7/2016	14-1	late	0	21	51	226	0	0	15	1	0	0	314	0.0	17.5	14.8	19.7	0.0	0.0	11.9	0.3	0.0	0.0	64.2
9/8/2016	5-2	late	0	23	69	254	0	81	6461	185	0	0	7073	0.0	13.8	23.6	37.4	0.0	231.5	3569.5	39.2	0.0	0.0	3914.8
9/8/2016	5-1	late	20	62	80	470	1	12	408	36	1	1	1091	47.8	51.7	23.2	41.1	13.1	44.8	324.6	9.8	27.2	12.1	595.2
9/13/2016	6-1	late	0	0	0	5	0	0	0	0	0	0	5	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4
9/14/2016	10-1	late	1	41	60	603	0	0	12	6	0	0	723	2.4	34.2	17.4	52.7	0.0	0.0	9.6	1.6	0.0	0.0	117.8
9/14/2016	11-1	late	0	12	26	248	0	0	72	23	0	0	381	0.0	10.0	7.5	21.7	0.0	0.0	57.3	6.3	0.0	0.0	102.7
9/27/2016	16-2	late	0	0	3	8	0	0	0	0	0	0	11	0.0	0.0	0.9	0.7	0.0	0.0	0.0	0.0	0.0	0.0	1.6
9/27/2016	16-1	late	0	1	1	10	0	0	0	1	0	0	13	0.0	0.8	0.3	0.9	0.0	0.0	0.0	0.3	0.0	0.0	2.3
9/28/2016	2-1	late	0	0	0	10	0	0	0	0	0	0	10	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.9
9/28/2016	17-2	late	0	6	1	65	0	0	0	0	0	0	72	0.0	5.0	0.3	5.7	0.0	0.0	0.0	0.0	0.0	0.0	11.0
sum	all	late	37	362	576	3538	3	101	7253	384	12	5	12271	88.4	296.4	170.5	324.2	39.2	306.0	4199.5	93.4	367.2	75.5	5960.3



Appendix 4.1 Habitat maps of the two study sites farmland (a) and forested landscape (b) with movement tracks from 27 common noctule bats *Nyctalus noctula*, recorded by GPS loggers



Appendix 4.2 Effect plot from a binomial generalized linear mixed model showing the probability that the tagged noctule bat will encounter conspecifics, depending on landscape and movement mode. DM: directed movement, straight flight. ARM patch: area restricted movement leading to the formation of a spatially well-defined foraging patch. Bars depict the 95 % confidence intervals of the effect estimates.

PUBLICATION LIST

The following publications are part of this thesis:

Roeleke, M., Johannsen, L. & Voigt, C.C. (2018). How bats escape the competitive exclusion principle - Seasonal shift from intraspecific to interspecific competititon drives space use in a bat ensemble. *Frontiers in Ecology and Evolution*, 6, 101.

Roeleke, M., Teige, T., Hoffmeister, U., Klingler, F. & Voigt, C.C. (2018). Aerial-hawking bats adjust their use of space to the lunar cycle. *Movement Ecology*, 6, 11.

DECLARATION OF AUTHORSHIP

I hereby declare that I prepared this thesis independently under the guidance of my supervisor. All direct or indirect sources used are given as references. All contributions of co-authors are acknowledged.

Berlin, 09.02.2019 Manuel Roeleke