Resource selection and flight activity of Leisler's bats (*Nyctalus leisleri*) in Gundelfinger Wald during mating season

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”Flatter flatter Fledermaus,
flatterst in die Nacht hinaus.
Heute willst du mehr erleben,
als nur an der Decke kleben.

Du flatterst los geschwind und leise,
nimm mich mit auf deine Reise.
Wohin du fliegst das zeige mir,
flieg nur voraus ich folge dir.

...

Das war eine tolle Nacht,
der Flug mit dir hat Spaß gemacht.
Sag werden wir uns wiedersehen,
heut’ Abend nach dem schlafen gehen?”
[Kratzke, 2015]

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Abstract

Sex-specific behaviour as a result of asymmetric reproductive strategies is a common phenomenon in mammals. Most temperate bats, including Leisler's Bats (*Nyctalus leisleri*), are sexually segregated during breeding season in summer. Sex-specific behavioural patterns are well studied during this reproductive phase. During mating season in autumn, both sexes share resources such as roost sites. However, little is known about their nightly behaviour during this time of the year.

This study investigated resource selection and flight activity patterns of *N. leisleri* during mating season by using radio telemetry. Three females and four males were radio tracked for several nights each. Space use was analysed with a resource selection function (RSF) including habitat, hydrological, human disturbance and topographical variables. Flight activity during the course of the night was modelled with a generalised additive model (GAM) taking into account weather conditions.

Sex-specific effects were found for most of the spatial parameters examined. Home ranges and maximum distances from roost sites were two to three times larger for females compared to males. The overall effects of habitat, distance to urban area, distance to forest edge, slope and aspect on resource selection were sex-specific, while the effects of distance to day roost and distance to major roads differed only in effect size. For males, small distance to their roost sites and flat terrain were the main drivers of resource selection, while for females, all variables were of equal importance. Moreover, flight activity patterns throughout the night differed between sexes. Of the weather variables investigated, temperature had the strongest influence on flight activity, even though wind speed, precipitation and wind direction had a significant effect too.

These results indicate that, besides foraging behaviour, courtship behaviour of males has a strong influence of spatial and temporal activity patterns of Leisler's Bats during mating season. Even though females and males share roosts at least for short times, resource partitioning occurs at night. The findings of this study underline the seasonal variations in sex-specific resource requirements of bats. These are important to know in order to design effective conservation strategies for entire populations.

Zusammenfassung

Geschlechtsspezifisches Verhalten aufgrund asymmetrischer Fortpflanzungsstrategien ist ein häufiges Phänomen bei Säugetieren. Weibliche und männliche Fledermäuse der gemäßigten Zonen, darunter auch der Kleinabendsegler (*Nyctalus leisleri*), verbringen die Wochenstubenzeit im Sommer räumlich getrennt voneinander. Geschlechtsspezifische Verhaltensmuster während dieser Reproduktionsphase sind gut erforscht. Zur Paarungszeit im Herbst hingegen teilen sich beide Geschlechter Ressourcen wie zum Beispiel Tagesquartiere. Über ihr nächtliches Verhalten zu dieser Jahreszeit ist jedoch wenig bekannt.

Die vorliegende Studie untersuchte die Ressourcenauswahl und Flugaktivität von *N. leisleri* während der Paarungszeit mithilfe von Radiotelemetrie. Drei Weibchen und vier Männchen wurden jeweils für mehrere Nächte verfolgt. Die Raumnutzung wurde mit einer "resource selection function" (RSF) analysiert und untersuchte die Einflussvariablen Habitat sowie hydrologische, anthropogene und topographische Faktoren. Flugaktivität im Verlauf der Nacht wurde mithilfe eines "general additive model" (GAM) unter der Einbeziehung der Wetterbedingungen modelliert.

Für die meisten untersuchten Raumnutzungsparameter wurden geschlechtsspezifische Effekte festgestellt. Die Streifgebiete und die maximalen Distanzen zu den Tagesquartieren waren bei Weibchen zwei- bis dreimal größer als bei Männchen. Die Einflüsse des Habitats, der Entfernungen zu Siedlungsgebieten und Waldrändern, der Hangneigung und der Exposition auf die Ressourcenauswahl waren geschlechtsspezifisch, wohingegen die Einflüsse der Distanz zum Tagesquartier und zu größeren Straßen sich nur in der Effektgröße unterschieden. Für Männchen waren geringe Distanzen zu ihren Quartieren und flaches Gelände die Haupteinflussfaktoren der Ressourcenauswahl, bei Weibchen im Gegensatz waren alle Faktoren gleichermaßen einflussreich. Des Weiteren unterschieden sich die Muster der Flugaktivität beider Geschlechter im Verlauf der Nacht. Von den untersuchten Wetterfaktoren hatte Temperatur den größten Einfluss auf die Fledermausaktivität, obwohl auch Windgeschwindigkeit und Niederschlag sowie die Windrichtung einen signifikanten Einfluss hatten.

Diese Ergebnisse zeigen, dass neben dem Jagdverhalten auch das männliche Balzverhalten einen großen Einfluss auf räumliche und zeitliche Aktivitätsmuster der Kleinabendsegler zur Paarungszeit hat. Auch wenn Weibchen und Männchen ihre Tagesquartiere zumindest für kurze Zeit gemeinsam nutzen, findet während der Nacht Ressourcenteilung statt. Die Erkenntnisse dieser Studie betonen die saisonale Variation geschlechtsspezifischer Ressourcenanforderungen von Fledermäusen. Diese zu kennen ist essentiell, um effektive Schutzstrategien für gesamte Populationen zu entwerfen.

Chapter 1

Introduction

1.1 Sex-specific behavioural differences

Sex-specific differences in behaviour are known for many species of mammals. These behavioural differences are based on varying social and resource selection strategies and mainly reflect asymmetric reproductive strategies and parental investment [Trivers, 1972]. In order to maximize lifetime reproductive success, fitness costs and benefits are optimized by both sexes in different ways, resulting in differing activity budgets. Female mammals maximise fitness by investing more energy in breeding fewer offspring, as they are physiologically limited in the amount of offspring they can produce. Males in contrast attempt to secure as many mating opportunities as possible [Andersson, 1994], potentially in trade-off with other activities such as foraging [Alberts et al., 1996; Miquelle, 1990]. Sex-specific allocation of time to specific activities may result in sexual segregation in terms of resource use or spatial organization [Conradt, 1998; Ruckstuhl and Neuhaus, 2000, 2005].

Sexual segregation is common for temperate bats in summer. While females aggregate in large nursery colonies, males live in separate groups or solitary [Senior et al., 2005]. Depending on sex-specific requirements, sexual segregation is thought to reflect spatial variation in the distribution of adequate roosting and foraging areas [Barclay, 1991; Grindal et al., 1999]. Sex-specific differences in terms of roost selection, foraging activity and use of torpor are well documented during this time of the year [Grindal et al., 1999; Kerth and Morf, 2004; Dietz and Kalko, 2007; Broders and Forbes, 2004, e.g.]. Behavioural differences can be ascribed to higher energetic costs of females as they rear their offspring in summer [Kurta and Kunz, 1987; McLean and Speakman, 2000]. At the same time, males have low energetic demands associated only with self-maintenance and spermatogenesis [Racey and Entwistle, 2000].

During mating season, the degree of sexual segregation decreases and many bat species form mixed-sex aggregations [Furmankiewicz and Altringham, 2007; Parsons and Jones, 2003; Rivers et al., 2005; Veith et al., 2004]. However, sex-specific strategies are likely to remain. Females need to fill up their energy storages and to allocate fat reserves for migration and hibernation, while males in contrast may migrate over shorter distances or not at all and instead invest a lot of energy in mating and courtship behaviour [Fleming et al., 2003; Ibanez et al., 2009]. These asymmetric reproductive strategies are known, however, little is known about the sex-specific variations in activity budgets and strategies of resource use of bats during mating season.

1.2 Resource use and activity patterns of bats

Investigations of resource use by bats mainly focus on their habitat requirements. Modelling approaches are carried out at different scales, ranging from roost site or foraging site selection to a landscape scale [Bellamy and Altringham, 2015; Frey-Ehrenbold et al., 2013; Jaberg and Guisan, 2001; Rainho and Palmeirim, 2011; Roscioni et al., 2013; Sattler et al., 2007]. Besides habitat, ecological meaningful parameters include hydrological, topographical or human disturbance variables. Rainho and Palmeirim [2011] demonstrated the importance of distance parameters such as distance to roost site when modelling foraging habitat selection. Human disturbance factors relevant for bats include artificial lights and roads. [Abbott et al., 2012; Lesinski et al., 2011; Siemers and Schaub, 2011]. However, the response of bats on these factors seems to be species-specific [Kerth and Melber, 2009; Lacoeuilhe et al., 2014; Mathews et al., 2015].

Activity of bats is known to vary during the course of the night and to be influenced by weather conditions. Generally, the phase of highest activity is a short time after sunset, when insect abundance is highest and predation risk decreases in diminishing light [Ciechanowski et al., 2007; Rachwald et al., 2001; Rydell et al., 1996]. Low temperatures, strong winds and rain reduce flight activity [Arnett, 2005; Ahlén et al., 2007; Erickson and West, 2002]. When the conditions are very unfavourable, emergence from the roost may be delayed or even inhibited.

1.3 Study species

Leisler's bat (*Nyctalus leisleri*, Kuhl, 1817) is a medium-sized European forest bat (forearm length of 39-47mm) [Schober and Grimmberger, 1998; Dietz et al., 2007; Bogdanowicz and Ruprecht, 2004]. It is widespread only in Ireland and has a patchy distribution over the whole rest of Europe, reaching until north-west Africa and south-west Asia [Bogdanowicz and Ruprecht, 2004]. While the northern parts of Europe are only used in summer for nursery, the species migrates over long distances to swarming and hibernation sites in the South and West of Europe [Hutterer, 2005]. However, this migration behaviour seems to be sex-biased, with males travelling shorter distances or even staying in wintering areas [Fleming et al., 2003]. There are recordings of nursery colonies or individuals for almost all of Germany, while swarming and hibernating sites are known from south-western Germany [Schorcht and Boye, 2004; Kretzschmar et al., 2005]. Population sizes and developments are largely unclear [Schorcht and Boye, 2004], but due to the species wide distribution, it is listed under the category "least concern" [Hutson et al., 2008].

Leisler's bat is typically associated with forests [Meschede and Heller, 2000], roosting predominantly in natural tree cavities in broad-leaf forests [Ruczyński and Bogdanowicz, 2005; Ruczyński et al., 2010]. However, buildings may also be used for roosting [e.g. Shiel et al., 1999; Waters et al., 1999] as well as bat boxes in broadleaved or coniferous forests if natural roosts are rare [Dietz et al., 2007; Schorcht and Boye, 2004]. *N. leisleri* is an aerial hawker, hunting during flight in the open air-space. High wing loadings and aspect ratios allow a fast and efficient flight [Norberg and Rayner, 1987]. Foraging areas can be located several kilometers away from roost sites. Besides forests, a wide variety of different habitats are known to be used: edge structures, pastures, water, farmland and settlements [e.g. Harbusch et al., 2002; Russo and Jones, 2003; Szentkuti, 2006; Vaughan et al., 1997]. However, evidence of a distinct habitat preference is lacking, as habitat preferences varied remarkably between studies. Human disturbance parameters such as major roads are supposed to not affect the species negatively [Waters et al., 1999], presumably due its flight and foraging behaviour [Dietz et al., 2007]. Street lights are assumed to even attract Leisler's bats [Mathews et al. 2015; Shiel and Fairley 1998; 1999; Waters et al. 1999; but see Lacoeuilhe et al. 2014].

Nightly activity of the species is mainly characterized by a peak during the first part of the night. Thereafter, presumably depending on temperature, a second peak later on in the night is possible [Shiel and Fairley, 1998; Fuhrmann et al., 2002; Waters et al., 1999]. There is little information about the influence of weather conditions other than temperature on the species.

Mating season of *N. leisleri* is in autumn, roughly from mid August until mid October [Ohlendorf and Ohlendorf, 1998]. While females generally migrate from nursery to hibernation sites during this time [Hutterer, 2005], males occupy roost sites for mating, often at exposed positions such as hills [Ohlendorf and Ohlendorf, 1998]. From there, they try to attract as many females as possible from the north-east to south-west migration routes in order to form temporary harems [Dondini and Vergari, 2009]. Males spend a majority of the night with calling for females, either from one of their roosts, stationary from a tall tree, or during flight when they defend their territory [Ohlendorf and Ohlendorf, 1998; Von Helversen and Von Helversen, 1994]. It is assumed that female migration strongly influences mating behaviour, as it prevents formation of stable harems over time [Dondini and Vergari, 2009; Ohlendorf and Ohlendorf, 1998]. There is a first evidence that behaviour of *N. leisleri* during mating season differs depending on sex: Fuhrmann et al. [2002] radio tracked one male and one female in August and described differences home range size, habitat use and activity patterns.

1.4 Aim of the study

This study focuses on sex-specific behavioural differences of *N. leisleri* during mating season. As a result of differing reproductive strategies, resource use and activity patterns are hypothesised to differ between sexes.

In detail, the aim of this study was

(1) to describe the nightly behaviour of males and females during mating season,
(2) to investigate drivers of resource selection and to reveal sex-specific differences of these, and
(3) to analyse flight activity of females and males during the course of the night taking into account the influence of weather conditions.

Radio telemetry is the appropriate method to investigate nightly behaviour of bats, as it allows continuous tracking of individuals [Wilkinson and Bradbury, 1988]. Additionally, behavioural parameters can be assessed separately for both sexes. For this purpose, radio telemetry is in advantage over other sampling methods for bats such as mist netting or indirect detection by ultrasonic detectors that are rather used for inventories or population monitoring [Flaquer et al., 2007; Thomas and West, 1989].

Chapter 2

Methods

In order to investigate sex-specific differences in behaviour of *N.leisleri* during mating season, radio tracking data of individuals captured at a mating colony in south-western Germany was collected. In total, five female and four male individuals were tagged during a period of five weeks in August and September 2015. Of these, three females and four males were radio tracked successfully for several nights (more details on the tracked individuals in Appendix A). Capturing, tagging and radio tracking was conducted with permission of Regierungspräsidium Freiburg, Veterinär- und Lebensmittelüberwachungsbehörde (permit 35-9185.81/G-14/07).

2.1 Study site

Gundelfinger Wald close to Freiburg i. Brsg. (Baden-Württemberg, Germany; 48°3'E 7°52'N) is a forest patch with a size of roughly 500 ha, located on top of a small hill (around 260-350 m.a.s.l). It is known to be used by Leisler's bats as mating and hibernation site [R. Brinkmann, pers. communication]. The forest patch is located between the foothills of the Black forest dominated by coniferous forests and pastures in the east and the Rhine valley dominated by arable land and urban areas in the west. The forest patch itself is a diverse broadleaved forest dominated by beech (*Fagus sylvatica*) with remarkably high proportion of oaks (*Quercus petraea*). The oldest trees reach an age of roughly 200 years, offering many natural tree cavities in old and dead wood. Additionally, more than 50 bat boxes are available as roosting sites for bats, which makes monitoring of the colony feasible.

2.2 Tagging and tracking of bats

Bats were captured by hand from bat boxes during daytime. Until handling, they were kept individually in small cotton bags for short time. Prior to tagging, sex, weight, forearm length and reproductive status of individuals was determined. Marking by forearm banding ensured individual identification of re-catches. Only adult males in a reproductive state and adult females found together in a box with a reproducing male were chosen for the telemetry study.

Radio-transmitters (Ag317, Pip317 or Ag337 PicoPip tags, Biotrack Ltd., Wareham, UK) with a weight of 0.4-0.5 g were attached between the scapulae using medical skin glue (Sauer Hautkleber 50.01, Manfred Sauer GmbH, Lobbach, Germany). The glue was allowed to dry for 10 minutes before individuals were released into the same box where they were found. As recommended by Aldridge and Brigham [1988] and Kenward [1987], tag weight never exceeded 5% of the body mass of an individual. Due to the risk that an animal could loose its tag or fly far away, telemetry was always started during the first night after tagging. It was attempted to track each individual for at least two to three nights. A radio tracking session was a whole night from sunset to sunrise. During this time, a single individual was followed continuously. Radio tracking was mainly done by car. due to a custom-made construction, the direction of the strongest signal could be detected while driving. A three-element Yagi antenna was mounted above the drivers' window of an all-terrain vehicle and connected to a TRX-100-S radio tracking receiver (Wildlife Materials, IL, USA).

Radio tracking of the fast flying bats mainly meant to follow the signal as fast and as close as possible. In order to later on calculate an area where a bat was most likely located, GPS position of observer, compass bearing and relative signal strength were recorded. The latter was measured categorical as reduction of receiver gain to a level where the signal was just detectable and served as approximation of distance between transmitter and reviver (more details about the calculation of location areas in section 2.3.1). Positional fixes were attempted to be recorded every 5 to 10 minutes, depending on signal reception and movement speed of the bat.

When an individual was not moving, the homing-in on the animal method [White and Garrott, 1990] or triangulation were used. Trees, bat boxes or buildings that served as roost were attempted to be identified. A second set of antenna and receiver was used to follow the signal by foot. Triangulation was only used in few cases when an animal was inactive for periods too short to get close enough for homing-in.

Flight activity and periods of resting were recorded to-the-minute. Fluctuations of signal strength indicate movement of the animal during flight, whereas a steady signal indicates that the animal is not moving. One flight was defined by a period of movement between two periods without flight activity (which could be resting in a roost or displaying stationary in the case of males). Periods without transmitter contact were noted in the protocol sheet. Additionally, all animals' day roosts were identified daily for the total lifetime of transmitters (declaration of manufacturer: 11 days).

2.3 Data preparation and analyses

Firstly, location areas of bats were calculated from positional fixes (see section 2.3.1). A number of descriptive parameters of nightly behaviour were computed for females and males separately: home range size calculated as 100% minimum convex polygon (MCP), emergence from day roost, number of flights per night, duration of single flights and total time with and without flight activity during one night. These data were used for general description of bat behaviour. Further, in order to identify drivers of resource selection, a resource selection function (RSF) was used to compare used locations with those available in the study area (see section 2.3.2). Lastly, flight activity of females and males during the course of the night was analysed taking into account the influence of weather conditions (see section 2.3.3).

2.3.1 Calculation of bat locations

To calculate location areas of bats, position of observer, compass bearing of direction and distance between observer and bat were needed respectively. While the first two variables were collected in the field, distance between receiver and transmitter (corresponding to observer and bat) was unknown. Instead, relative signal strength was recorded for each positional fix and used to calculate distance. Correlation between these two variables was modelled with experimentally obtained data of relative signal strength for known distances between transmitter and receiver. To simulate a flying bat, a transmitter was attached to a pole and hold up by a person (3 and 5 m above ground for two sessions, respectively). GPS positions and signal strengths were recorded by a second person in a car with antenna mounted as during telemetry nights, while the person holding the transmitter was allowed to move in a radius of two meters around a particular location. Because signal strength was expected to be affected not only by distance to transmitter but to a small extend also by habitat type and topography, the experiment was repeated in the three habitat categories forest, open land (pasture or farmland) and urban area as well as in varying terrain. Trees, buildings or topographical obstacles between transmitter an receiver are likely to attenuate the signal. In order to be representative for locations used by the tagged bats, this experiment was conducted in proximity to Gundelfinger Wald.

Because a non-linear effect of signal strength was expected, generalized additive mixed models (GAMMs)[1] [Wood, 2006]) with signal strength as smoothed term and experimental session as random term were used to model distance (distance was log-transformed to achieve normal distribution of residuals). Only the habitat at the observer's location was known, but not the actual habitat between observer and bat. For this reason, a first model included only relative signal strength as predictor. Predicted distances derived from this model together with the respective observer location and compass bearing allowed to estimate the bats' locations. In order to recalibrate these locations based on the habitat between observer and bat, a second model additionally included habitat as fixed effect (with weights adjusting for variance heterogeneity between habitat levels [Zuur et al., 2007]). Including topography into the model did not improve model fit. Recalibrated distances were predicted from the second model for each habitat category. Finally, habitat proportions along straight lines between estimated bat locations and respective observer locations were extracted from a reclassified digital landscape map (Basis DLM BW [LGL, 2009]) , e.g. 56% forest and 46% open land or 100% urban area. These proportions were used to weight the recalibrated distances for different habitat categories derived from the second model. Summaries and plotted predictions of both models can be found in Appendix C.

A buffer was assigned around each bat location representing the 95% confidence interval. This buffer area represents the area, where a bat most likely was located. As signal strength was recorded categorical, the recording error resulting from rounding to a signal strength level was taken into account for the calculation of buffer size as well as the standard deviation of the model. For the few occasions when triangulation was used, bat location was defined as the intersection point of bearings instead of using the approach described above[2]. A buffer of 50 m was assigned to the intersections points. For short flights around roosts and displaying sites, the spatial mean of an animals roosts was used as bat location with a buffer of 300 m. Ohlendorf and Ohlendorf [1998] and Von Helversen and Von Helversen [1994] reported courtship flights within a 300 m radius around roost sites. Additionally, to account for inaccuracy of GPS locations, buffer size was increased by 15 m for all bat locations.

2.3.2 Resource selection function

A resource selection function (RSF) is defined as any function that is proportional to the probability of use by an organism [Manly et al., 2002]. Spatial units selected by animals are conceived as resources. Predictor variables associated with these spatial units can be regarded as resource variables or covariates. In this study, a RSF is estimated from presence/available data obtained by radio telemetry. Radio telemetry can identify locations used by animals, but the number of possible available locations is infinite. For the RSF, all recorded locations of flying bats were used. Additionally, one location per inactive period was included, in order to avoid pseudo-replication. A 100% MCP was calculated for the locations of all individuals[3]. For each presence location, 50 available locations were randomly created within this MCP enlarged by a buffer equally sized to the biggest bat location buffer[4]. Further, characteristics such as ID, sex and buffer size of presence

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[1] R package *mgcv*

[2] R package *sigloc*

[3] R package *adehabitatHR*

[4] R packages *sp* and *rgeos*

locations were assigned to the corresponding 50 randomly drawn available locations. Presence locations were scored one whereas available locations (as a sample of available resource units) were scored zero in terms of use.

A set of predictor variables was selected a priori based on expected ecological requirements of *N. leisleri*. Besides distance to roost site, habitat, hydrological, topographical and human disturbance variables were chosen (Table 2.1). GIS data from multiple sources was used to extract environmental variables for all presence and available locations[5]. Distances to a point, line or the borders of a polygon feature (namely day roost, road, water, forest edge and urban area) and aspect were calculated for presence and available location points. For distance to urban area and forest edge, negative values were assigned to a point within the urban area or forest, respectively. Aspect was reclassified into five categories: flat (if slope was less than 5°), north, east, south and west. Elevation and slope were calculated for each raster cell within the presence and available location buffers followed by computing the mean value within the buffer. The habitat source layer (Basis DLM BW [LGL, 2009]) was reclassified into new categories, using the dominant category within a buffer for analysis. Reclassification resulted in nine habitat categories: urban area, arable land, pasture, vineyards, fruit trees, broad-leaved forest, mixed forest, coniferous forest and water.

As prevailing statistical model of the RSF, a binomial generalized linear mixed model (GLMM) applying a logistic regression with use as response variable and ID as random term was attempted to be used. Due to low sample size, normality of the random effect was not met and instead, a GLM with ID as fixed effect term was used to account for dependency problems. Due to the use of presence/available data, the GLM should be seen as an estimating function rather than for statistical interference [Boyce et al., 2002]. All predictors shown in table 2.1 were tested for multi-collinearity (correlation coefficient $\geq$ 0.7) [Zuur et al., 2007]. Alternative full models were build by avoiding to include collinear predictors in the same model. Sex was interacted with all environmental variables (all predictors besides ID and observer, table 2.1) to test for sex-specific differences. Additionally, squared terms were included for continuous variables. Model selection was based on the Akaike information criterion (AIC). Using AIC as model selection criterion helps to identify the model that accounts for the most variation with the fewest variables [Burnham and Anderson, 2003]. From the alternative full models, the one with best fit was used and reduced by stepwise backwards selection[6]. Interactions or explanatory variables were dropped until no more lowering of AIC could be achieved. If a variable was dropped but its respective squared term remained in the model, the automated step selection function was stopped and continued manually instead.

For model predictions, the following RSF equation was used:

$$w(x) = exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_i x_i)$$

where $w(x)$ is the relative probability of selection, x is the predictor variable and β is the coefficient of the predictor value obtained by the GLM Manly et al. [2002]. 95% confidence intervals of model predictions were created by drawing random coefficients from 95% confidence intervals of a normal distribution with mean and standard deviation of the respective coefficient and applying them in the RSF equation.

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[5] R packages *raster*, *rgeos* and *geosphere*

[6] R package *stast*

Table 2.1: Predictor variables used to fit a generalized linear model (GLM) in order to analyse resource selection of *N. leisleri* with a resource selection function (RSF). Predictor variables were chosen based on expected ecological requirements of the species.

predictor variable	nature of predictor variable	description	source layer
Distance variable			
dist_dayroost	continuous (0-19970m)	euclidean distance between location point and previous day roost of a bat	
Habitat variables			
habitat	categorial (urban area, arable land, pasture, vineyards, fruit trees, broad-leaved forest, mixed forest, coniferous forest, water)	dominant habitat within a location buffer	Basis DLM BW [LGL, 2009]
dist_forestedge	continuous (-531-1187m)	euclidean distance between a location point and nearest outer forest edge	Basis DLM BW [LGL, 2009]
Human disturbance variables			
dist_road	continuous (0-4516m)	euclidean distance between a location point and nearest major road	Basis DLM BW [LGL, 2009]
dist_urban	continuous (-446-3369m)	euclidean distance between a location point and nearest town or city	Basis DLM BW [LGL, 2009]
Hydrological variable			
dist_water	continuous (0-1021m)	euclidean distance between a location point and nearest water course	watercourses [LUBW, 2015]
Topographical variables			
aspect	categorial (flat, north, east, south, west)	aspect at a location point, flat if slope $<5°$	DEM [LGL, 2009]
elevation	continuous (194-1238m)	mean elevation within a location buffer	DEM [LGL, 2009]
slope	continuous (3-38°)	mean slope within a location buffer	DEM [LGL, 2009]
Others			
ID	categorial (eight different individuals)	individual ID	
sex	categorial (female, male)	sex of an individual	
observer	categorial (three different observers)	name of the observer	

2.3.3 Flight activity model

To investigate the relationship between flight activity and nighttime as well as weather conditions, to-the-minute data of all tracked individuals was used. Every minute when an animal was flying was defined as active whereas minutes when individuals were resting or males were displaying without flight activity were defined as passive. Air temperature and humidity were recorded by data loggers in three meters height close to the day roosts of tracked bats in Gundelfinger Wald. Data of wind speed, wind direction and precipitation were provided by a weather station in Freiburg[7] [LUBW, 2015]. Wind measures were taken in ten meters hight, whereas precipitation was recorded at three meters height. All weather variables were recorded with an interval of 30 minutes. To obtain a value for every measurement of flight activity, weather variables were interpolated linearly for every minute except for wind direction and precipitation, where the closest value was used respectively[8]. Nighttime was calculated as a variable ranging from zero (sunset) to one (sunrise) in order to account for differences in night length throughout the study period.

A binomial generalized additive model (GAM) with nighttime, wind direction and ID as smoothed terms was used to model flight activity[9]. Flight activity was expected to have several peaks in the course of the night, therefore a smoothed term with cubic regression spline and shrinkage factor was appropriate for the predictor nighttime. To detect sex-specific differences in nightly behavior, nighttime was interacted with sex. As wind direction was measured in degrees, a circular regression spline was used. Individual ID was included in the model as random effect smooth. This has the same performance as using a GAMM, but is advantageous in terms of computing speed for larger data sets. Based on expected relationships of flight activity and the predictors temperature, humidity, wind speed and precipitation, both linear and quadratic terms of these were included in the model.

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[7] monitoring station No 4462, Fehrenbachallee 1, 79106 Freiburg

[8] R package *wd*

[9] R package *mgvc*

Chapter 3

Results

3.1 Descriptive statistics of female and male behaviour

General nightly behaviour differed between females and males. Especially females appeared to be restless, some of them roamed over long distances and long periods. Males in contrast spent a lot of time in the forest close to their roost sites. Individuals seldom stayed at a certain area for longer times or visited spots several times. Therefore, identification of distinct foraging areas was only possible in a few cases (e.g. a foraging area was visited several times for short periods by the same male during several nights, but this was an exceptional observation).

Besides the described behavioural differences, several measured parameters differed between sexes: Home range sizes and maximum distances were remarkably larger for females compared to males. In contrast, the number of flights per night was lower for females, whereas the duration of single flights was longer. Further, total time spent flying was higher and, as a result of that, total time without flight activity was lower for females (Table 3.1). Home ranges were variable in size and shape, also within sexes. They overlapped partly between individuals and sexes, whereby overlap occurred mostly in proximity to day roosts (Fig. 3.1). Due to low sample size, these patterns are merely descriptive.

During the study period, *N. leisleri* mostly roosted in bat boxes and natural tree cavities, but females were also located in buildings. Day roosts of females were widespread compared to those of males, which were clustered around the location where they were first found. Both females and males changed their day roosts regularly, using up to seven different day roosts during a maximum monitoring period of 16 days (additional information on day roost use in Appendix B).

Table 3.1: Parameters describing nightly behaviour of three female and four male *N. leisleri* radio tracked continuously for several nights each.

parameter	females		males	
	mean±SD	range	mean±SD	range
emergence from day roost (min after sunset)	17±13	4-39	27±35	3-130
number of flights per night	4±3	1-10	11±8	0-26
duration of flights (min)	59±139	1-560	22±47	1-283
total time of flight activity (min per night)	277±239	38-637	199±113	0-378
total time without flight activity (min per night)	320±253	11-662	407±128	179-680
home range size (km^2)	89.29±82.9	17.4-180	23.7±25.2	5.8-59.9
max. distance from day roost (km)	8.7±7.0	0.5-19.8	4.7±2.5	1.2-9.8

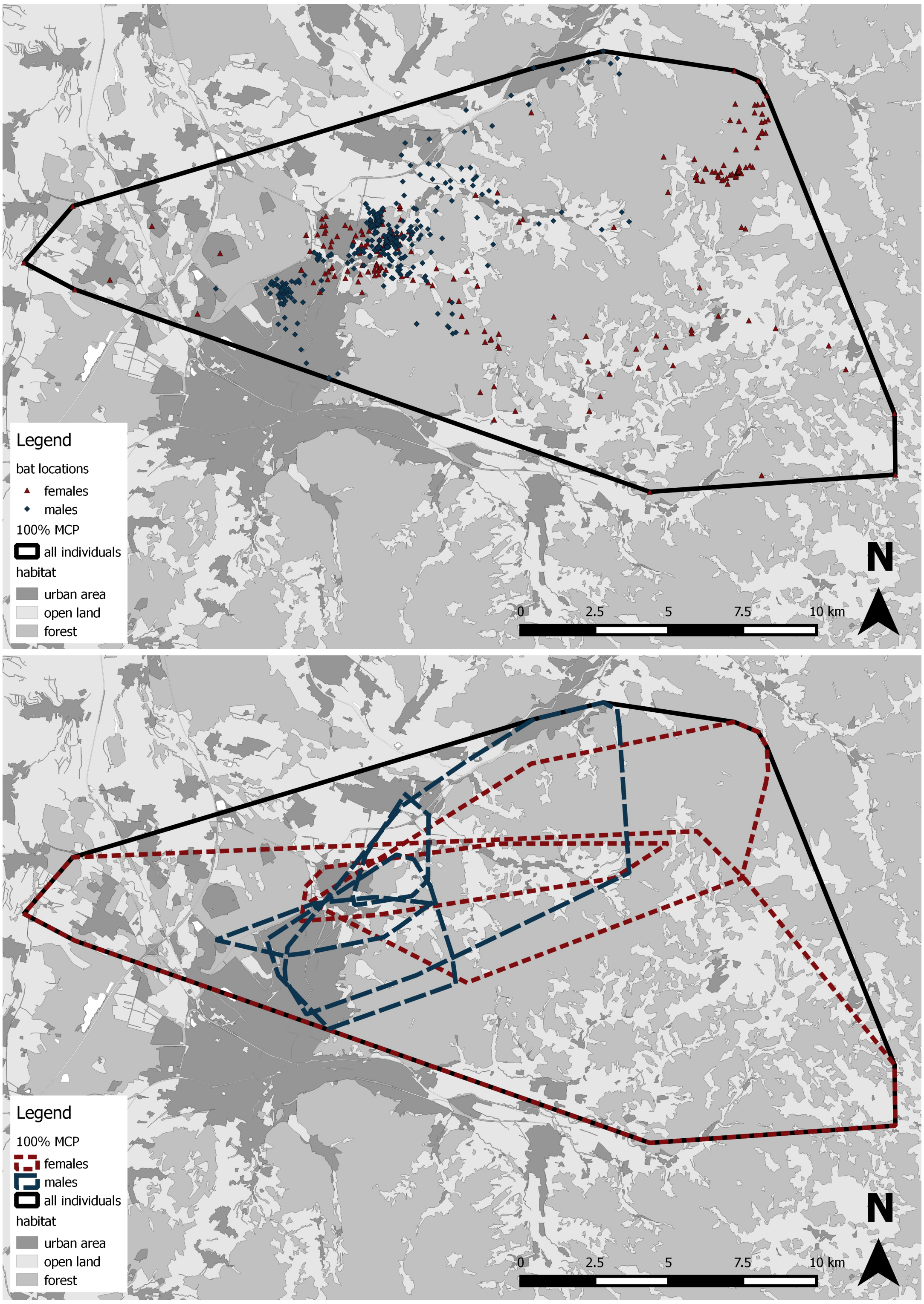

Figure 3.1: Upper map: Study area with 709 locations of four female (red) and four male (blue) *N. leisleri*. Lower map: Home ranges of three females and four males were calculated as 100% minimum convey polygon (MCP) for each individual. The 100% MCP of all individuals is shown in black. Background map: habitat categories, modified form Basis DLM BW [LGL, 2009]

3.2 Calculation of bat locations

The distance between receiver and transmitter increased with reduced signal strength (Fig. 3.2). Including habitat as fixed factor improved model fit significantly (summaries of both GAMMs in Appendix C). At equal distances, signal strength was reduced in forests and urban areas compared to open lands. The maximum range of transmitters was approximately 1 to 1.2 km during the experiment. Depending on the predicted distances, buffer size representing the 95% confidence interval of a location varied (46.7 ±73.2m, mean ±SD, Fig. 3.3).

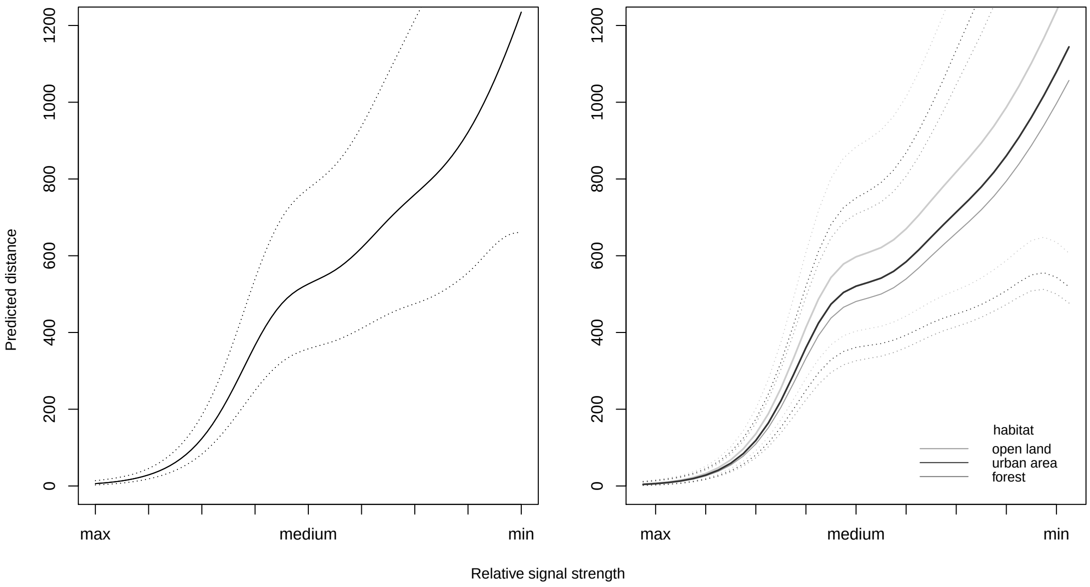

Figure 3.2: Predictions of distance between receiver and transmitter (corresponding to observer and bat) depending on relative signal strengtht. Distance was modelled with two different generalised additive mixed models (GAMMs). A first GAMM included only relative signal strength as predictor (left), a second one included additionally habitat for recalibration (right). Data of relative signal strength and known distances was obtained experimentally.

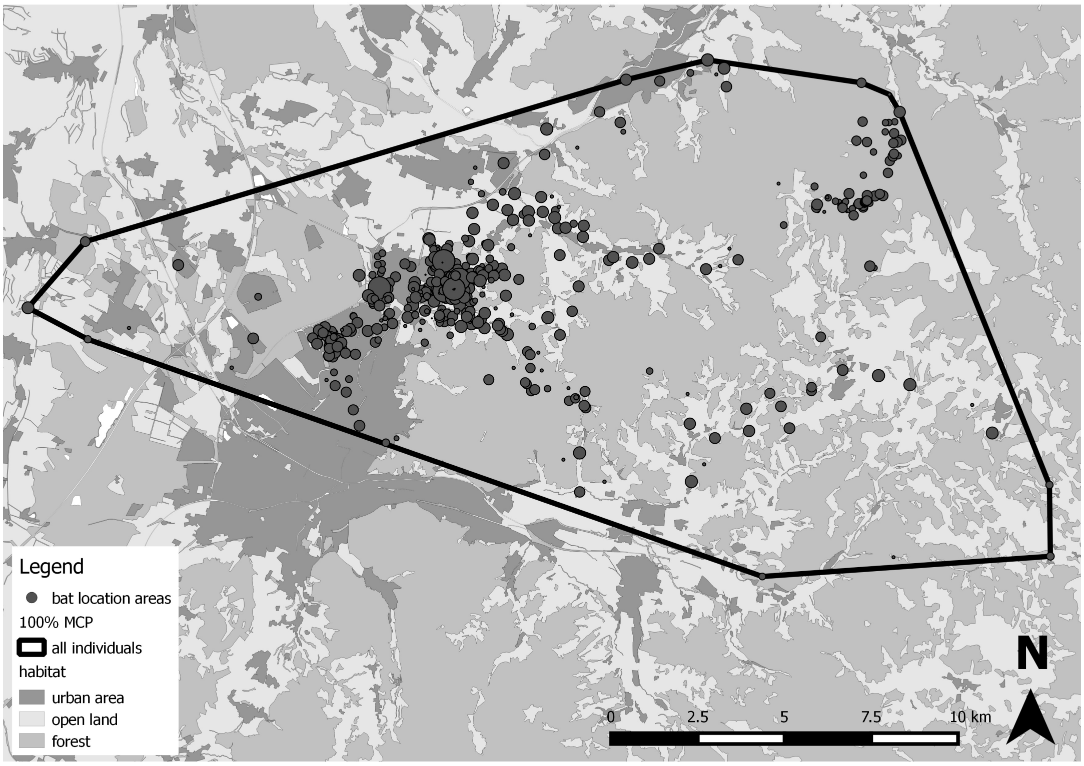

Figure 3.3: Map of the study area with 709 bat locations areas. The differently sized areas represent the 95% confidence interval of bat locations. These were calculated from the observers location, a compas bearing, and a distance estimated from the relative signal strength (modelled with a generalized additive mixed model (GAMM) taking into account the habitat). The different buffer sizes are a result of the standard deviation increasing with distance between observer and bat. The 100% minimum convex polygon (MCP) of all individuals is shown in black. Background map: habitat categories, modified form Basis DLM BW [LGL, 2009]

3.3 Resource selection by *N. leisleri*

Factors explaining resource selection by female and male *N. leisleri* in this study was identified by applying a RSF on a GLM fitted with 709 presence and the 50-fold number of available locations. Elevation was collinear with distances to day roost, urban areas and major roads but explained less variation in the data than these. Consequently, it was excluded from the full model in order to avoid multi-collinearity of predictors. The interaction sex : dist_water as well as observer and slope^2 were dropped as a result of model selection (details about model selection and summary of the final model in Appendix D).

Model predictions revealed sex-specific effects for predictors. The overall effects of habitat, distance to urban area, distance to forest edge, slope and aspect differed for females and males, whereas the effects of distance to day roost and distance to major roads differed only in effect size (Fig. 3.4 and 3.5). In terms of habitat selection, females selected for coniferous forests and slightly for urban areas, whereas males slightly preferred broad leaved forests (Fig. 3.4). Increasing distance to city and deceasing distance to forest edge had very slight effects on selection, positively for females and negatively for males (Fig. 3.4 and 3.5). Increasing slope had no effect on selection for females but a strong negative effect for males. The aspects north and east were selected by females over the other aspects and flat terrain, whereas males showed no selection pattern (Fig. 3.5). Both males and females selected locations further away from roads, even though the effect was more pronounced for males (Fig. 3.5). Independent of sex, decreasing distance to water had a positive effect on resource selection for *N. leisleri* (Fig. 3.4).

The main driver for selection by males clearly was distance to day roost, followed by slope. For females in contrast, no driver of a similar importance could be observed. However, habitat followed by aspect had the highest relative probabilities of selection (Fig. 3.4 and 3.5).

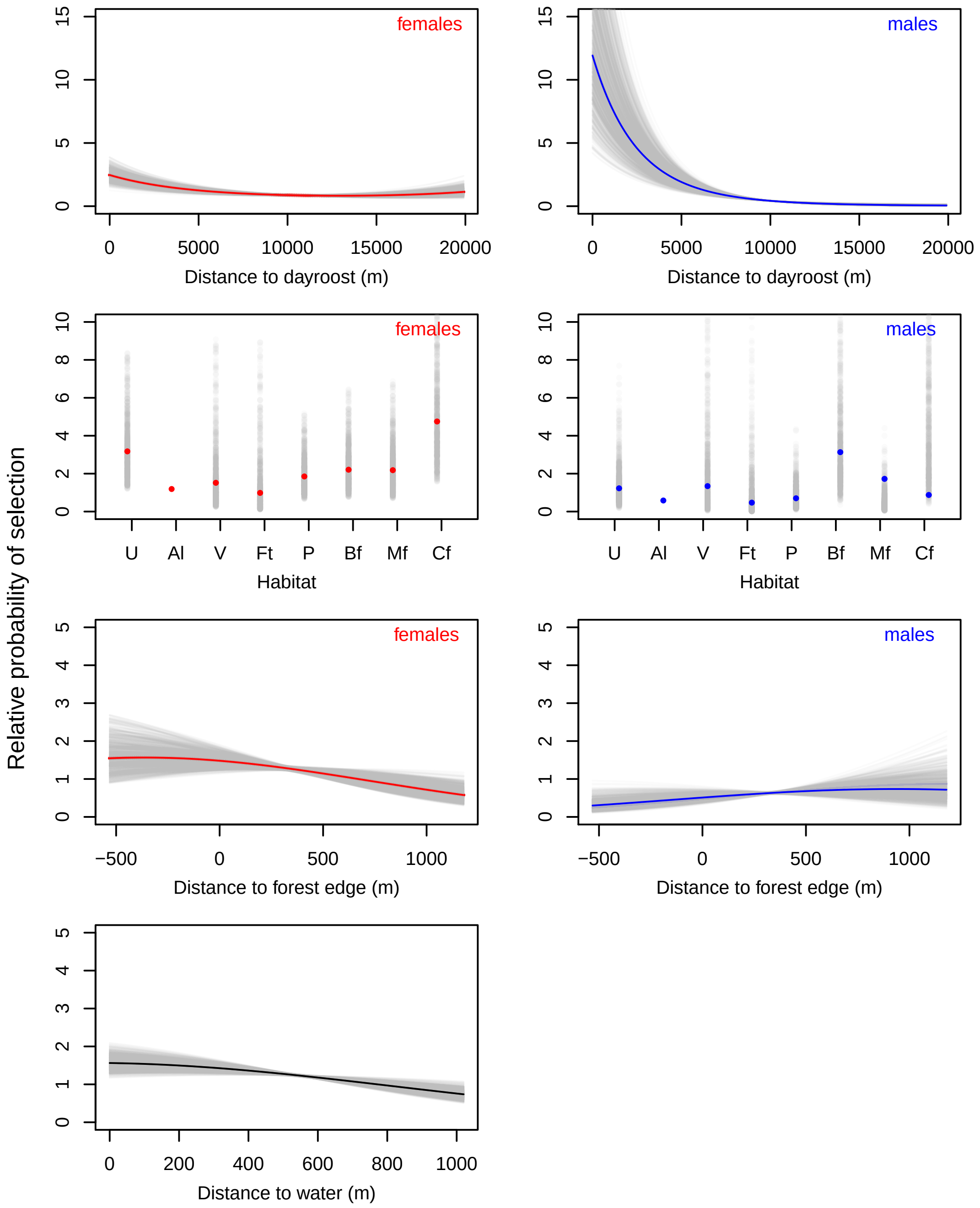

Figure 3.4: Predicted relative probability of selection of a resource unit by *N. leisleri* depending on the variables distance to day roost, habitat, distance to forest edge and water. Predictions of all variables but distance to water are made for females (red) and males (blue) separately. The y-axis is scaled depending on the relative probability of selection of a variable respectively. Habitat categories are urban area (U), arable land (Al), vineyards (V), fruit trees (Ft), pasture (P), broadleaved forest (Bf), mixed forest (Mf) and coniferous forest (Cf). Shaded areas represent the 95% confidence interval of the predictions. Predictions are made with a resource selection function (RSF) based on a binomial generalised linear model (GLM) using 709 presence and the 50-fold of available locations. Presence locations originated from four females and four males radio tracked continuously for several nights, available locations were randomly distributed within the 100% minimum convex polygon (MCP) of all individuals.

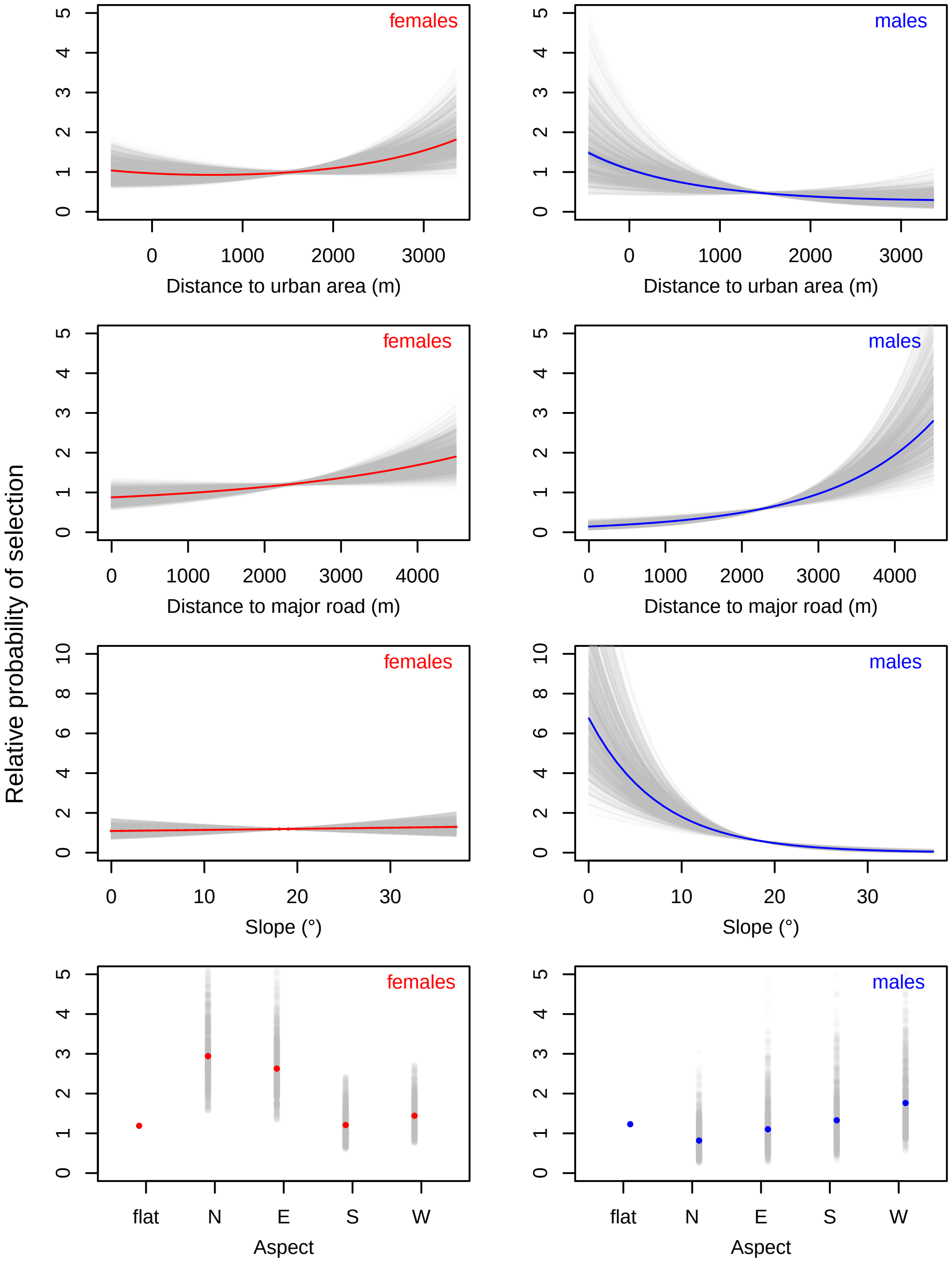

Figure 3.5: Predicted relative probability of selection of a resource unit by *N. leisleri* depending on the variables distance to urban area and major road, slope and aspect. Predictions of all variables are made for females (red) and males (blue) separately. The y-axis is scaled depending on the relative probability of selection of a variable respectively. Shaded areas represent the 95% confidence interval of the predictions. Predictions are made with a resource selection function (RSF) based on a binomial generalised linear model (GLM) using 709 presence and the 50-fold of available locations. Presence locations originated from four females and four males radio tracked continuously for several nights, available locations were randomly distributed within the 100% minimum convex polygon (MCP) of all individuals.

3.4 Flight activity of *N. leisleri*

Flight activity of *N. leisleri* was modelled by using 13008 to-the-minute recordings of four females and four males. It was shown to be dependent on nighttime and weather conditions (Table 3.2 and Fig. 3.6). The effect of nighttime on flight activity differed between sexes. For females, two distinct peaks of flight activity were predicted, a stronger one just after sunset and a second, less pronounced peak in the last third of the night. For males in contrast, only one distinct peak after sunset and two barely pronounced ones later during the night were predicted (Fig. 3.6). However, overall activity did not differ between sexes (Table 3.2). Higher temperature favoured flight activity of *N. leisleri* until a peak around 22°C, after which flight activity was decreasing again. Further, south wind, low wind speeds and precipitations had slight positive effects on flight activity, whereas humidity was insignificant (Table 3.2 and Fig. 3.6).

Table 3.2: Model summary of the generalised additive model (GAM) used to model flight activity of *N. leisleri*. The model is based on 13008 to-the-minute recordings of four females and four males tracked continuously for several nights.

Parametric coefficients

Predictor variable	Estimate	Std.Error	z value	Pr(>|z |)	
Intercept	-10.935	1.792	-10.798	<2e-16	***
humidity	-0.02679	0.03100	-0.864	0.38742	
humidity^2	3.908e-05	2.173e-04	0.180	0.85726	
wind speed	0.3020	0.1298	2.327	0.01996	*
wind speed^2	-0.1919	0.03870	-4.959	7.1e-07	***
temperature	2.161	0.09047	23.891	<2e-16	***
temperature^2	-0.04872	0.002413	-20.193	<2e-16	***
precipitation	1.461	0.5884	2.483	0.01304	*
precipitation^2	-1.491	0.5014	-2.974	0.00294	**
sex male	-0.8209	1.910	-0.430	0.66735	

Approximate significance of smooth terms

Predictor variable	edf	Ref.df	Chi.sq	p-value	
s(wind direction)	1.976	2.000	522.1	<2e-16	***
s(nighttime) : sex female	8.916	8.998	523.5	<2e-16	***
s(nighttime) : sex male	8.510	8.932	490.8	<2e-16	***
s(ID)	5.975	6.000	1161.2	<2e-16	***

Signif. codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05 , ‘.’ 0.1, ‘ ’ 1
R-sq.(adj) = 0.393 Deviance explained = 34.7%

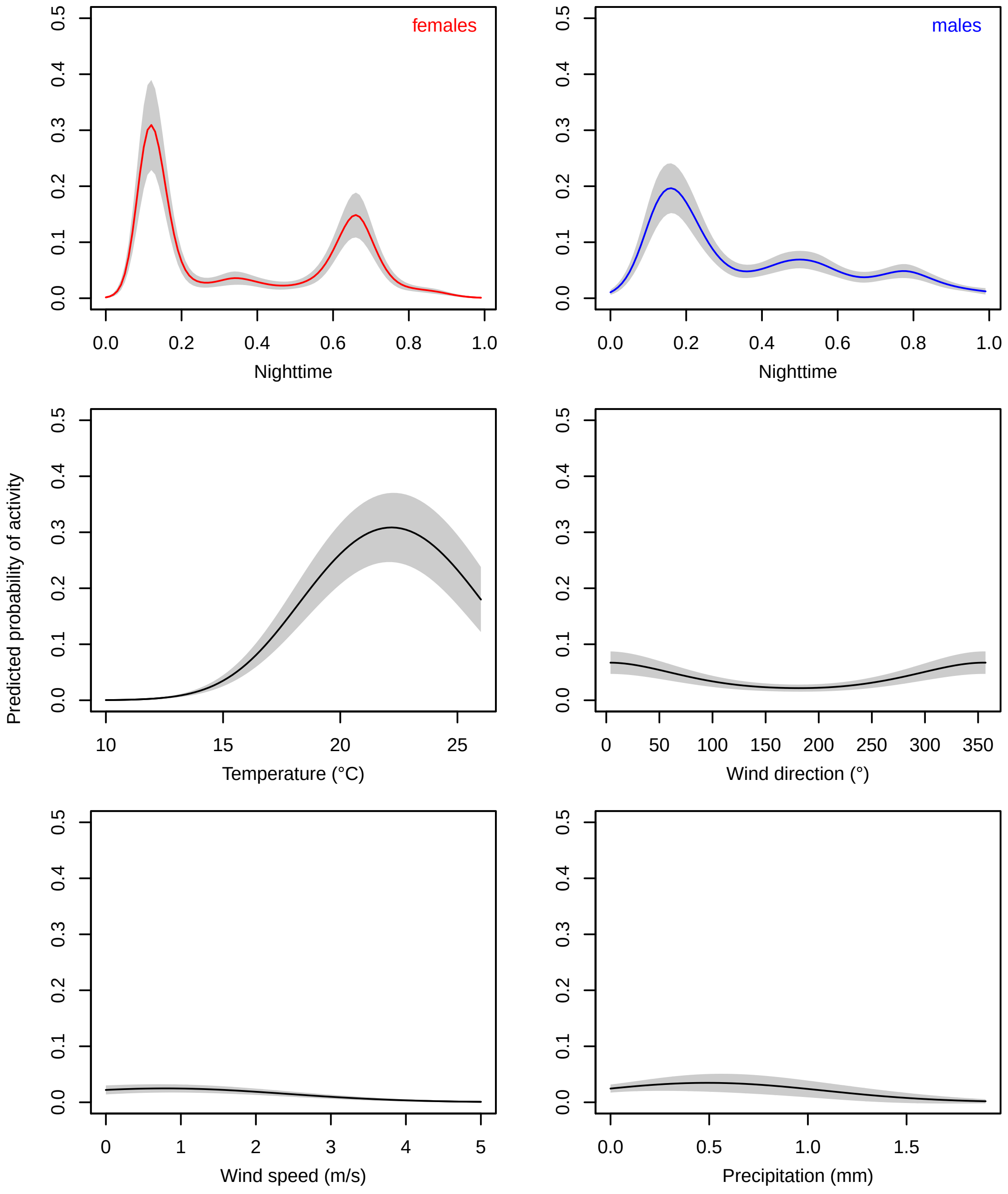

Figure 3.6: Predictions of the generalised additive model (GAM) used to model flight activity of *N. leisleri* depending on nighttime and weather conditions. Nighttime represents the time between sunset (0) and sunrise (1) adjusted for different night lengths. The effect of nighttime is predicted for females (red) and males (blue) separately, while the influence of weather conditions is predicted for both sexes together. The model is based on 13008 to-the-minute recordings of four females and four males tracked continuously for several nights. Shaded areas represent the 95% confidence interval of the predictions.

Chapter 4

Discussion

The present study reveals sex-specific differences in nightly behaviour, resource selection and flight activity of *N. leisleri* during mating season. These behavioural differences are likely to reflect asymmetric reproduction strategies.

4.1 Nightly behaviour in female and male *N. leisleri*

Spacious roaming of females and territoriality of males support the anecdotal observations of Fuhrmann et al. [2002]. These behavioural patterns are likely to be related not only to foraging but also to social motivations related to mating. Females may, besides foraging, search for other displaying males, while males most likely try to attract females to their mating territory. Accordingly, females had much larger home ranges than males and the maximum recorded distance from roost site was twice as much for females compared to males. The observed home range sizes by far exceed those reported in previous studies. Here, the maximum home range size was 180 km^2, which is about 10 or even 30 times larger than the maximum sizes reported by Waters et al. [1999] and Fuhrmann et al. [2002] in autumn. Only Szentkuti [2006] stated home ranges of a similar dimension. Accordingly, maximum recorded distances from roost sites in this study are among the highest documented for *N. leisleri* , but exceed theses of precious studies only by a small proportion [Schorcht and Boye, 2002; Shiel et al., 1999; Szentkuti, 2006; Waters et al., 1999]. Both sexes showed variable sizes and shapes of home ranges. This indicates different individual requirements in terms of energy availability and demands but also flexibility in resource use. Partly overlap of home ranges implies that intra-specific competition is not crucial for the species. Müller et al. [2012] showed that aerial hawkers respond aggregative on foraging sites with high abundance of prey.

Further, the number of flights observed in this study reflect a behavioural difference in male and female Leisler's bats during mating time. Compared to females, males undertook far more flights but with shorter durations of each single flight. Most of these flights probably were short courtship flights. Only few are assumed to have been foraging flights. During these courtship flights, males defended their territory by calling [Ohlendorf and Ohlendorf, 1998; Von Helversen and Von Helversen, 1994]. Numbers of flights recorded for females are similar to those reported by Shiel et al. [1999].

4.2 Resource selection by *N. leisleri*

Resource selection by *N. leisleri* during mating season was shown to depend on a number of distance, habitat, human disturbance, hydrological and topographical factors. The effect of some of these factors revealed to be sex-specific. Further, relative importance of single factors differed remarkably between sexes.

Distance to day roost was the most important driver of resource selection by males. They were clearly restricted to resource units in proximity to their roost sites. During mating season, males occupy mating sites consisting of several clustered roosts that they defend against other males [Ohlendorf and Ohlendorf, 1998; Von Helversen and Von Helversen, 1994]. This small-scale territorial courtship behaviour seems to strongly influence their space use and thereby also their foraging behaviour. A similar restriction to sites close to its territory was described by Fuhrmann et al. [2002] for one tracked male *N. leisleri* in August. Also females selected for locations closer to roost sites. However, this factor was of much less importance for them and other ecological features had a similar influence.

Habitat selection by *N. leisleri* differed between sexes. While females selected for urban areas and even stronger for coniferous forest, males showed little preference with a slight selection for broadleaved forest, the habitat surrounding their roost sites. Forest in general seemed to have little influence on resource selection by Leisler's bats, with a slight positive trend for females and a slight negative one for males. An effect of forest edges could not be shown, possibly due to restricted accuracy of locations. Further, inner forest edges such as forest roads or clearings were not included in the analysis due to a lack of base data, but may be of similar importance [Harbusch et al., 2002; Lesiński et al., 2007; Russ and Montgomery, 2002; Vandevelde et al., 2014]. A broad range of studies on habitat use of *N. leisleri* in different geographical areas was conducted during the last 20 years, but a clear general habitat preference can not be drawn. Surveys with acoustic methods obtained varying results for habitats mainly used by Leisler's bats. These were for example woodland and its edges, settlements, farmland, pasture and water [Kaňuch et al., 2008; Russ et al., 2003; Russo and Jones, 2003; Shiel and Fairley, 1998; Vandevelde et al., 2014; Vaughan et al., 1997]. Harbusch et al. [2002] and Shiel et al. [1999] conducted telemetry studies and reported use of mainly forest edges, pasture or water. However, habitat selection as a ratio of used vs. non-used or available habitats was only stated by three studies. These reported selection for parkland, deciduous woodland edge, pasture and water [Russ and Montgomery, 2002; Szentkuti, 2006; Waters et al., 1999].

Leisler's bats were often observed to be associated with water in previous studies [Harbusch et al., 2002; Kaňuch et al., 2008; Shiel et al., 1999; Vaughan et al., 1997]. Here, water was analysed as continuous distance parameter [Rainho and Palmeirim, 2011]. *N. leisleri* showed a slight selection for resource units closer to water, regardless of sex. Still, due to restricted accuracy of locations, it remains unclear if bats preferably foraged over watercourses or only in habitats associated with these.

Street lights have been demonstrated to attract *N. leisleri* in several studies [Mathews et al. 2015; Shiel and Fairley 1998; 1999; Waters et al. 1999; but see Lacoeuilhe et al. 2014]. Attractiveness of artificial lights on bats can be explained by increased insects abundance, even though this seems to be dependent on the wavelength of light [Rydell, 1992]. Distance to nearest town or city, the parameter investigated in this study, was regarded to be an appropriate measure for artificial light. In a recent study, this variable explained two third of light at night (besides time after sunset, nebulosity and moon phase) [Lacoeuilhe et al., 2014]. Here, resource units within or close to urban areas were slightly selected by males, whereas for females a slight opposing effect was observed. Even tough females selected for urban areas as described above, selection for resource units further away from urban areas seemed to be even stronger.

A selection of resource units further away from major roads was found for both sexes. Major roads have been shown to negatively influence overall bat activity, also in greater distances where a direct effect of noise and pollution seems unlikely [Berthinussen and Altringham, 2012]. Even though traffic noise reduced foraging efficiency of the greater mouse-eared bat (*Myotis myotis*), such an effect is not expected for *N. leisleri* due to generally different foraging strategies [Dietz et al., 2007]. Waters et al. [1999] even reported selection by *N. leisleri* for a major road bordered by hedgerows and street lights. Also a barrier effect of roads that was reported for other bat species [Abbott et al., 2012; Kerth and Melber, 2009] appears not to be present for *N. leisleri*, which flies in heights far above roads or tree crowns [Dietz et al., 2007; Shiel et al., 1999]. Even though one would expect *N. leisleri* to be unaffected by roads, the results of the present study reveal the opposite effect. Still, it is possible that the observed selection is not an actual avoidance of major roads but a preference for another unknown confounding factor. Major roads in the study area are mainly located in the valleys, and distance to roads was, amongst others, correlated with elevation.

Topographical features have received few attention in the context of resource selection by *N. leisleri* so far. In this study, a sex-specific influence of slope and aspect on resource selection was shown. While males selected for flat terrain, females did not show any preference. Accordingly, no effect of aspect was shown for males, whereas females selected for northern and eastern slopes. While males avoided the Black Forest foothills but stayed in the plain or in the valleys, females were possibly searching for other displaying males. Jaberg and Guisan [2001] described *N. leisleri* to occur independent from elevation, but this evidence could be biased due to the sampling method applied. Here, elevation was excluded from the model underlying the RSF, as it was highly correlated with distances to day roost, urban areas and roads. However, these variables affect resource selection by *N. leisleri* in different ways, and consequently, a possible effect of elevation can not be concluded easily. It remains unclear which of these variables is a determining or a confounding factor.

Besides the spatial restriction of males to resource units close to their roost sites, recourse selection patterns in this study are difficult to interpret or to put into a broader context. Recent studies mostly analysed habitat use in summer on female nursery colonies or from spring to autumn without putting an emphasis on a certain season or sex. The present study in contrast addresses the specific question of sex-specific resource use during mating season. Consequently, comparisons are difficult and generalisation of other studies should be avoided. A distinct overall habitat preference of the species is lacking so far and there are several possible reasons for this: Firstly, it can be the result of varying or partly inadequate sampling methods [Gannon et al., 2003]. Collins and Jones [2009] revealed restrictions of the use of bat detectors at ground level for high flying species such as *N. leisleri*. Especially in forests, calls were recorded at tree crown level but not from ground, which would lead to biased results, and many of the studies done used acoustic methods. Another explanation may be geographic variation, as studies were conducted all over Europe. Leisler's bat is an opportunistic hunter [Dietz et al., 2007] that may be very flexible in terms of adapting to different environments surrounding its roosting sites, which would result in varying habitat use adapted to local conditions. Alternatively, it is possible that space use of *N. leisleri* may be primarily related to insect distribution in the open air space [Müller et al., 2012]. The species is known to fly in great heights [Shiel et al., 1999], where insect patches may be associated rather with air movements and temperature fluctuations than with habitat features at ground level [Chapman et al., 2008; Russ and Montgomery, 2002].

4.3 Flight activity of *N. leisleri*

Nightly flight activity patterns of *N. leisleri* were shown to vary depending on sex. Additionally, flight activity was linked to temperature and to a very small extent to other meteorological variables. Most of the variability in flight activity of the species can be explained by varying availability of prey [Ciechanowski et al., 2007; Erickson and West, 2002]. The described meteorological variables most likely influence the abundance of air-borne insects which in return influences the activity of bats. However, the behaviour of males seems to be strongly influenced not only be the necessity of food intake but also by mating behaviour. Activity of both males and females was highest in the first third of the night, with a distinct peak soon after sunset. This observation matches with activity patterns described for Leisler's bats in summer [Shiel and Fairley, 1998; Fuhrmann et al., 2002; Rachwald et al., 2001; Waters et al., 1999] and is most likely related to high abundance of airborne insects [Rydell et al., 1996]. Thereafter, activity patterns differ between sexes. While activity of females peaked a second time during the last third of the night, possibly in relation of another peak of insect abundance [Rydell et al., 1996], activity of males was represented by two relatively small peaks during the rest of the night. After a first foraging trip, males showed pronounced courtship behaviour, characterized by alternating periods of calling with and without flight activity [Ohlendorf and Ohlendorf, 1998; Von Helversen and Von Helversen, 1994]. These activity patterns confirm the anecdotal observations of Fuhrmann et al. [2002] who radio tracked one male and one female in autumn .

In comparison to nighttime, a smaller amount of variability in flight activity was explained by weather conditions. Of these, temperature had the strongest influence, a correlation widely known for bats including *N. leisleri* [Fiedler, 2004; Erickson and West, 2002; Schorcht and Boye, 2002; Shiel and Fairley, 1998; Vaughan et al., 1997]. Here, an increase of bat activity with rising temperature was observed until around 22°C. With temperatures higher than that activity decreased, probably corresponding to the time directly after sunset when the bats did not yet emerge from their roosts. The observed negative effects of increasing wind speeds, rainfall and winds from south were significant but had a relatively small contribution to explain the overall variability of flight activity. Rain and stormy weather were reported to be negatively related to bat activity [e.g. Arnett, 2005; Erickson and West, 2002]. The influence of rain was not fully investigated during this study, as field work was not carried out in rainy nights. The negative effect of wind speed on bat activity was studied relatively often in the context of bat fatalities at wind turbines [Ahlén et al., 2007; Fiedler, 2004; Russo and Jones, 2003] and may as well be related to insect abundance [Santer, 2012]. However, due to differences in foraging strategy and flight capability, the importance of this factor probably varies depending on species. Further, northerly winds and low humidity were reported to favour bat activity [Arnett, 2005; Rydell et al., 2010]. Northerly winds may be correlated to favourable large-scale weather situation. Additionally, winds from north were shown to induce aggregations of air-borne insects such as moths which use these winds on their southwards migration in autumn [Chapman et al., 2008]. However, the absolute values of meteorological variables used to predict flight activity in this study have to be regarded with caution, as they were not recorded at the bat's position respectively. Conditions such as wind speeds or temperatures may have differed strongly between the measurement station and the bat's location, which sometimes was several hundred meters of altitude higher. Still, the general trends observed in this study should be valid.

4.4 Methodological strengths and restrictions

Radio telemetry is widely used to investigate nightly behaviour of bats [O'Mara et al., 2014]. So far, it represents the best available method to obtain detailed information on spatial and temporal activity patterns of this taxon, as individuals can be monitored continuously. Satellite transmitters are only used on much larger bats in the tropics [Richter and Cumming, 2008; Smith et al., 2011], but they need to be improved in form of drastic weight reduction before use on small bats in temperate zones will be possible.

Radio telemetry of highly mobile bats is a challenging task. Leisler's bats often fly relatively fast and in straight lines [Shiel et al., 1999]. In this study, due to topography and road network in the study area, continuous tracking was not always possible. Per night, individuals were lost for

70±62 minutes (mean±SD). It can be assumed that home ranges as well as distances from roost sites are even larger than those reported. Further, this could have led to biased results of the RSF because of underestimation of the area of available resource units.

Accuracy of locations is another issue when using radio telemetry. Triangulation is often used to obtain locations of adequate accuracy, but it needs to be done simultaneous by two observers when tracking highly mobile animals such as *N. leisleri* [e.g. Kerth and Melber, 2009; Schorcht and Boye, 2002]. Here, a method applicable for a single observer was developed in order to estimate areas where an animal was most likely located. The calculated point locations with a 95% confidence interval as buffer around them led to satisfactory results in terms of location accuracy.

Adequate sample size is a critical requirement for statistical analyses. In the present study, sample size was lower than primarily aimed for. This was a result of a transmitter failure, an animal leaving the study area and the ecologically limited study period. However, the amount of locations and activity measurements collected seemed reasonable for a statistical analysis of resource selection and flight activity. MCP areas are probably not saturated, as tracking period per individual, which was in tread-off with a higher sample size, was relatively short.

4.5 Conclusions

As in many species of mammals, female and male bats pursue different reproductive strategies in order to maximize lifetime reproductive fitness. While females spend more energy in breeding of offspring during summer, males have to invest in successful mating in autumn. The results of the present study emphasise the hypothesis that resource use and activity patterns of female and male *N. leisleri* differ during mating season. These sex-specific differences in behaviour are likely to be a result of differing energy demands and activity budgets related to asymmetric reproductive strategies.

Generally, insect availability is the main driver in resource selection and activity patterns of bats. However, mating willingness of males seems to have a strong influence on nightly behaviour in autumn. Even though males and females share roost sites for mating at least for short times, resource partitioning occurs at night.

In order to design effective conservation strategies for entire populations, knowledge about habitat requirements of both sexes of a species is essential. The existence of seasonal variations in local sexual segregation and sex-specific resource use during different periods of the year underline the need for detailed analysis of sex-specific requirements throughout the year.

Acknowledgements

This thesis is the final result of a six-months learning process. It can neither express the struggles nor the times of enthusiasm I experienced on the way. The long nights spent tracking bats or the days filled with error messages in R made me doubt at some points, but I had great support by various people during this time! I wish to thank all of those who contributed to this project in one or another way. It would not have been possible without you!

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Appendix A

Additional information on tagged bats

Table A.1: Information on body condition, tagging and tracking of five female and four male *N. leisleri*. Individuals were captured during daytime from bat boxes in Gundelfinger Wald.

	ID	band No.	date tagged	forearm length (cm)	weight (g)	number of telemetry nights	nuber of days with transmitter contact [a]
females	F1	E439864	25.08.2015	45,6	15,5	2	6
	F2	E422579	01.09.2015	44,6	15,3	2	5
	F3	E422582	11.09.2015	44,5	12,8	0[b]	0
	F4	E422582	18.09.2015	45,4	12,3	0,1[c]	1
	F5	E439867	23.09.2015	42,3	11,5	3	10
males	M1	E422622	25.08.2015	44,2	13,1	2,5 [d]	15
	M2	E419011	04.09.2015	44,5	13,7	3	9
	M3	E419009	11.09.2015	43,5	14,9	4[e]	15
	M4	E419022	18.09.2015	43,1	13,6	3	15

[a] until an individual left the study area or battery failure
[b] transmitter failure
[c] individual was lost 45 minutes after sunset of the first telemetry night
[d] third telemetry night only until 1am
[e] including one night without any activity

Figure A.1: Photographs of two *N. leisleri* with radio transmitters. PicoPip tags (Biotrack Ltd., Wareham, UK) with a weight of 0.5 g were attached between the scapulae of the bat using medical skin glue. Reflecting tape on the tag should enable visibility of the bat when illuminated. In the lower picture, the forearm band used for individual identification is visible too. Source of the upper picture: FrInaT GmbH.

Appendix B

Additional information on day roost use

Table B.1: Parameters describing day roost use of five female and four male *N. leisleri*. Day roost locations were in and around Gundelfinger Wald. Individuals with transmitter were located daily for the total lifetime of transmitter battery, or until an individual left the study area.

	females					males			
ID	F1	F2	F3[a]	F4[b]	F5	M1	M2	M3	M4
total number of day roost detections	7	6	1	2	11	16	19	16	6
number of different day roosts	2	2	1	2	5	7	3	5	4
mean number of consecutive days in the same day roost	1.6	1	-	2	2.4	1.2	2	1.5	2
proportion of days spent in a bat box	0.14	0.33	1	0.5	0.09	0.13	0.1	0.94	0.6
proportion of days spent in a natural tree cavity	0.86	0	0	0.5	0.09	0.88	0.9	0.06	0.94
proportion of days spent in a building	0	0.67	0	0	0.82	0	0	0	0

[a] transmitter failure

[b] individual lost in the beginning of the first telemetry night

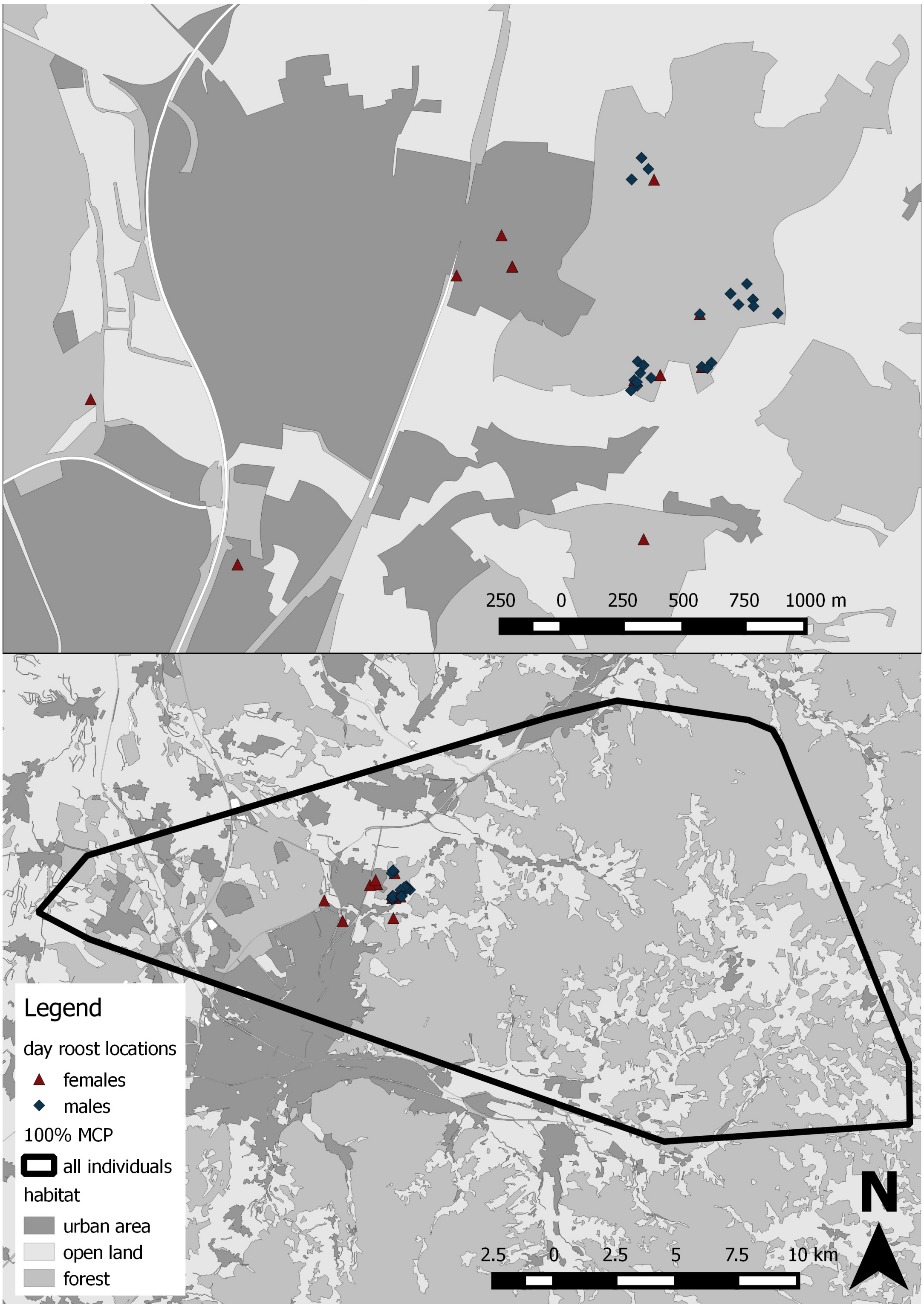

Figure B.1: Map of day roost locations of five female (red) and four male (blue) *N. leisleri* in and around Gundelfinger Wald. Zoomed map: local distribution day roosts. Overview map: location of day roosts within the study area, represented by the 100% minimum convex polygon (MCP) of all individuals (black). Background map: habitat categories, modified form Basis DLM BW [LGL, 2009]

Appendix C

Model summaries of GAMMs used to predict distances between observer and bat

Table C.1: Summary of the first generalized additive mixed model (GAMM) used to predict distances between observer and bat (receiver and transmitter).

Parametric coefficients

Predictor variable	Estimate	Std.Error	z value	Pr(>|z |)	
Intercept	5.7460	0.1888	30.43	<2e-16	***

Approximate significance of smooth terms

Predictor variable	edf	Ref.df	Chi.sq	p-value	
s(signal strength)	4.887	4.887	95.12	<2e-16	***

Signif. codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05 , ‘.’ 0.1, ‘ ’ 1
AIC: 125.3303, R-sq.(adj) = 0.757

Table C.2: Summary of the second generalized additive mixed model (GAMM) used to predict distances between observer and bat (receiver and transmitter). Reference category for Habitat is urban area.

Parametric coefficients

Predictor variable	Estimate	Std.Error	z value	Pr(>|z |)	
Intercept	5.71566	0.18230	31.353	<2e-16	***
Habitat forest	-0.07958	0.09610	-0.828	0.410	
Habitat open land	0.13711	0.10002	1.371	0.174	

Approximate significance of smooth terms

Predictor variable	edf	Ref.df	Chi.sq	p-value	
s(signal strength)	5.034	5.034	98.28	<2e-16	***

Signif. codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05 , ‘.’ 0.1, ‘ ’ 1
AIC: 118.3683, R-sq.(adj) = 0.761

Appendix D

Step selection and summary of the GLM underlying the RSF

Table D.1: Stepwise backwards selection of the best full generalised linear model (GLM) based on Akaike information criterion (AIC). The best full model included all predictors except elevation which was collinear with other predictors. Step selection was performed with the function *step* (package *stats* in R). The automated function was stopped only if a variable was dropped but its squared term remained in the model.

Step	Term sequentially dropped	AIC	ΔAIC
BEST FULL MODEL		4001.5	
step1	- sex : dist_water	3999.9	1.6
step2	- observer	3998.4	1.5
step3	- slope^2	3997.0	1.4

Table D.2: Summary of the final binomial generalised linear model (GLM) used for prediction of with the resource selection function (RSF). The model is based on 709 presence and the 50-fold number of available locations of four female and four male *N leisleri.* Reference categories in the model summary are Sex female, Habitat arable land, ID F1 and Aspect flat.

Predictor variable	Estimate	Std.Error	z value	Pr(>|z |)	
Intercept	-6.68820	0.56023	-11.938	<2e-16	***
sex male	-0.97537	0.08902	-10.957	<2e-16	***
dist_dayroost	-2.86689	0.68848	-4.164	3.13e-05	***
dist_dayroost^2	0.77362	0.06446	12.002	<2e-16	***
Habitat broadleaved forest	0.61870	0.54841	1.128	0.259249	
Habitat coniferous forest	1.38512	0.56516	2.451	0.014252	*
Habitat fruit trees	-0.18987	1.12712	-0.168	0.866224	
Habitat mixed forest	0.60713	0.58825	1.032	0.302026	
Habitat pastures	0.44247	0.52877	0.837	0.402712	
Habitat urban	0.98176	0.50299	1.952	0.050956	.
Habitat vineyards	0.24269	0.91590	0.265	0.791028	
Habitat water	-10.20375	396.00839	-0.026	0.979444	
dist_forestedge	-0.15212	0.16641	-0.914	0.360630	
dist_forestedge^2	-0.16397	0.04274	-3.836	0.000125	***
dist_water	-0.02604	0.06319	-0.412	0.680277	
dist_water^2	-0.20030	0.05573	-3.594	0.000325	***
dist_urban	-0.13875	0.17247	-0.804	0.421116	
dist_urban^2	0.32369	0.05943	5.447	5.12e-08	***
dist_road	0.13255	0.12616	1.051	0.293409	
dist_road^2	0.10159	0.05632	1.804	0.071263	.
slope	0.05199	0.13929	0.373	0.708950	
Aspect north	0.90560	0.32146	2.817	0.004845	**
Aspect east	0.79309	0.34628	2.290	0.022005	*
Aspect south	0.01631	0.35712	0.046	0.963583	
Aspect west	0.19308	0.32757	0.589	0.555575	
ID F2	-0.01843	0.22527	-0.082	0.934810	
ID F4	-0.14622	0.41924	-0.349	0.727263	
ID F5	0.03364	0.22494	0.150	0.881106	
ID M1	-0.71272	0.16880	-4.222	2.42e-05	***
ID M2	-0.53947	0.17642	-3.058	0.002228	**
ID M3	-0.11879	0.16884	-0.704	0.481710	
ID M4	NA	NA	NA	NA	
sex male : dist_dayroost	-1.33129	0.25928	-5.135	2.83e-07	***
sex male : Habitat broadleaved forest	1.06287	0.63179	1.682	0.092511	.
sex male : Habitat coniferous forest	-0.97770	0.78461	-1.246	0.212729	
sex male : Habitat fruit trees	-0.02380	1.26830	-0.019	0.985029	
sex male : Habitat mixed forest	0.47703	0.76138	0.627	0.530964	
sex male : Habitat pastures	-0.25706	0.61468	-0.418	0.675795	
sex male : Habitat urban	-0.23861	0.57224	-0.417	0.676696	
sex male : Habitat vineyards	0.59081	1.04141	0.567	0.570501	
sex male : Habitat water	1.26107	488.08143	0.003	0.997938	
sex male : dist_forestedge	0.54160	0.19866	2.726	0.006405	**
sex male : dist_urban	-0.64846	0.28051	-2.312	0.020795	*
sex male : dist_road	0.65511	0.17424	3.760	0.000170	***
sex male : slope	-1.52328	0.24988	-6.096	1.09e-09	***
sex male : Aspect north	-0.56655	0.43917	-1.290	0.197040	
sex male : Aspect east	-0.15555	0.48645	-0.320	0.749149	
sex male : Aspect south	0.80710	0.44982	1.794	0.072768	.
sex male : Aspect west	0.91312	0.40675	2.245	0.024771	*

Signif. codes: ‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05 , ‘.’ 0.1, ‘ ’ 1

Selbstständigkeitserklärung

Erklärung

Hiermit versichere ich, die vorliegende Arbeit selbständig verfasst zu haben. Ich habe keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und alle wörtlich oder sinngemäß aus anderen Werken übernommenen Inhalte als solche kenntlich gemacht.

Die eingereichte Masterarbeit war oder ist weder vollständig noch in wesentlichen Teilen Gegenstand eines anderen Prüfungsverfahrens. Die elektronische Version der eingereichten Masterarbeit stimmt in Inhalt und Formatierung mit den auf Papier ausgedruckten Exemplaren überein.

Freiburg, 14. März 2016