RESEARCH ARTICLE

Movement responses of common noctule bats to the illuminated urban landscape

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Abstract

Context Cities are a challenging habitat for obligate nocturnal mammals because of the ubiquitous use of artificial light at night (ALAN). How nocturnal animals move in an urban landscape, particularly in response to ALAN is largely unknown.

Objectives We studied the movement responses, foraging and commuting, of common noctules (*Nyctalus noctula*) to urban landscape features in general and ALAN in particular.

Methods We equipped 20 bats with miniaturized GPS loggers in the Berlin metropolitan area and related spatial positions of bats to anthropogenic and natural landscape features and levels of ALAN.

Results Common noctules foraged close to ALAN only next to bodies of water or well vegetated areas, probably to exploit swarms of insects lured by street lights. In contrast, they avoided illuminated roads, irrespective of vegetation cover nearby. Predictive maps identified most of the metropolitan area as non-favoured by this species because of high levels of impervious surfaces and ALAN. Dark corridors were used by common noctules for commuting and thus likely improved the permeability of the city landscape.

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Conclusions We conclude that the spatial use of common noctules, previously considered to be more tolerant to light than other bats, is largely constrained by ALAN. Our study is the first individual-based GPS tracking study to show sensitive responses of nocturnal wildlife to light pollution. Approaches to protect urban biodiversity need to include ALAN to safeguard the larger network of dark habitats for bats and other nocturnal species in cities.

Keywords Urbanization · GPS tracking · Artificial light at night · ALAN · Habitat use · Preference · Movement · Common noctule bat

Introduction

The proportion of humans living in cities is increasing, leading to an expansion of urban environments worldwide (Grimm et al. 2008; Seto et al. 2011, 2012; UNPD 2012). This urban sprawl causes manifold changes in ecosystems, ranging from shifts in local climates (ambient temperature, humidity and wind), decreased habitat connectivity caused by high levels of impervious surfaces (surfaces sealed by buildings, concrete or roads) to increased disturbance by anthropogenic stressors such as noise, artificial light at night (ALAN) and pollutants (Sadler et al. 2006; Grimm et al. 2008; Kyba and Hölker 2013). As a consequence, many wildlife species avoid urban environments. Yet some species cope well with city landscapes and are even synurbic (Baker and Harris 2007; Russo and Ancilotto 2015). One reason for the success of urban wildlife is their ability for regulatory and acclimatory responses such as adjusting their behaviour accordingly (McDonnell and Hahs 2015). For example, urban wildlife may postpone foraging to the crepuscular or night time to reduce interactions with humans (Tigas et al. 2002; Lowry et al. 2013). Other species, such as bats, may be exposed to few interactions with humans anyways, owing to a strictly nocturnal lifestyle. Yet even when restricting activities to the night, nocturnal animals are exposed to anthropogenic stressors, such as ALAN (Longcore and Rich 2004; Rich and Longcore 2006; Hölker et al. 2010). On a global scale, the consequences of ALAN on wildlife species are poorly studied compared to the vast literature on how land use change or deforestation

affects wildlife. As a strictly nocturnal taxon, bats are highly vulnerable to the detrimental effects of ALAN (Voigt et al. 2018; Zeale et al. 2018). Indeed, over the past decade experimental research has revealed strong adverse effects of ALAN on bats (e.g. Rydell 1992; Stone et al. 2009; Russo et al. 2017), but only recently studies have looked into landscape scale effects of ALAN on bats (Hale et al. 2012; Luck et al. 2013; Hale et al. 2015; Mathews et al. 2015; Azam et al. 2016; Zeale et al. 2018; Pauwels et al. 2019; Straka et al. 2019).

In general, some bat species are known to benefit from ALAN in urban environments, at least when foraging (Rydell 1992; Russo and Ancilotto 2015). Over the past decades, evidence has accumulated that the majority of bat species avoid ALAN (Voigt et al. 2018). For example, bats bypass illuminated commuting routes (Stone et al. 2009; Zeale et al. 2018), foraging places (Polak et al. 2011) and drinking sites (Russo et al. 2017). Moreover, ALAN can substantially reduce habitat quality and disconnect habitats (Hale et al. 2012, 2015; Mathews et al. 2015), leading to the suggestion that lowering illumination may re-establish habitat connectivity in urban landscapes (Laforge et al. 2019). Some studies suggested that the guild of open-adapted bat species, i.e. rapid flyers in the open space with relatively low-frequency echolocation calls, are insensitive to urban characteristics (Luck et al. 2013), or even may take advantage of the illuminated urban landscape (Threlfall et al. 2011; Laforge et al. 2019). Overall, our knowledge on how bats use the urban landscape is still sketchy, even though such a knowledge may be needed to protect urban bats in particular and urban biodiversity in general. Also, bats are highly relevant during planning processes; at least in Europe where all species are legally protected by the E.U. habitat directive (92/43/EEC). Thus, understanding how urban bats cope with ALAN is key for formulating effective management recommendations that help to protect and promote urban biodiversity.

Here, we used an individual-based GPS tracking approach to study the spatial response of bats to urban characteristics. Specifically, we asked how common noctule bats (*Nyctalus noctula*) respond to natural and anthropogenic landscape features when commuting or foraging, and in particular how ALAN affects commuting and foraging in an urban landscape. We selected common noctule bats, since this species

belongs to the guild of open-adapted species, which were previously considered to be insensitive to urban characteristics or even to exploit urban landscapes (Threlfall et al. 2011; Luck et al. 2013). However, this notion is based on acoustic recordings, which are usually ground-based, covering an area of maximum 20–30 m height. Open-adapted species are often flying higher than this (Roeleke et al. 2016, 2018) and therefore response behaviours of bats foraging in the open space is difficult to detect with ground-based recordings. Therefore, by using miniaturized GPS tracking we aimed at establishing a more comprehensive picture on how open-space foraging bats respond to urban characteristics. Since common noctule bats are known to forage in twilight (Roeleke et al. 2016; Zeale et al. 2018), we hypothesized that this species may be indeed tolerant to ALAN. If common noctule bats are tolerant to ALAN, we predicted that tagged common noctules should not avoid areas with high illuminance levels when foraging and commuting. However, if they are sensitive to ALAN they should rather avoid areas illuminated at night. Further, we hypothesized that common noctules use linear landscape features in a city environment, since they have been observed using forest edges and hedgerows for commuting and foraging above farmland (Roeleke et al. 2016; Heim et al. 2016, 2017). Consequently, we predicted that they prefer to be active close to roads and railroad tracks, irrespective of the level of ALAN at these structures.

Materials and methods

Study area

The study area was located in the district of Marzahn-Hellersdorf in northeast Berlin and consisted largely of residential and commercial areas, with a high proportion of large pre-fab buildings in the north, gradually outnumbered by smaller houses in the south (Umweltatlas Berlin 2010). Interspersed urban green spaces such as parks, cemeteries and succession areas covered about 12% of the area, forests, groves and shrubs made up about 13% and standing water bodies covered 2% of the total area. Outside the city borders, the landscape was dominated by intense farmland (15%) with small patches of forests and groves and small villages. Within the city borders, land area

covered by rails, roads and car parks amounted 11% of the total area. The small river 'Wuhle' crossed the study area in north–south direction. While the city and settlements were brightly illuminated, especially along streets, larger green spaces in the city and especially the landscape beyond the city boundaries were less illuminated at night (Kuechly et al. 2012).

Experimental work

All work was conducted under the animal care and ethics approval of the federal agency (C113-G0114/15) and the approval of the conservation agency (IE 224-OA-AS/G/1167.2). Between June and early September 2015 and between July and August in 2016 and 2017, we captured 20 male common noctule bats at natural and artificial daytime roosts in the parks 'Parkfriedhof Marzahn' and 'Schlosspark Biesdorf', two larger parks which are not or only partly illuminated by street lamps, respectively. All daytime roosts were in the darker section of the parks. In each bat, we measured body mass (g) and forearm length (mm) using spring balances and calliper, respectively.

GPS data acquisition

We attached a single GPS logger (Robin, CellGuide Ltd., Tel Aviv, Israel; Vesper, ASD technologies inc., Haifa, Israel) to the back of each captured bat using medical latex glue (Sauer Hautkleber, Manfred Sauer Germany). In 2016 and 2017, we added a small VHF transmitter (Telemetrie Dessau, Germany) to each GPS logger to improve the relocation of bats and tags. GPS loggers were on average 10% of a bat's body mass and thus above the widely accepted 5% threshold value. Yet, both conservation and animal welfare agencies granted permission (see above) to conduct this study in light of the insights gained by this study for the protection of this species. To check for adverse health effects, we performed a linear model with body mass changes as response variable to see if tag mass and duration of attachment affected body mass changes between capture and recapture of bats. From the 2017 dataset for which we have comprehensive data, we used the body masses of recaptured bats that were tagged (n = 5) and those that remained untagged (n = 15), the Julian day, forearm length (as a measure of size) and sex as covariates in the analysis. The model showed that body mass changes were

significantly affected by date of capture ($F_{1,14} = 6.7$, $p = 0.021$), with body mass losses more frequently observed early than in the late season. All other factors remained non-significant (sex: $F_{1,14} = 0.001$, $p = 0.99$; tag: $F_{1,14} = 0.056$, $p = 0.82$, forearm length: $F_{1,14} = 0.88$, $p = 0.36$; length between capture and recapture: $F_{1,14} = 6.7$, $p = 0.086$). Thus, body mass changes did not differ between tagged and untagged bats in the same location and during the same season.

GPS locations were recorded every 30 s from 30 min before sunset until dawn [Table S1 in electronic supplementary material (ESM)]. The earliest starting time was 18:33 CEST (mean = 20:18 CEST) and the latest ending time was 2:46 CEST (mean = 23:07 CEST). We ignored GPS locations with extremely large (> 1000 m) horizontal or vertical positional errors from further analysis. For a first inspection, we visualised the individual flight paths in QGIS 2.14 (QGIS Development Team 2017) and removed locations from bats resting in a roost. We interpreted large gaps (> 3 min) in the recording of GPS locations as roosting, as the GPS signals were not received when bats stayed inside roosts. GPS locations were split into one or more trips per animal. We defined one trip as comprising the movement path between subsequent roosting events (as defined above). In the rare case of battery or signal failure during a trip, we still used the partly recorded trip in our analysis. For each trip, we quantified the number of GPS locations, duration, flight speed and turning angle between subsequent locations.

Landscape information (habitats, linear structures, ALAN)

For the spatial analysis of movement paths, we merged land use maps of Berlin (Umweltatlas Berlin 2010) and Brandenburg (LfU 2015). Further, we summarised > 200 land use categories to obtain eight categories relevant for bats according to previous studies (Kronwitter 1988; Gaisler et al. 1998; Bartonicka and Zukal 2003; Hale et al. 2012; Ciechanowski 2015). For more details, see the habitat categorization table (Table S2) in the supplement. We obtained information on ALAN from an aerial survey (Kuechly et al. 2012).

We used logistic regressions to test the effect of predictor variables on the space utilisation of bats. We obtained GPS records (presences) in the field and then

created the necessary pseudo-absences (Hirzel et al. 2002) by rotating each flight path around its origin by a random angle (Calenge 2006). The origin was the location of the roost from which a bat emerged. By following this approach, we maintained individual movement constraints with respect to travel speed and angle of the trajectory during all analyses (Martin et al. 2008). We defined preference of a certain covariate, specifically level of illumination, level of impervious surface, level of vegetation, distance to roads, distance to water bodies, distance to railways upon their availability (Beyer et al. 2010).

Statistical analyses

We followed a hierarchical approach. First, we created a model distinguishing commuting from foraging behaviour (hereafter called 'behaviour models'). Second, we tested preference for environmental predictors within these behavioural categories with a use-availability design (see below; hereafter called "preference models").

Assignment of movement behaviour types to GPS locations

We used the R package moveHMM (Michelot et al. 2015) to identify two movement behaviours based on step length and turning angle. These movement behaviours were then assigned to the respective GPS locations. The first movement behaviour, quasi-linear movement as proxy of commuting behaviour (commuting), was defined as a fast, near-linear flight, characterised by high flight speed (computed from step length in 30 s GPS interval, step length about 225 m) and small turning angles (degree turned from one to the next step, turning angle about 15°). We defined area-restricted search as a proxy for foraging behaviour, characterized by relatively low flight speed (step length about 40 m) and large turning angles (about 165°). For each time point, we assessed the quality of the assignment by computing the probability of being in one of the states (Michelot et al. 2016). To avoid locations with high uncertainty, we tagged all locations showing values < 0.8 probability as undefined and excluded them from the movement behaviour model. We reclassified locations showing very short and abrupt changes in activity within a homogenous sequence of movement. For example, we

reclassified one 'commuting' location as 'foraging' when identified within a sequence of 'foraging' locations. We created two temporal buffers of ± 1.5 min, within which the focal location was assigned to foraging if this behaviour was shown on the majority of all locations contained in the buffer. Remaining 'single' locations were then reclassified to the movement behaviours shown in the surrounding locations (42 out of 3,129 locations). The reclassification was done for each trip, so that the first and last few locations of trips were not compared to data of another trip. A final plot of each trip and the whole flight path of every individual served as a last visual check to verify the plausibility of the assignment (Fig. S8 in ESM).

Data extraction

For data extraction at every GPS location, we used the median error (29.9 m) as radius of a circular area. This approach accounted for the horizontal positional error. For the circle around each GPS location, we calculated the proportion of each land use category and the median brightness of ALAN (Pebesma and Bivand 2005; Bivand et al. 2013). We excluded locations without light measurements (90 out of 3129 GPS locations = 2.8%). Then, we measured the minimum distance of each location (GPS and rotated track location) to the closest landscape structure element (railways, routes of individual transport, waterways). Finally, we identified frequently selected landscape features of common noctules by computing the proportion of GPS locations for each land use category and the rotated tracks using Jacobs index D (Jacobs 1974).

Data analysis

We tested three sets of logistic models in a generalized linear mixed-modelling (GLMM) framework (Bates et al. 2015; Table S3 in ESM). First, we applied a set of models to explain the movement behaviours using a Boolean response, indicating 'commuting' vs. 'foraging' (i.e., 'behaviour models'). Consecutively, we separated the GPS locations by their assigned behaviour (cf. section "Assignment of movement behaviour types to GPS locations"). For each behaviour type, we tested a set of models to explain the selection for specific areas using a binomial

response variable [GPS locations (use) vs. rotated locations (availability)]; hereafter called 'foraging preference models' and 'commuting preference models'. We included 'individual ID' and 'year' as crossed random effects. All environmental predictors (cf. 'landscape information paragraph' in ESM) were independent of each other, as all calculated Pearson's correlation coefficients remained < 0.7. For the 'preference models' an abundance weighting was conducted to account for the unequal replications of GPS localisations and rotated locations (1:5 relationship; Bates et al. 2015). We inspected linearity of predictors using generalised additive models (GAMs) and included a landscape variable to the power of two if a non-linear pattern was detected. By doing so, we modelled non-linear responses to linear landscape structures, as necessary for 'distance to railways', 'distance to roads' and 'distance to bodies of water' (Fig. S4 in ESM). We specified the interaction term of each landscape structure with light. The 'behaviour models' included only GPS locations with behaviour defined either as 'commuting' or 'foraging'. Locations with 'undefined' behaviour were excluded (n = 78, 2.6% of all locations). Abundance weighting was unnecessary as unequal numbers of GPS locations resulted from the conducted behaviour. To evaluate the predictive power of fixed effects, we compared the candidate models' AIC values to those of the respective null models (Table S7 in ESM). To check for robustness of our analysis due to spatiotemporal autocorrelation, we ran candidate models with subsets of the data (every 2nd, 5th and 10th value, respectively). The applied Durbin-Watson test for temporal autocorrelation became non-significant ($p > 0.3$) when every fifth or tenth sample was used (Hartig 2018). Similarly, DHARMa Moran's I test for spatial autocorrelation became non-significant ($p > 0.3$) when every fifth or tenth sample was used (Hartig 2018). The discovered patterns remained the same when reducing the number of samples by increasing the sampling interval. Hence, we ruled out effects of spatiotemporal autocorrelation. Residuals of the selected final models did not deviate from normality by visual inspection. The behaviour models were weakly skewed to positive residuals while both preference models were weakly skewed towards negative values. Finally, we selected the model offering the highest predictive power and reasonable complexity indicated by the lowest AIC (ΔAIC 1st–

2nd > 30). Preparation of spatial data, data extraction and modelling were done in R 3.4.0 (R Core Team 2017). Mapping of spatial data, splitting of flight paths into 'trips' and the reclassification of land use categories were conducted with QGIS 2.14.15 (QGIS Development Team 2017). Finally, we predicted the probability of the conducted movement based on linear environmental predictors using the final behaviour model across the whole urban landscape. Consecutively, we predicted the selected areas when a specific behaviour was conducted based on the corresponding preference model for the same area. All models were developed in the study area entailing the district Marzahn-Hellersdorf in the north-east part of Berlin and used to predict probability maps for the whole metropolitan area of Berlin.

In a last step, we compared our results to another study of bat diversity in Berlin (Straka et al. 2019). To confirm the quality of the predicted probability maps, we correlated (Spearman rank correlation) the measured acoustic activity of common noctule bats recorded independently during an acoustic bat activity survey in Berlin (Straka et al. 2019), with values extracted from our prediction maps at the same locations. To incorporate the size of the surveyed sites of Straka et al. (2019) we used a 100 m buffer to extract the predicted probability. The acoustic bat survey was performed on urban grasslands and common noctule bats have been present at all sites.

Results

We recorded 41 flight trips of 20 male noctule bats (*Nyctalus noctula*) during 1-3 days of individual tracking. On average, common noctules emerged from their roosts at about 21:35 (hh:mm, median; Table S1). The median length of all trips was 7.3 km (min: 2.5 km, max: 18.2 km; Table S1 in ESM). All bats moved about 2.4 km (median) away from the roost (min: 0.5 km, max 15.7 km; Table S1). On average common noctules travelled 17.6 ± 9.3 km (mean ± one standard deviation). When commuting, bats flew at a median speed of 7.7 ± 7.0 m/s with turning angles (-180 to $180°$) averaging $-5.0 \pm 95.6°$. During foraging, bats flew at an average speed of 6.2 ± 5.2 m/s using turning angles of $2.5 \pm 109.3°$. The behaviour classification led to 13,164 foraging locations, 4602 commuting locations

and 468 unclassified locations. Following this, bats foraged at 72% and commuted at 25% of the recorded GPS locations. About 2.6% of all locations remained unclassified.

In a first step, we compared the landscape utilization of all recorded bats with the simulated pattern derived from rotated tracks using Jacobs index (Fig. 1). As described before, we refer to percentage values as the relative proportion of a land use category in a circular area of about 30 m around the GPS location, called buffer zone. Foraging common noctules selected bodies of water and open space with > 50% impervious surface in the buffer zone while neglecting developed areas regardless of the extent of impervious surfaces (Fig. 1). All other habitat types were avoided to varying degrees (sorted from least to strongest avoidance: Agricultural area, open cultural landscapes, urban green space, forests, developed areas with > 50% impervious surfaces, developed areas with < 50% impervious surfaces in the buffer zone; Fig. 1). Commuting bats flew more likely above bodies of water, above agricultural areas and above urban green spaces (< 50% impervious surface in the buffer zone) than expected by chance. Commuting bats showed neither preference for nor avoidance of forests, yet they avoided all other habitat categories (sorted from least to strongest avoidance: open space with > 50% impervious surface, open cultural landscapes, developed areas with > 50% impervious surface and developed areas with < 50% impervious surface in the buffer zone; Fig. 1).

Factors influencing flight behaviour

Common noctules were less likely to commute than to forage over areas with a large proportion of open space, irrespective of the level of illumination and available vegetation cover (Fig. 2A). This pattern changed to a clear preference of foraging in well illuminated areas when open space and vegetation cover was available. Yet, in most cases confidence intervals were large (Fig. 2A). Close to railways, common noctules performed mostly foraging behaviour, particularly when areas were illuminated, irrespective of adjacent vegetation (Fig. 2B). Close to roads, common noctules performed both foraging and commuting; yet, the large confidence intervals indicated that foraging and commuting behaviour were both likely to occur close to roads (Fig. 2C). In
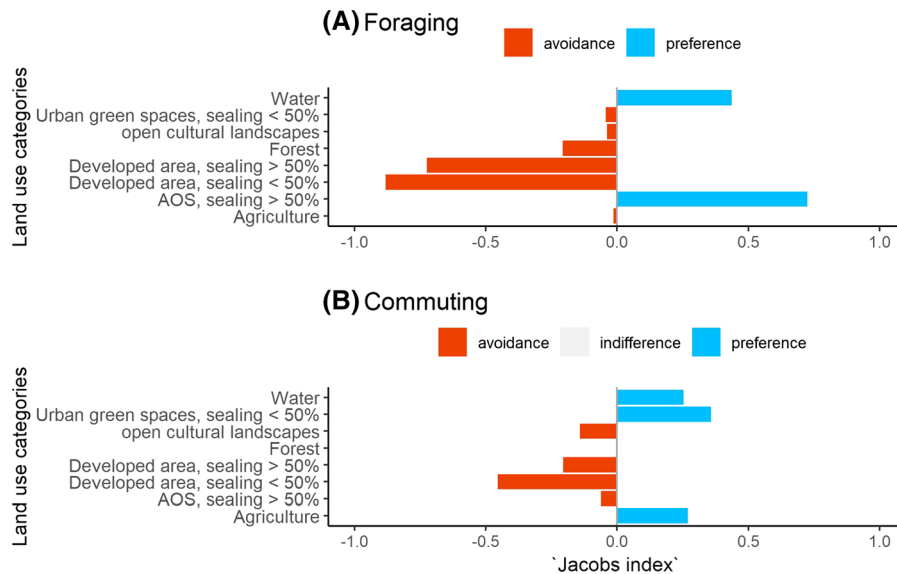
Fig. 1 Exploitation of land use categories by common noctule bats (*Nyctalus noctula*) in the Berlin metropolitan area according to Jacobs index (Jacobs 1974). The analysis was done separately for GPS locations showing foraging (**A**) or commuting behaviour (**B**). The y-axis shows all landscape categories and the x-axis the computed Jacobs index. AOS stands for aerial open space. When the Jacobs index was zero no bar is shown (see **B**). The percentage of sealing refers to the percentage of impervious surfaces in the buffer zone

general, common noctules foraged most often at intermediate distance (> 100 m) to roads and when illumination levels were relatively high, irrespective of the vegetation cover in adjacent areas (Fig. 2C). When being close to bodies of water, common noctules were more likely to forage than to commute. However, bats were more likely to forage at bodies of water with increasing levels of illumination (Fig. 2D) and more likely to commute over bodies of water with low levels of riverine vegetation.

Foraging common noctules (Fig. 2E–H and Table S6 in ESM) avoided small open spaces (< 20% coverage in the buffer zone), irrespective of the extent of nearby vegetation (Fig. 2E). When extensive open spaces (> 50% in the buffer zone) were available, bats selected high levels of illumination, particularly when vegetation was present. The narrow confidence intervals for the effect of high vegetation cover underline the importance of vegetation for common noctules when foraging in areas where open space is dominating (> 80% in buffer zone; Fig. 2E). Foraging common noctules did not select areas close to railways (Fig. 2F). Common noctules were usually not observed at illuminated roads (Fig. 2G), but rather at some distance to roads

(100 to 500 m), particularly when the area was heavily illuminated and when vegetation cover was high (Fig. 2G). Bodies of water were preferred by foraging common noctules, irrespective of illumination if the vegetation cover was high (> 50% in the buffer zone, Fig. 2H). With increasing distance to bodies of water, foraging common noctules selected more densely vegetated areas and neglected areas with low vegetation cover (Fig. 2H).

When commuting, common noctules selected dark areas regardless of available open space and regardless of vegetation cover (Fig. 2I–L and Table S6 in ESM). Specifically, common noctules commuted in dark areas next to railways, tolerating higher levels of illumination only when vegetation cover was low (Fig. 2J). The tracked common noctules selected dark areas when commuting close to roads (Fig. 2K). However, bats commuted most often far away from roads (> 500 m) regardless of the level of illumination or vegetation (Fig. 2K). The most frequently used commuting areas were close to bodies of water, independent of illumination or vegetation (Fig. 2L).
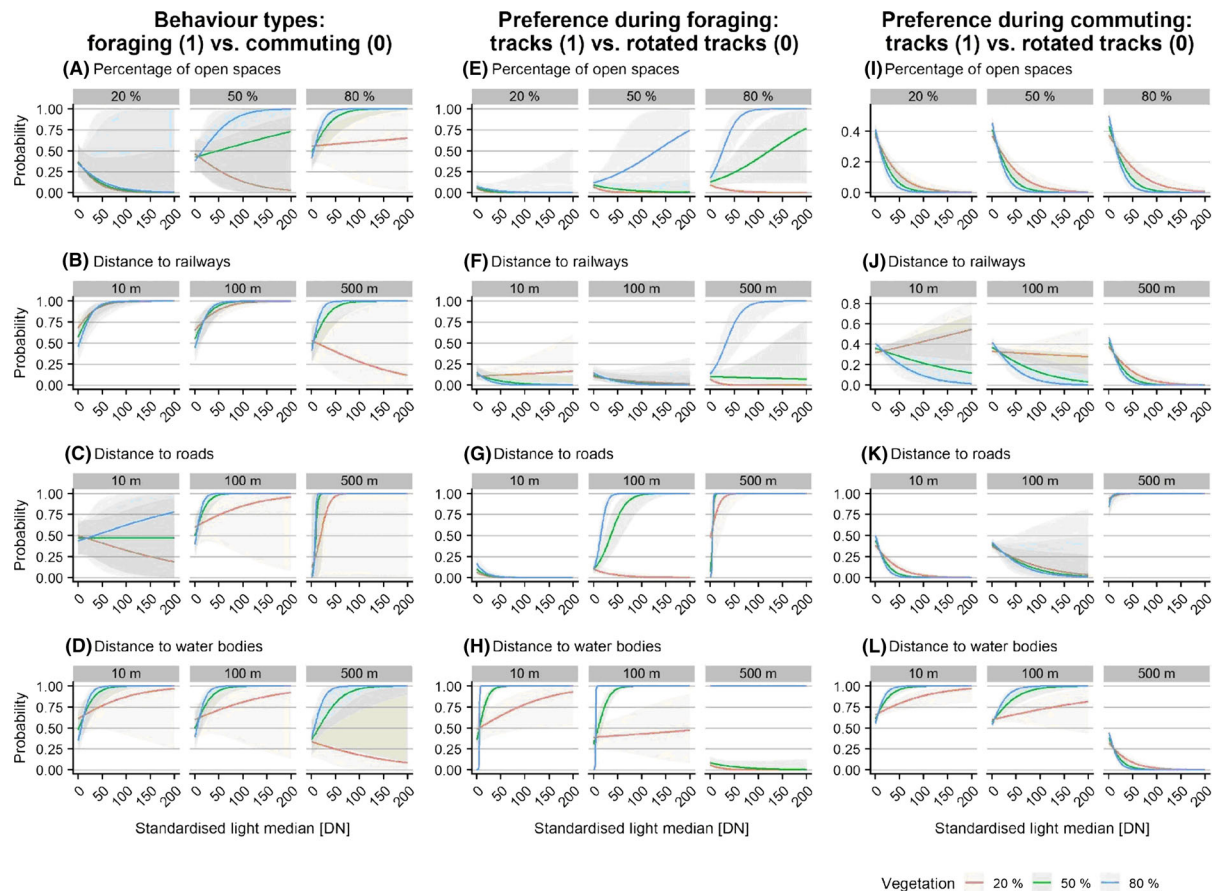
Fig. 2 Effect plots showing the influence of landscape use categories on the conducted movement behaviours (left columns) of common noctule bats (*Nyctalus noctula*), and the selected landscape structures during foraging (middle column) and commuting (right column). Each panel shows the probability of presence at the y axis and relative light intensity (0 = dark, 200 = bright) at the x axis. One row of graphs (horizontal plot triplet) summarizes the findings for one specific land use category. The three colors of lines represent 20% (red), 50% (green) and 80% vegetation cover (blue) in the buffer zone. (Color figure online)
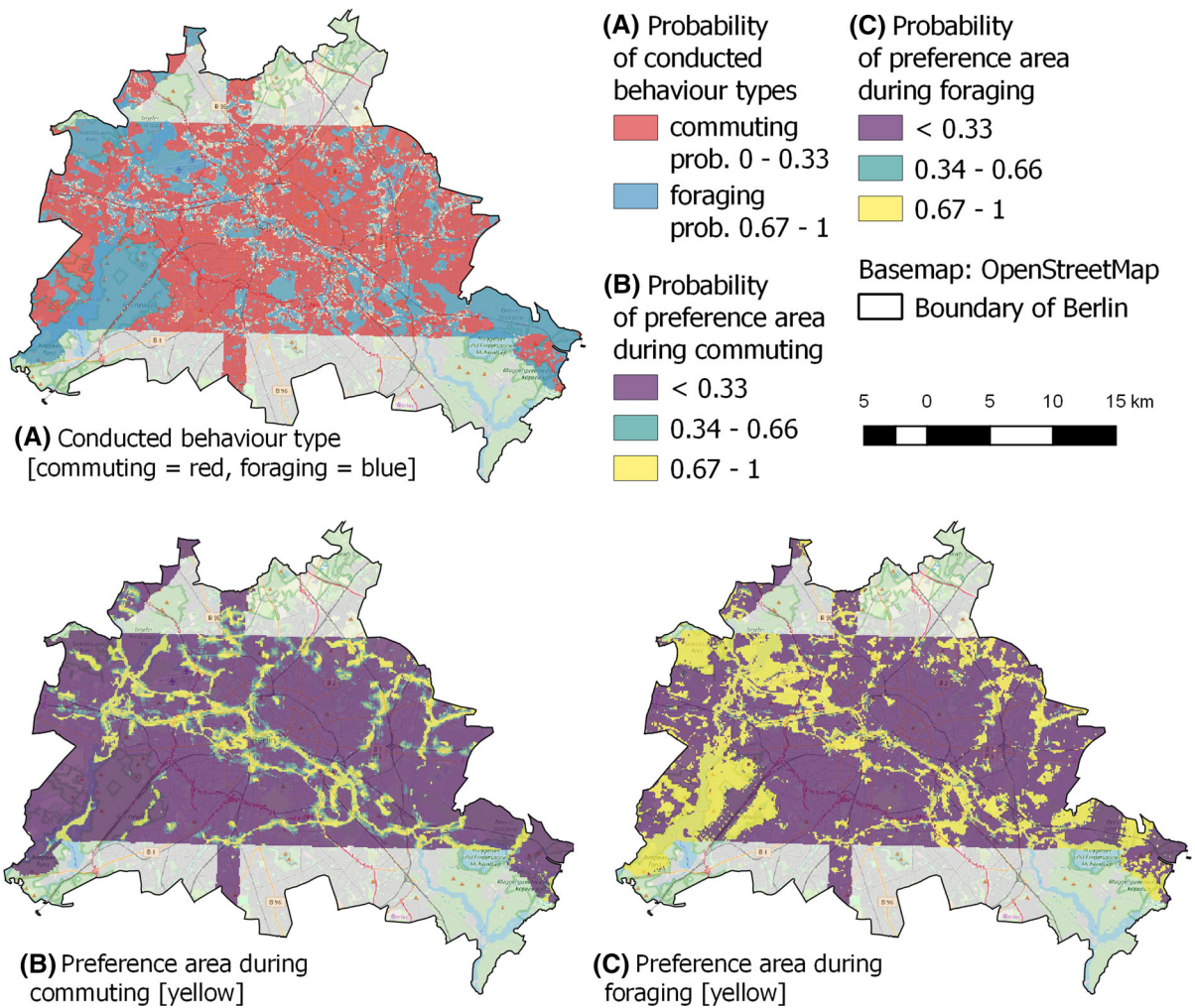
Predictive map for preference and behaviour of noctule bats

The derived maps extrapolate the space use of common noctules based on the analysed environmental predictors at a given location in the Berlin metropolitan area (Fig. 3). We identified large green areas such as urban forests and landscape parks in the north south-west and south-east as well as the abandoned airport Tempelhof to be likely areas for foraging common noctule bats, while the remaining majority of the urban landscape seems to be commuting area interspersed with several small foraging patches (Fig. 3A). The map Fig. 3B highlights a limitation of suitable commuting corridors, consisting of the network of waterways (rivers and channels) and open spaces (Fig. S5 in ESM). The predicted foraging preference map instead followed the distribution of urban vegetation in the Berlin metropolitan area and indicates extensive green structures as preferred foraging grounds (Fig. 3C).

We evaluated our predictive maps by comparing the local probability values with the acoustic activity of bats obtained from sites throughout Berlin (Straka et al. 2019). A correlation test showed that our model predicted more foraging than commuting at sites with high acoustic activity of common noctules ($r_s = 0.42$, $p = 0.07$). Moreover, our model predicted commuting for sites with a low acoustic activity of common noctules ($r_s = -0.52$, $p = 0.02$). Lastly, we could not find a correlation between the probability of foraging

(A) Conducted behaviour type
[commuting = red, foraging = blue]

(A) Probability of conducted behaviour types
- commuting prob. 0 - 0.33
- foraging prob. 0.67 - 1

(B) Probability of preference area during commuting
- < 0.33
- 0.34 - 0.66
- 0.67 - 1

(C) Probability of preference area during foraging
- < 0.33
- 0.34 - 0.66
- 0.67 - 1

Basemap: OpenStreetMap
Boundary of Berlin

5 0 5 10 15 km

(B) Preference area during commuting [yellow]

(C) Preference area during foraging [yellow]

Fig. 3 Predictive probability map showing the movement behaviour of common noctule bats (*Nyctalus noctula*) in the Berlin metropolitan area: **A** shows areas where bats most likely commute (probability close to 0) or forage (probability close to 1), **B** shows the predicted corridors of commuting bats, and **C** shows the predicted foraging grounds of common noctules

and the acoustic activity of common noctule bats at the sites ($r_s = 0.28$, $p = 0.25$).

Discussion

Using miniaturized GPS loggers, we studied the spatial behaviour of common noctule bats (*Nyctalus noctula*) in the metropolitan area of Berlin to shed light on how urban bats respond to habitat features of the city landscape, especially to artificial light at night (ALAN). Our models highlight that common noctules were mostly repelled by ALAN, except near bodies of water or when being far away from roads and when

vegetation cover was high. Indeed, common noctules avoided flying next to roads when roads were illuminated, which questions the relevance of illuminated roads as linear landscape elements and as foraging areas for noctule bats in cities. Possibly, insect biomass was lower close to roads than in adjacent areas, making foraging at roads inefficient for common noctules. Alternatively, traffic noise may have constrained the efficacy of foraging with biosonar (Siemers and Schaub 2011). The high likelihood for common noctules to be present next to bodies of water with high levels of ALAN may be caused by insects that accumulate at lanterns after having emerged from an aquatic larval stage into the winged adult stage.

While urban water sites are crucial for urban bats (i.e. for drinking, foraging and commuting) not all urban bat species can take advantage of these sites when they are lit (Straka et al. 2016). However, it seems that in the case of noctule bats, these sites are even more frequently used when they are lit.

Overall, our model suggested that common noctules tolerated ALAN only when foraging but avoided ALAN when commuting. Consequently, dark corridors seem to be key for connecting patchily distributed foraging areas in the urban matrix. The two established predictive maps for preference and movement behaviour of common noctules emphasize the relevance of bodies of water, forests and landscape parks for foraging common noctules in the Berlin metropolitan area. Yet, these maps also pinpoint to the low value of heavily urbanized areas for bats, even for open-adapted bats such as common noctules. This confirms earlier studies in pipistrelle bats that even bats that are tolerant to some levels of ALAN in a foraging context may ultimately suffer from high levels of illumination in urban areas (Hale et al. 2012, 2015).

Constraints and validation of our models

Our model was based on a variety of landscape features of different quality. For example, we used a general measure of ALAN obtained from aerial surveys of light pollution conducted in 2010 (Kuechly et al. 2012). Therefore, information on ALAN may have been partly outdated in our study, considering the most recent transition of lighting schemes, e.g. from mercury high pressure vapour lamps to energy efficient sodium vapour lamps and LED throughout the European Union. Additionally, this aerial survey did not distinguish between lighting types or specific wavelength spectra. Yet, a recent study has shown that the activity of common noctules did not change in relation to the colour of emitted light (Spoelstra et al. 2017). Thus, a change in the wavelength spectrum of the current street lamps in our study area might not have a strong effect on the outcome of our models. Additionally, we neglected in our model that bats flew at varying altitudes above ground and were thus exposed possibly to other levels of ALAN than measured by Kuechly et al. from aerial surveys. Consequently, exposition of noctule bats to ALAN may have differed from those levels of illumination considered in our models. Lastly, we cannot formulate

threshold values for the context-specific tolerance of noctule bats towards ALAN since the used light parameter did not provide absolute values but rather a general proxy of local illumination from artificial sources (Kuechly et al. 2012). In summary, we cannot rule out the possibility that the aforementioned factors and limitations may have biased our analysis to a certain extent. However, locations of street lanterns have most likely not changed over the past decade and all other parameters, such as the location of roads and railroads remained constant in almost all cases. Therefore, we argue that the potential bias caused by referring to old information might only be small.

To validate our prediction maps, we compared our predictve maps to data from an acoustical survey that recorded common noctule bats in the Berlin metropolitan area (Straka et al. 2019). As foraging bats emit many more calls at foraging sites than at commuting sites, the marginal significant positive correlation of predicted foraging behaviour and acoustic activity of common noctule bats validates the outcome of our behavioural model. The negative correlation of local preference of commuting noctules with the acoustic activity of common noctules indicates that the preference model for commuting noctules correctly predicted areas with low acoustic bat activity as commuting areas; a reasonable pattern when bats pass an area rapidly during the fast commute. The non-significant correlation of predicted local preference of foraging bats and acoustic bat activity may result from the specific study design of Straka et al. (2019). The study was designed to record acoustic activity of all bat species at urban grasslands where bats were known to forage. As a result, all sites were suitable foraging grounds, and differences between the predicted probability of foraging bats and the acoustic activity of bats was most likely caused by random effects.

Predicting the space use of urban bats across the Berlin metropolitan area

In our study, we focused on the spatial behaviour of male bats because of legal constraints imposed by the conservation agencies and for the reason of practicability. However, for the long-term survival of urban bat populations, it is essential that female bats can cope with anthropogenic stressors, including ALAN. One of our previous GPS tracking studies highlighted

that female and male noctule bats may employ different foraging and migrating strategies (Roeleke et al. 2016; Lehnert et al. 2018). Further, it has been documented that habitat use of common noctules may vary throughout the reproductive season (Mackie and Racey 2007). Since we lack information about how female common noctules respond to ALAN in the Berlin metropolitan area, we must remain cautious in extrapolating future population scenarios based on male movement patterns alone. Nonetheless, our predictive maps provide a first baseline for predicting how common noctules use the metropolitan area of Berlin. Our preference map highlights on the one hand that the largest part of the Berlin metropolitan areas seem to be not suitable for foraging common noctules, probably because insect biomass is low when the extent of impervious surfaces is high and vegetation cover is low. On the other hand, the specific topography of Berlin with its network of rivers and channels and also its extensive landscape parks make the urban landscape permeable for bats. This highlights the need to protect dark, green corridors. Such commuting corridors may offer common noctules the combined benefit of relative warm roosts in the urban heat island and the accessibility of a high insect biomass in rural areas. However, the expected urban sprawl in the metropolitan area of Berlin may cause suburban areas to deteriorate over time so that more central colonies of common noctules may become disconnected from more suitable habitats at the edge of the metropolitan area. Maintaining a network of dark corridors may facilitate movements of nocturnal animals and may thus preserve urban biodiversity. Our predictive maps highlight areas particularly sensitive as commuting corridors or foraging habitats and thus inform stakeholders, such as the authorities responsible for regional planning of outdoor lighting, where to avoid or reduce the level of ALAN.

Conclusions

We show that common noctules foraging in urban landscapes selected areas close to bodies of water adjacent to vegetation or illuminated and well vegetated open areas. Commuting noctule bats avoided illuminated areas but rather selected dark and open structured corridors such as the network of rivers, channels and urban green spaces. The lack of such a corridor network may increase the degree of isolation between urban colonies even in a highly mobile bat species like the common noctule. Consequently, dark corridors and food patches with a high vegetation cover need to be preserved to sustain populations of common noctules and other bats in urban environments. Our study is the first individual based GPS tracking study to show how urban wildlife responds to light pollution. Since GPS approaches enabled us to monitor bats even when flying at higher altitudes, our approach seems to be superior over previous approaches using ground-based acoustic recordings. The limitations of ground-based acoustic recordings, i.e. covering only a space of 20–30 m height above microphones, may explain the contrasting findings of our and previous work. Whereas previous studies suggested that open-adapted bats such as common noctules are not responding to urban characteristics, our GPS study shows that even species of this guild respond sensitive to urban characteristics, including ALAN.

Author contributions CCV conceived the study. CCV, YY and SKS ensured funding and designed methodology. JMS, JB, TT and CCV conducted field work. JMS, JB, SKS and PG analysed the data. CCV, JMS, JB and PG wrote the draft manuscript and all authors commented on it.

Compliance with ethical standards

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