



Mathematisch-Naturwissenschaftliche Fakultät

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Suggested citation referring to the original publication:
Ecological Processes 6 (2014) 24
DOI <https://doi.org/10.1186/s13717-017-0091-7>
ISSN (online) 2192-1709

Postprint archived at the Institutional Repository of the Potsdam University in:
Postprints der Universität Potsdam
Mathematisch-Naturwissenschaftliche Reihe ; 826
ISSN 1866-8372
<https://nbn-resolving.org/urn:nbn:de:kobv:517-opus4-428166>
DOI <https://doi.org/10.25932/publishup-42816>

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Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields

Olga Heim^{1,2*}, Lukas Lorenz², Stephanie Kramer-Schadt¹, Kirsten Jung³, Christian C. Voigt^{1,4} and Jana A. Eccard²

Abstract

Introduction: Bats are threatened by agricultural intensification, and although bat ecology in agricultural landscapes is in the focus of current research, the effects of interacting spatiotemporal factors on species-specific bat activity above farmland remain understudied. Our aim was to identify spatiotemporal factors and their interactions relevant for the activity of bat species above conventionally managed arable fields.

Methods: We repeatedly monitored relative bat activity above open arable fields in Germany using acoustic monitoring. We used site-related biotic and abiotic factors and landscape characteristics across five spatial scales, their combinations, and interactions to identify those factors which best explain variation in bat activity.

Results: Numerous interactions between landscape characteristics and the insect abundance affected bat activity above fields. For instance, *Pipistrellus pipistrellus* became more active with increasing insect abundance, but only above fields with a low proportion of woody vegetation cover in the surroundings. Additionally, the level of bat activity in summer depended on landscape characteristics. For example, the activity of *Pipistrellus nathusii* was relatively low in summer above fields that were surrounded by vegetation patches with a high degree of edge complexity (e.g., hedgerow). However, the activity remained at a relatively high level and did not differ between seasons above fields that were surrounded by vegetation patches with a low degree of edge complexity (e.g., roundly shaped forest patch).

Conclusions: Our results revealed that landscape characteristics and their interactions with insect abundance affected bat activity above conventionally managed fields and highlighted the opportunistic foraging behavior of bats. To improve the conditions for bats in agricultural landscapes, we recommend re-establishing landscape heterogeneity to protect aquatic habitats and to increase arthropod availability.

Keywords: AgroScapeLabs, European bat species, Agriculture, Landscape, Multi-scale habitat modeling, Ecosystem service, Conservation

Introduction

Agriculture has shaped landscapes and influenced the behavior of wildlife over thousands of years. In the last century, intensification of agricultural land use led to increased field sizes and a reduced heterogeneity of farmland in many regions of the world. Additionally, an

increased amount of chemicals and industrial fertilizers is applied by heavy machinery. These land-use changes have altered the prospects of many species across taxa, often leading to drastic declines of wildlife populations and biodiversity loss in agricultural landscapes (Foley et al. 2005; Lüscher et al. 2014; Stoate et al. 2001; Tschardt et al. 2005) on a range of spatial scales (e.g., Matson et al. 1997; Wenzel et al. 2006).

In the year 2011, about 38% of the global land area was used by agriculture with about 30% of it covered by arable land (FAO 2015, date accessed: 05.11.2016; see

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also Additional file 1). In the face of a growing world population and the predicted agricultural land expansion and further intensification (Tilman et al. 2011; Tilman et al. 2001), it becomes increasingly important to understand the ecological dynamics in agricultural landscapes in order to mitigate environmental degradation and to sustain ecosystem functioning in the future.

In this context, European bats (Chiroptera) represent a specifically interesting taxon for two reasons. Firstly, the negative consequences of agricultural intensification, such as habitat loss, fragmentation, and reduced prey abundance, are known to affect bat populations (Dietz et al. 2007; Mickleburgh et al. 2002) and have led to severe population declines, resulting in the current level of protection in Europe (Council of the European Union 1992). Secondly, bats might act as biological pest control agents in agricultural landscapes (Maine and Boyles 2015; Puig-Montserrat et al. 2015) which highlights their value as a component of temperate zone agroecosystems. With the increasing perception of bats as ecosystem service providers in agroecosystems (Boyles et al. 2011; Kunz et al. 2011), researchers started to investigate a range of different spatiotemporal effects on bat activity in agricultural landscapes. On a local scale, prey availability, diversity, and land-use intensity affect the activity of bats above farmland (Wickramasinghe et al. 2003). On a landscape scale, several factors, such as specific landscape elements (Akasaka et al. 2012; Lentini et al. 2012), landscape composition, and configuration (Frey-Ehrenbold et al. 2013; Kalda et al. 2014) are known to affect bat activity and diversity above farmland. Hereby, the spatial scale of landscape characteristics which affect bat activity can differ between bat species (Akasaka et al. 2012; Lintott et al. 2016). Due to species-specific adaptations in wing morphology (Norberg and Rayner 1987), bat species differ in flight characteristics, such as flight speed and maneuverability. These flight characteristics are associated with the bat species' mobility which can affect the spatial scale of habitat use (Bader et al. 2015). In addition, the habitat use of bats in agricultural landscapes changes with the season (Ciechanowski 2015; Heim et al. 2016) since it is tightly associated with the annual reproductive life cycle of most European bat species (Mackie and Racey 2007; Racey and Swift 1985).

Although previous studies investigated a large set of factors which are relevant for bat activity in agricultural landscapes, only a few included conventionally managed arable fields or focused on bat activity above arable fields (e.g., Ciechanowski 2015; Heim et al. 2016; Kelm et al. 2014; Lentini et al. 2012; Roeleke et al. 2016; Wickramasinghe et al. 2003). Additionally, studies that investigate not only specific factors but also their interactions are rare. For instance, by relating land-use intensity, insect abundance, and forest proximity to foraging attempts of

bats, Treitler et al. (2016) found more foraging attempts on grasslands near forests, yet only on extensively managed grasslands. Furthermore, Heim et al. (2015) found that the forest extent in the surrounding landscape of grasslands can be more important for bat activity above grasslands during early summer compared to late summer. Thus, more studies which investigate the interactions of effects from different spatiotemporal scales are needed in order to improve our understanding of how and why bats use the agricultural landscape and which factors determine their movements, including their foraging activity. Such information could help in making conservation efforts for these bat species more efficient.

Here, we aim at identifying a set of spatiotemporal factors and their interactions which are relevant for species-specific bat activity above conventionally managed arable fields. We distinguished between relative bat activity and foraging activity, as bats may forage above fields but also cross them while commuting between roosts and foraging sites. We predicted that the relative activity of bats above arable fields will be largely affected by large-scale landscape characteristics (e.g., composition, configuration) while relative foraging activity will be largely affected by local characteristics (e.g., prey availability, crop type, vegetation height).

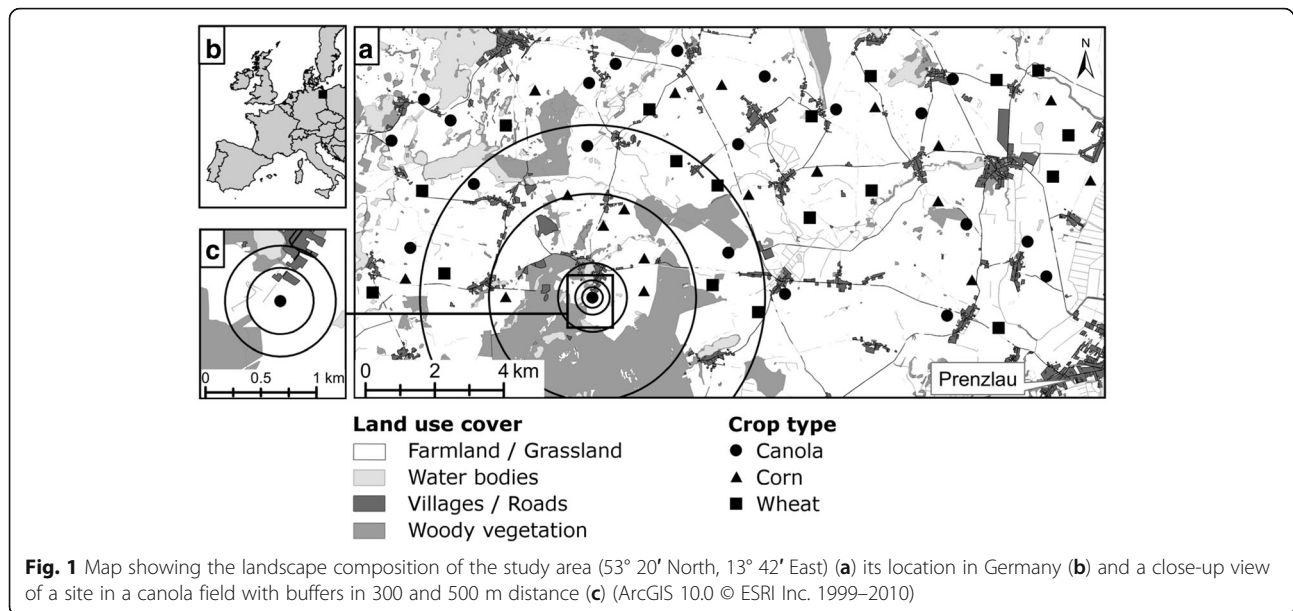
We hypothesized that the bat species' mobility is associated with the spatial scale of landscape characteristics which affect bat activity. In particular, we predicted that the relative activity of highly mobile bat species will be explained best by landscape characteristics on a relatively large spatial scale compared to the activity of less mobile bat species which should predominantly respond to landscape characteristics on a relatively small spatial scale.

Methods

Study area

We conducted our study within the framework of the "Agricultural Landscape Laboratories" (AgroScapeLabs, www.bbib.org/scapelabs.html). The study area of the AgroScapeLabs covers about 291 km² and is located in the Uckermark region (53° 20' North, 13° 42' East, Brandenburg, Germany, Fig. 1, for further details also refer to Heim et al. 2016).

This region is specifically interesting for our purpose as the amalgamation of small farms during socialist years (Behrens 2005) and the land-use change of the last 50 years resulted in large-scale changes creating large field units (20–75 ha; Katzschner 2011). These fields dominate the scenery and cover about 66% of the study area. Remnant forest patches (13%), grasslands (10%), water bodies (6%), and built-up areas (5%) represent a minor feature of the landscape. During summer, ambient temperature averages 17.4 ± 0.9 °C in Brandenburg (mean \pm STD calculated based on data from 1981 to



2010 of the DWD 2016) with a precipitation of 567.1 ± 81.8 mm per year (mean \pm STD calculated based on data from 1881 to 2016 of the DWD 2017).

Study design

The study design used here follows closely the design in the publication of Heim et al. (2016) as both studies were conducted simultaneously. We selected arable fields cultivated with corn ($N=18$), canola ($N=18$), and wheat ($N=17$) since these were frequently used crop types in the study region. These crop types are economically important, as wheat and corn are two of the top five most produced crops in the European Union in 2014 (157 and 61 Mtpa), while canola was produced to a lesser amount of about 24 Mtpa (FAO 2015). From May to September 2012, we repeatedly assessed relative bat activity on a total of 53 arable fields (Fig. 1) by using a passive acoustic monitoring approach (Batcorder 500 kHz sample rate, 16 bits; EcoObs GmbH, Nuremberg, Germany). We aimed at monitoring each site once per month. In total, each field was sampled one to four times with a mean value of 2.5 times.

Batcorders were located in >150 m distance to landscape elements, such as forest edges, hedges, water bodies, and built-up areas to avoid recording bat activity which is influenced by an edge effect at such landscape elements (Heim et al. in prep.; Kelm et al. 2014). Recordings of bat activity were conducted only during nights with no or light wind and no rain. We randomly selected six sites of different crop types for monitoring on any given night and recorded bat activity simultaneously with one Batcorder per site within the first 3.5 h after sunset, which includes the first peak of nocturnal

bat activity (Rydell et al. 1996). Hereby, the Batcorder thresholds were set to -36 dB and a critical frequency of 16 kHz. For further details, please refer to Heim et al. (2016).

Bat species identification

Out of the 24 bat species occurring in Germany, the following 13 bat species are known to occur regularly within the study region: *Nyctalus noctula*, *Nyctalus leisleri*, *Eptesicus serotinus*, *Vespertilio murinus*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Pipistrellus nathusii*, *Plecotus auritus*, *Barbastella barbastellus*, *Myotis myotis*, *Myotis nattereri*, *Myotis brandtii*, and *Myotis daubentonii* (Teubner et al. 2008). We decided to identify bat species manually to avoid potential misidentifications of common bat species by automatic identification software (Russo and Voigt 2016; Rydell et al. 2017). The procedure of bat species identification closely follows the procedure in the publication of Heim et al. (2016). We measured start, peak, and end frequencies of at least two calls per recording using Avisoft SASLab Pro (version 5.1.0, Avisoft Bioacoustics, Berlin Germany; settings: Hamming window, FFT = 512, overlap = 93.75%; time resolution = 0.064 ms, frequency resolution = 0.977 kHz). To identify the bat species, we compared the call shape and the measured frequencies with published data (e.g., Miller and Degn 1981; Obrist et al. 2004; Parsons and Jones 2000; Pfalzer and Kusch 2003; Russo and Jones 2003; Rydell 1990; Skiba 2003; for details, see Additional file 2).

Relative insect abundance

For the assessment of the relative abundance and diversity of airborne insects, we caught flying arthropods at

night using interception flight traps each equipped with a UV-light, a light sensor, and a plastic bottle filled with 70% ethanol attached to the cone of the trap. We trapped insects parallel to the recordings of the Batcorders. We used a distance of approximately 50 m to the recording site to avoid a bias of the insect trapping on the recorded bat activity, as bats might be attracted by the light of the insect trap. In the morning, insects were transferred into 99.8% ethanol for preservation. Later, we counted and categorized insects to order level using a stereomicroscope and identification keys (Köhler 2014). Additionally, we computed the Shannon Diversity Index per site on order level, based on the insect orders which occur in the study region. The insects which were caught on ground level (3 m above ground) might not represent the diet of bat species which forage at greater heights. Therefore, we included factors such as the local crop type, height, and vegetative status, which might affect insect abundance, diversity, or community composition on a larger scale, into our analysis. Thus, for each recording night and for each arable field, we estimated the crop height by measuring the height of several individual plants using a folding ruler (accuracy = ± 5 –10 mm) and documented the growth status of the crop based on two classes (1 = growing stage, empty field, or harvested; 2 = blooming and fruit building stage).

Landscape analysis

We used biotope and land-use vector maps of the federal districts of Brandenburg (BTLN 2009) and Mecklenburg-Western Pomerania (LUNG 2005). We reclassified landscape elements into six categories (see also Additional file 3): (i) agriculturally used areas (arable fields, grasslands); (ii) natural and semi-natural woody vegetation patches (forests, tree groups, tree lines, hedgerows); (iii) water bodies (≥ 1 ha, lakes, rivers); (iv) built-up area (buildings, sealed areas); (v) roads (streets, highways, railway); and (vii) kettle holes (< 1 ha; remnant small water bodies). We used ArcGIS 10.0 (© ESRI Inc. 1999–2010) to create buffers of 300, 500, 1000, 3000, and 5000 m radii around the monitoring sites (Fig. 1). Hereby, the selection of the buffer zone ranges was based on the nightly flight distances from the roost reported for the bat species that occur in the study region (Dietz et al. 2007; Entwistle et al. 1996; Nicholls and Racey 2006a; Roeleke et al. 2016). With Patch Analyst 5.0.1.60 (Rempel et al. 2012), we analyzed different characteristics of the above-defined landscape elements. We assessed aspects of landscape composition by calculating the percentage of land covered [$(\sum \text{land use area}/\text{buffer area}) \cdot 100\%$] by natural and semi-natural woody vegetation, water bodies, and built-up area patches within the respective buffer area to describe the amount of non-agriculturally used habitats. In order to describe aspects

of landscape configuration, we assessed the shape complexity of natural and semi-natural woody vegetation patches [m/ha] by calculating the mean perimeter-area ratio for this habitat category. In addition, we included the density of kettle holes [ha^{-1}] and the density of roads [m/ha] per buffer area, as kettle holes are very characteristic for this young glacial landscape and roads are known to influence bat activity on arable fields (Voigt and Kingston 2016; please see Additional file 4 for descriptive statistics).

Statistics

All statistical analyses were done in R (R Core Team 2014) and calculations of response variables are similar to the calculations in Heim et al. (2016). Following the one-zero time sampling approach (Martin and Bateson 1993), we divided a given night into 1-min intervals and counted the number of intervals with species-specific bat calls (Miller 2001) including both feeding buzzes and search calls. To obtain the measure *relative bat activity* for each species (hereafter: activity), we built a proportion based on the previously counted bat call intervals and the total number of 1-min intervals in a given night and site. To obtain the measure *relative foraging activity* for each species (hereafter: foraging activity), we counted the number of species-specific echolocation call sequences that indicate the pursuit of an insect, a so-called final buzz. Then, we counted the number of intervals with species-specific feeding buzzes and related this to the number of species-specific bat call intervals per night and site. Since both response variables are proportions, we used the binomial error distribution with the logit link in all following generalized linear mixed effects models (GLMMs).

Prior to model building, we tested for collinearity among explanatory variables using Spearman's rank correlation and included only variables with $\rho < 0.7$ in the same model (Dormann et al. 2013). As we were not primarily interested in the effects of abiotic factors (temperature, relative humidity, cloud cover, wind speed) although they are known to affect bat activity (Ciechanowski et al. 2007), we only controlled for factors which were significantly correlated with the response variable within the respective models in a preceding analysis. As a result, we added the ambient air temperature to candidate models which explained activity and foraging activity of *N. noctula* ($\text{BA}_p: \rho = 0.27, p < 0.01$; $\text{FA}_p: \rho = 0.34, p < 0.001$) and *P. pygmaeus* ($\text{BA}_p: \rho = 0.26, p < 0.01$; $\text{FA}_p: \rho = 0.22, p < 0.05$), respectively. As seasonality is known to have a strong effect on bat activity in agricultural landscapes (Heim et al. 2016), we included Julian day as a covariate into all models. Furthermore, we log-transformed insect abundance, kettle hole density, and the percentage of water cover and of vegetation cover

and scaled all variables before fitting GLMMs. Prior to model fitting, we explored the shape of the relationship between response and explanatory variables via generalized additive mixed models (mgcv::gamm4, Wood and Scheipl 2014). For that, we used the full model, a cubic regression basis and a random factor for recording site and fitted smoothing splines with four knots. Only the covariate “season” was associated with the activity of *N. noctula*, *P. pipistrellus*, and *P. pygmaeus* in a quadratic manner. Thus, we added a second order polynomial function of the covariate season to the respective set of candidate GLMMs.

The resulting 29 candidate models were based on our hypotheses and can be divided into four spatiotemporal factor sets based on local predictors (assessed on the scale of the site), landscape predictors across different spatial scales (landscape), temporal predictors (season) and their combinations, and the null model (Table 1).

The first set contained models with local factors (crop type, height and status, insect abundance, and diversity), while the second set contained models with factors representing landscape characteristics only (Table 1). Hereby, variables in each section interacted with the season to identify whether effects change across seasons. In the third section, site-related variables were allowed to interact with each other and the season. In the fourth section of models, we combined landscape factors from

each spatial scale with site-related factors and allowed them to interact with each other and with the season. This section contained also the global models with variables from all subsections combined (Table 1). For each species and response variable, we fitted all 29 GLMMs with the ID of the respective recording site as a random factor. We included an observation-level random effect where each data point received a unique level of a random effect, into the model of the activity of *N. noctula* to correct for overdispersion of the residuals (Harrison 2014). We checked the model fit by examining model residuals graphically using binned plots and tested for spatial autocorrelation (package ncf (Bjornstad 2016) based on Moran’s I). Hereby, we did not detect any signs of spatial autocorrelation in the residuals of the models. Then, we compared and ranked candidate models using the Akaike information criterion corrected for small sample sizes (AICc). By comparing all models to the null model, we tested whether any additional covariates explained more variance than the null model. By comparing the models from the first and second section to the third and fourth section, we tested whether and which combination of factor sets explains species-specific activity and foraging activity best or whether only landscape, local, or temporal effects are relevant. Furthermore, we were able to identify either one or several important spatial scales at which landscape characteristics explain

Table 1 Candidate models are grouped into four factor sets and the null model: models with covariates related to local conditions at the site, models containing measures of landscape characteristics across five spatial scales, one model with a combination of local covariates, and models with various combinations of local and landscape-related covariates

| | Model no. | Scale [km] | Insect | | Crop | | | Cover [%] | | | Complexity | Density | | Season |
|------------------------------|-----------|----------------|----------------|-------------------|------------------|--------|------------------|------------|-------|----------|-------------------|----------------------------|-------------------|------------------|
| | | | Abundance | Diversity | Height [cm] | Status | Type | Vegetation | Water | Built-up | Vegetation [m/ha] | Kettle [ha ⁻¹] | Road [m/ha] | |
| Null model | 1 | | | | | | | | | | | | | |
| Local | 2 | | (+) | (+) ^a | | | | | | | | | | + ^a |
| | 3 | | | | + ^a | | | | | | | | | + ^a |
| | 4 | | | | | (+) | (+) ^a | | | | | | | + ^a |
| Landscape | 5–8 | 0.3–3 | | | | | | (+) | (+) | (+) | (+) | (+) | (+) | + ^a |
| | 9 | 5 | | | | | | | (+) | (+) | (+) | | (+) ^a | + ^a |
| | 10 | 5 | | | | | | (+) | (+) | | | (+) | (+) ^a | + ^a |
| Local combined | 11 | | (+) | (+) ^{ab} | + ^{b,c} | | | | | | | | | + ^{a,c} |
| Local and landscape combined | 12–15 | 0.3–3 | + ^b | | | | | (+) | (+) | (+) | (+) | (+) | (+) ^{ab} | + ^a |
| | 16 | 5 | + ^b | | | | | (+) | (+) | (+) | | | (+) ^{ab} | + ^a |
| | 17 | 5 | + ^b | | | | | (+) | (+) | | (+) | | (+) ^{ab} | + ^a |
| | 18–21 | 0.3–3 | | | (+) | | | (+) | (+) | (+) | (+) | (+) | (+) ^{ab} | + ^a |
| | 22 | 5 | | | (+) | | | (+) | (+) | (+) | | | (+) ^{ab} | + ^a |
| | 23 | 5 | | | (+) | | | (+) | (+) | | (+) | | (+) ^{ab} | + ^a |
| | 24–27 | 0.3–3 | + ^b | | (+) | | | (+) | (+) | (+) | (+) | (+) | (+) ^{ab} | + ^a |
| | 28 | 5 | + ^b | | (+) | | | (+) | (+) | (+) | | | (+) ^{ab} | + ^a |
| 29 | 5 | + ^b | | (+) | | | (+) | (+) | | (+) | | (+) ^{ab} | + ^a | |

Abbreviations: kettle density of kettle holes (small water bodies), season Julian day, + covariate included in model, +^{a,b} superscript letters indicate interactions: covariates with the same letter interact with each other; the interaction applies to all factors within the brackets

bat and foraging activity best. If no single best model with an AICc weight (w_i) of ≥ 0.9 could be identified after model ranking, we compiled a 90% confidence set of models (Burnham and Anderson 2002). In those cases where nested models occurred within the 90% confidence set of models, we selected the most parsimonious model for inference (for an overview of 90% confidence set of models, see Additional file 5). In a further step, we inspected the estimates of all covariates in the model and present only those covariates which showed an effect.

Results

Overall bat activity and comparison of overall activity between bat species

Out of 7409 bat recordings with at least two echolocation calls, we identified 6543 recordings (88.3%) to species level, 345 (4.7%) recordings to single-genus level (*M. bra/dau*, *Pipistrellus* sp., *Myotis* sp.), and 521 (7%) recordings to multi-genus level (Nyctaloid, unidentifiable; see also Additional file 6). Out of the 34,138 1-min intervals from 28 nights where a bat could have been recorded, only 3766 1-min intervals contained bat calls, which equaled an overall bat activity of about 11%. Out of these 3,766 1-min intervals, 12.4% were associated with feeding buzzes (Additional file 6).

Nyctalus noctula was the most frequently recorded bat species, making up about 35% of all recordings and occurring in about 85% of recording occasions (Additional file 6), while the three pipistrelles *P. nathusii*, *P. pygmaeus*, and *P. pipistrellus* were less often recorded (16, 11, and 6%, respectively). Although the three pipistrelles were less active than *N. noctula*, they occurred in about 55 to 80% of recording occasions (Additional file 6).

With about 3 and 0.7%, respectively, *M. bra/dau* and *M. nattereri* were the least often recorded species (Additional file 6). Since GLMMs for these bat species did not converge or fitted badly, they had to be excluded from further analyses.

Local and landscape-scale effects

Bat activity was best explained by a combination of landscape characteristics and local factors (Table 2, for details on random effects, see Additional file 7). The only exception was the activity of *P. pygmaeus*, which was best explained exclusively by landscape characteristics and the season (Table 2, Additional file 8).

We found that landscape characteristics often affected the correlation between insect abundance and bat activity (Fig. 2, see Additional file 9 for a tabular overview).

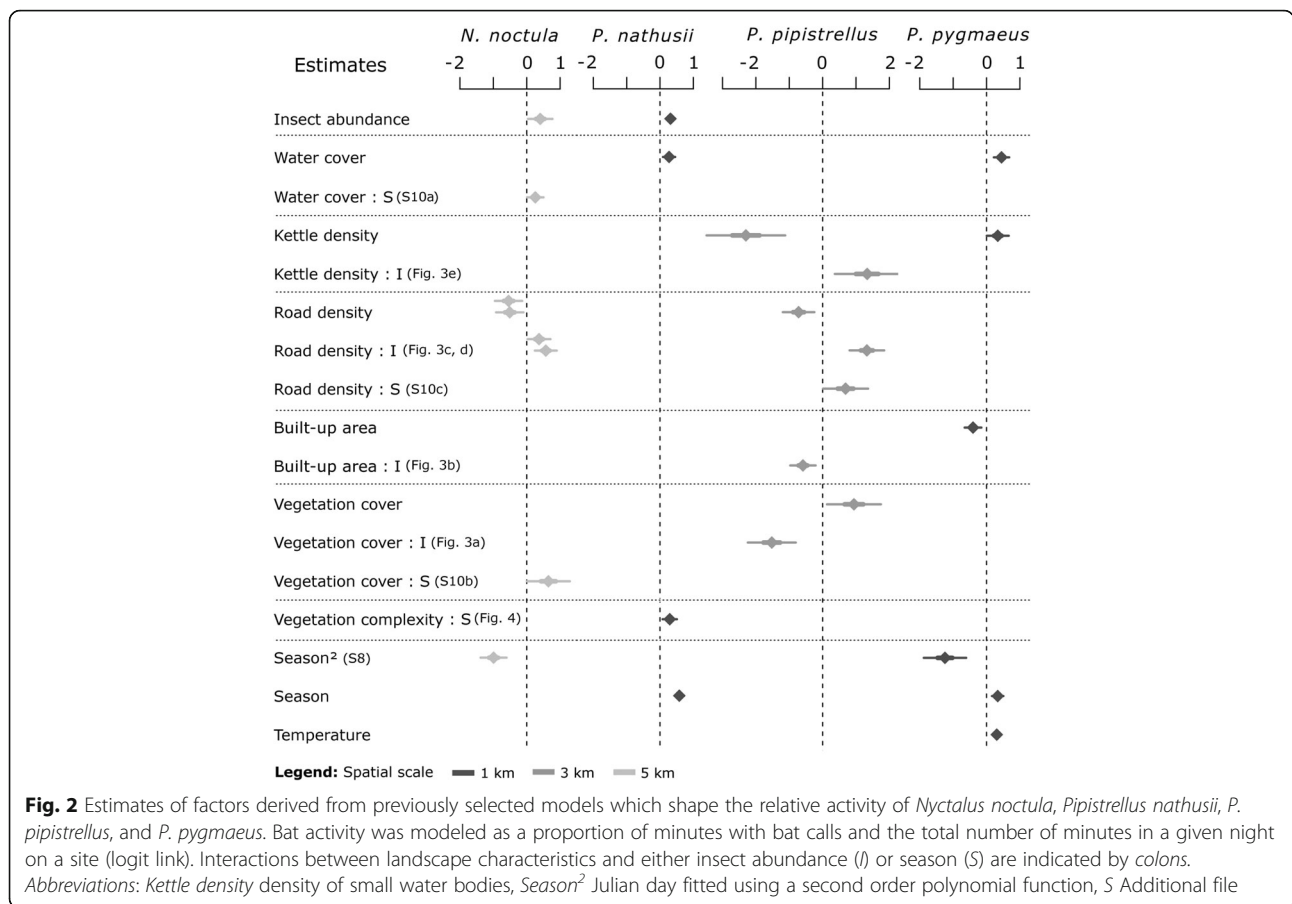
In particular, the direction of this correlation shifted depending on the condition of landscape characteristics (Fig. 3).

For example, *P. pipistrellus* activity decreased with increasing insect abundance above fields with a high proportion of woody vegetation cover and built-up area (Fig. 3a, b). On fields with a low proportion of woody vegetation cover and built-up area, *P. pipistrellus* bats were more active when insect abundance was high. In contrast to this pattern, we found that the activity of *N. noctula*, for instance, was positively correlated with insect abundance above fields surrounded by a relatively high density of roads (Fig. 3c). Similarly, *P. pipistrellus* bats were more active with increasing insect abundance above fields with a relatively high road and kettle hole density (Fig. 3d, e). In contrast, on fields with a relatively

Table 2 Summary of the best generalized linear mixed effect models fitted to species-specific relative bat activity (BA_p) and foraging activity (FA_p) using the binomial error distribution. All 29 candidate models (see *model no.* in Table 1) were compared via AICc to identify the best model ($w_i \geq 0.9$; w_i is the weight of evidence of a model given the set of models; based on Burnham and Anderson (2002)). If no best model was found, we used the 90% confidence set of models for inference by summing up models from top to bottom until the accumulated number of weights reached $w_i = 0.9$ ($\sum w_i$). Here, we present only the most parsimonious models, so that $\sum w_i$ values are smaller than 0.9 (complete overview in Additional file 5)

| | Factor sets | Scale [km] | df | log(L) | AICc | Δ_i | w_i | $\sum w_i$ | $R^2_{cond.}$ | Model no. |
|------------------------------|------------------------------|------------|----|---------|-------|------------|-------|------------|---------------|-----------|
| BA _p | | | | | | | | | | |
| <i>Nyctalus noctula</i> | Local and landscape combined | 5 | 19 | -370.96 | 786.6 | 0 | 0.50 | 0.61 | 0.25 | 17 |
| | | 5 | 19 | -372.46 | 789.6 | 3.00 | 0.11 | | 0.25 | 16 |
| <i>Pipistrellus nathusii</i> | Local and landscape combined | 1 | 22 | -284.21 | 621.5 | 0 | 0.39 | 0.60 | 0.25 | 14 |
| <i>P. pipistrellus</i> | Local and landscape combined | 3 | 23 | -178.79 | 413.6 | 0 | 0.75 | 0.75 | 0.30 | 15 |
| <i>P. pygmaeus</i> | Landscape | 1 | 17 | -247.74 | 534.7 | 0 | 0.64 | 0.64 | 0.33 | 7 |
| FA _p | | | | | | | | | | |
| <i>N. noctula</i> | Local combined | | 12 | -124.66 | 275.9 | 0 | 0.99 | 0.99 | 0.23 | 11 |
| <i>P. nathusii</i> | Local combined | | 11 | -60.22 | 144.6 | 0 | 0.99 | 0.99 | 0.40 | 11 |
| <i>P. pygmaeus</i> | Null model | | 2 | -68.79 | 141.7 | 0 | 0.66 | 0.66 | 0 | 1 |

Abbreviations: $\log(L)$ log likelihood, AICc Akaike information criterion corrected for small sample sizes, Δ_i difference in AICc values related to the best model, $R^2_{cond.}$ conditional pseudo R^2 gives the explained model variation including random factors



low road and kettle hole density, *P. pipistrellus* bats were less active with increasing insect abundance.

Spatial scale of landscape effects

In accordance with our expectations, the activity of *N. noctula* and *P. pygmaeus* was best explained by landscape characteristics at 5 and 1 km, respectively. However, the activity of *P. pipistrellus* was best explained by landscape characteristics on a 3-km scale, while the activity of *P. nathusii* was best explained by landscape characteristics on a 1-km scale (Table 2).

Degree of bat activity during summer depends on landscape characteristics

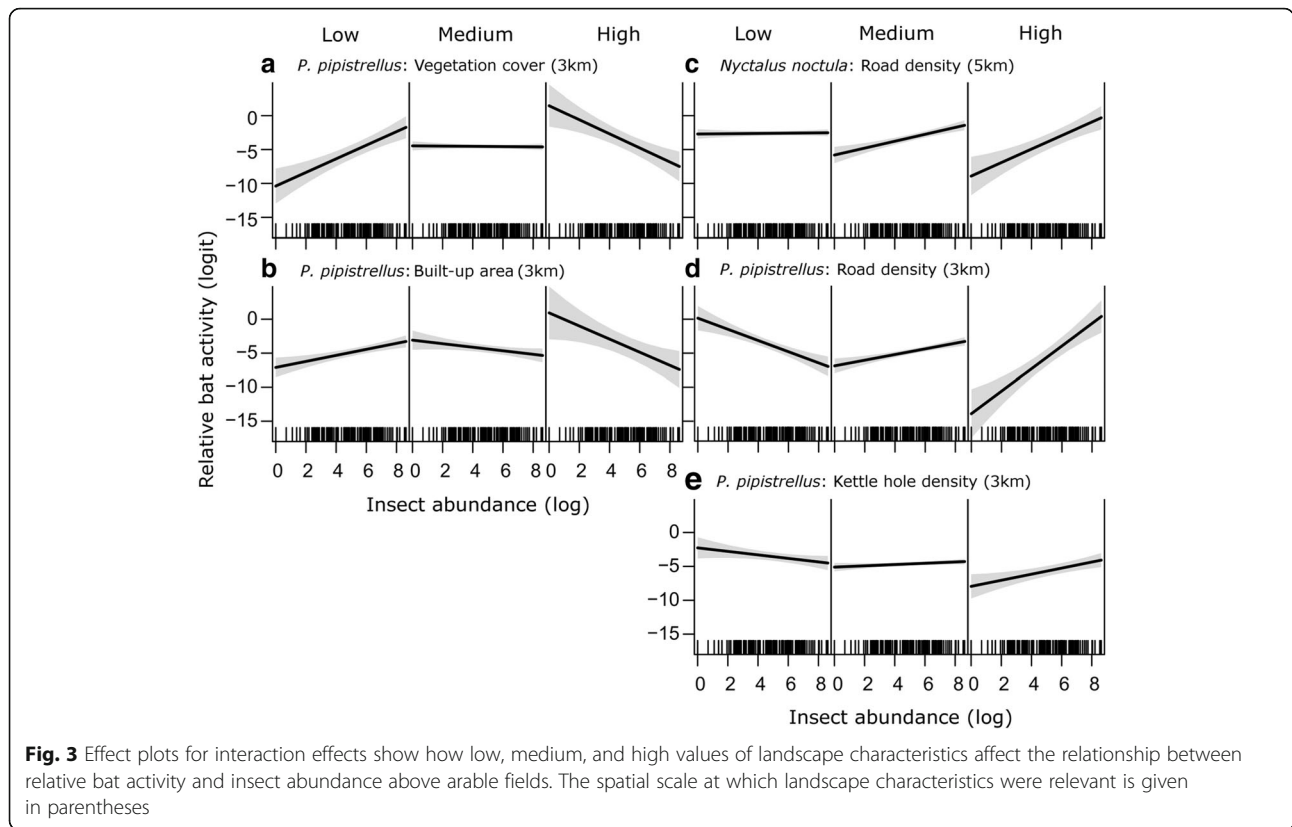
Interactions of landscape characteristics with the season occurred only in the models of *N. noctula*, *P. nathusii*, and *P. pipistrellus* (Fig. 2). In particular, depending on the parameter value of a landscape characteristic (low, medium, or high), bat activity above the arable field either varied across seasons or remained relatively high and independent of the season (Fig. 4, Additional file 10).

For example, the activity of *P. nathusii* was lowest in June/July and increased until September above fields that were surrounded by vegetation patches with a

relatively high degree of edge complexity (Fig. 4). However, the activity of *P. nathusii* did not differ between seasons above fields with a relatively low degree of vegetation complexity in the surrounding landscape. We found similar patterns in the interactive effects of water and vegetation cover with the season which influenced the activity of *N. noctula* and in the interactive effect of road density with the season which influenced the activity of *P. pipistrellus* (Additional file 10). Interestingly, all these patterns indicate that the changes in bat activity were strongest in summer, whereas activity in autumn remained on a relatively high and constant level.

Comparison of relevant effects across bat species

The activity of the three pipistrelles *P. nathusii*, *P. pipistrellus*, and *P. pygmaeus* was affected by similar landscape characteristics on similar spatial scales, however partially in opposite ways (Fig. 2). For instance, the amount of water cover and the density of kettle holes were associated positively with the activity of *P. pygmaeus*, while the kettle hole density was negatively associated with the activity of *P. pipistrellus*. Also, the activity of *P. pipistrellus* was positively associated with built-up areas, which were negatively related to the activity of *P. pygmaeus*. In addition, we found a



positive effect of the percentage of woody vegetation cover on the activity of *P. pipistrellus* above farmland. Interestingly, the activity of *P. nathusii* was positively associated with the amount of water cover on the scale of 1 km which was also the case for *P. pygmaeus* and for *N. noctula*, however on a larger spatial scale and in interaction with the season.

Effects on species-specific foraging activity

The foraging activity of *N. noctula* and *P. nathusii* was best explained by a combination of factors related to

prey availability and crop characteristics on the arable field and seasonal effects (Table 2, for information on random effects, see Additional file 7).

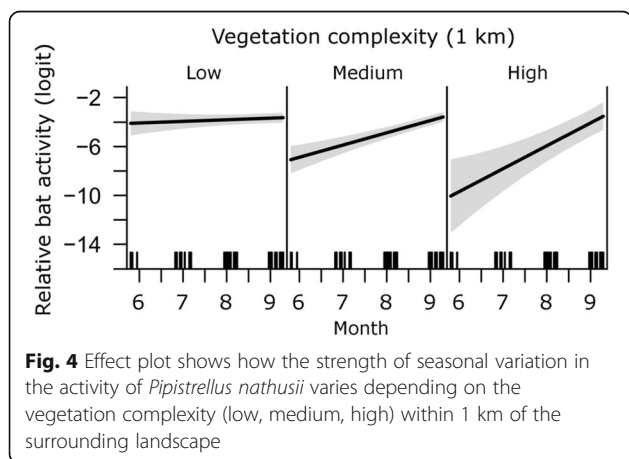
In general, crop height, insect diversity, and abundance on the sampled fields varied in the course of the recording period (Fig. 5).

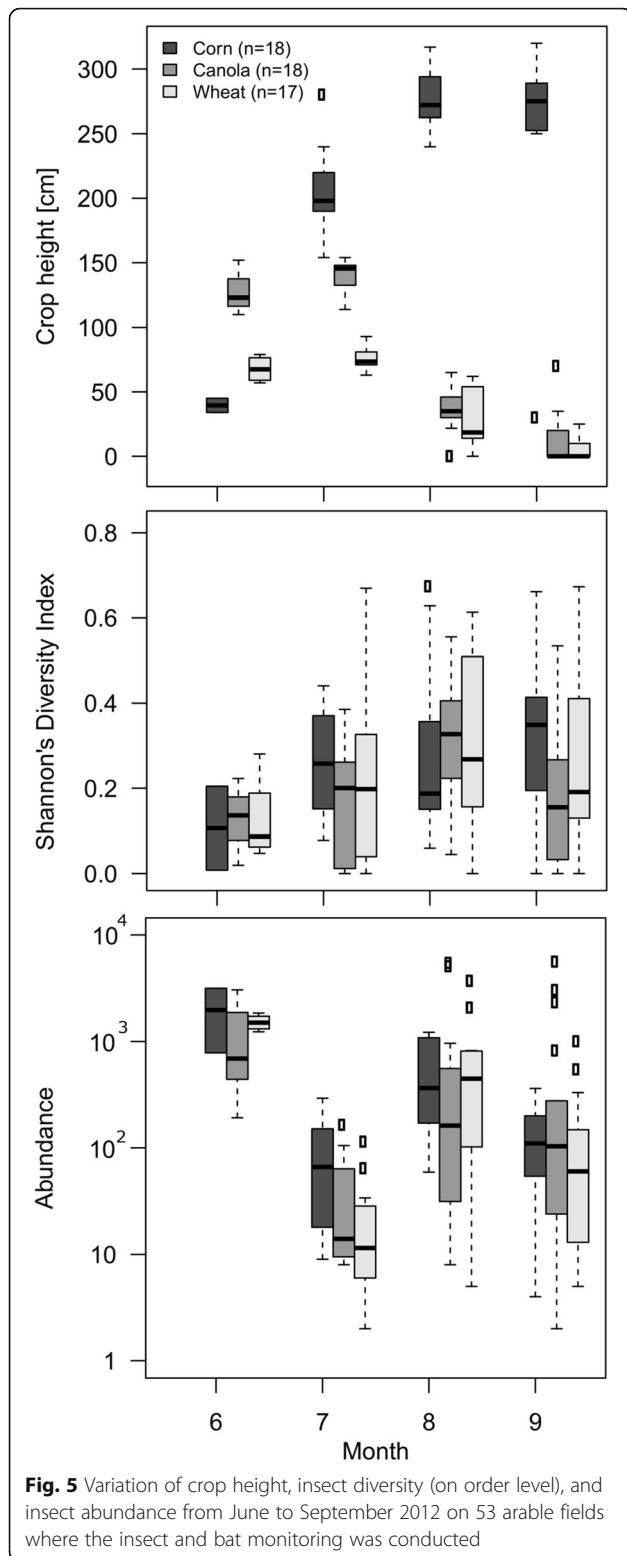
Overall, about 79% of the insects captured on all fields belonged to the order of Diptera (Additional file 11). The majority of the remaining insects belonged to the orders Coleoptera, Heteroptera, and Lepidoptera (about 10, 6, and 2%, respectively).

Foraging activity of both *N. noctula* and *P. nathusii* was positively affected by the crop height (Fig. 6), which interacted with the insect diversity in the model of *N. noctula* and with the insect abundance in the model of *P. nathusii* (Fig. 6, see Additional file 12 for tabular representation).

Hereby, *N. noctula* bats foraged most intensively at low to medium insect diversity values on fields with very tall crops (Fig. 7a). In contrast, *P. nathusii* foraged most intensively on fields with tall crops independent of whether insect abundance was high or low (Fig. 7b).

Furthermore, we found that the foraging activity of *N. noctula* increased across months with the highest activity in September, whereas the foraging activity of *P. nathusii* was highest in June and decreased linearly until September. Interestingly, none of the used factors could





explain the foraging activity of *P. pygmaeus* above fields, while the foraging activity of *P. pipistrellus* could not be modeled due to insufficient numbers of recorded feeding buzzes.

Discussion

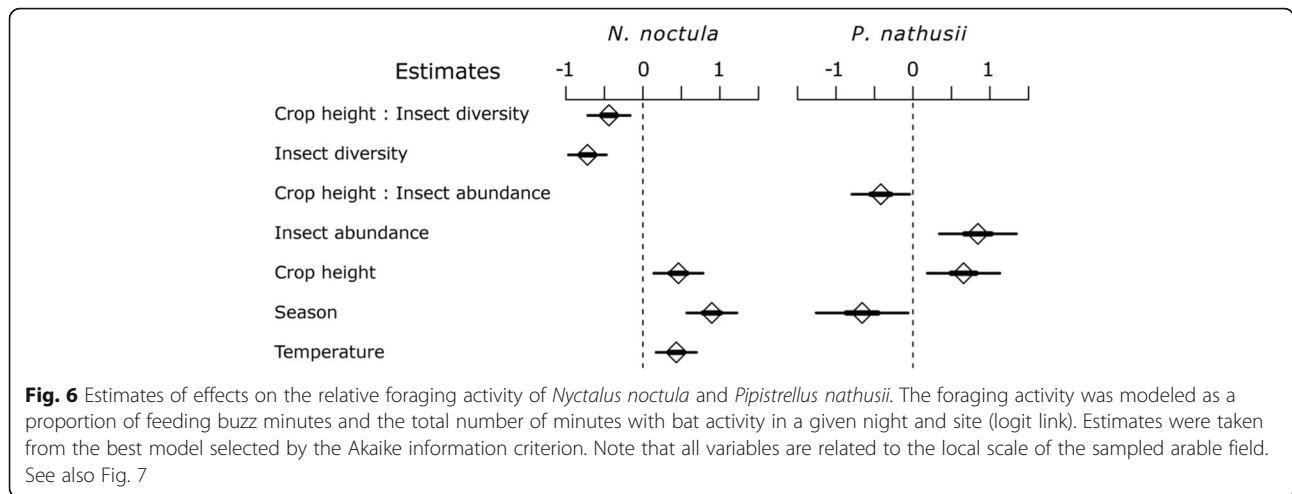
We asked how European bat species use arable fields in a landscape dominated by conventional agriculture. To answer this question, we recorded the relative activity and foraging activity of bats at our study site in Germany which is dominated by intense agriculture.

We found a relatively low overall bat activity above arable fields compared to the bat activity above grasslands and in woodlands in a heterogeneously structured landscape only 50 km away from our study site (Heim et al. 2015; Jung et al. 2012; Treitler et al. 2016). The predominant bat species at our study site was *N. noctula*, followed by *P. nathusii*, *P. pipistrellus*, and *P. pygmaeus*. Bats belonging to the genus *Myotis* were least abundant. A combination of landscape scale, local, and seasonal effects explained the activity of most of the investigated bats.

In particular, we discovered that the influence of landscape characteristics could shift the correlation between bat activity and insect abundance into both positive and negative directions depending on the landscape characteristic condition, such as a high or low amount of water cover, and the type, such as whether it is water cover or road density. Furthermore, we found that the effect of landscape characteristics on the activity of *N. noctula* and *P. nathusii* above arable fields was associated with stronger variation in bat activity during summer compared to autumn. Finally, we found that the foraging activity of *N. noctula* and *P. nathusii* was explained by similar factors (crop height, insect related factors, and season). Yet, differences in the effects of relevant factors between bat species suggest that bats, although using the same foraging strategy of aerial hawking, might behave differently while foraging above arable fields.

Species-specific activity patterns

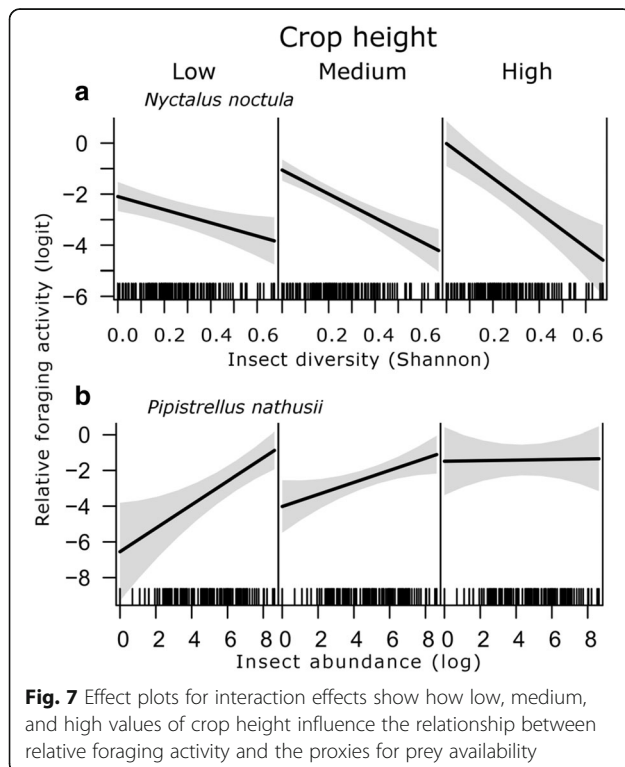
The observed differences in overall activity levels across bat species in this study were similar to those reported for grasslands embedded in a heterogeneously structured landscape about 50 km away from our study region (e.g., Heim et al. 2015; Jung et al. 2012; Treitler et al. 2016). The high abundance of *N. noctula* may best be explained by the numerous maternity roosts which are located in the study area. Furthermore, the differences in overall activity levels between bat species might reflect not only the abundance patterns but also their preferences for specific habitats (see Additional file 13 for details). *Nyctalus noctula* is well adapted to forage in the open space, while *P. pipistrellus* and *P. pygmaeus* use mostly the contact zone between arable fields and forests or hedges, the so-called edge-space (Heim et al. unpublished data). *Myotis* species are well adapted to forage in cluttered space and are therefore expected to avoid open space. Interestingly, although *P. nathusii* is categorized as an edge-space species, it appears to use the open



space to a higher degree compared to the other two pipistrelle species (Kelm et al. 2014) and appears to be less dependent on linear woody landscape elements.

Landscape characteristics affect the relationship between bat activity and insect abundance

We found two distinct ways how landscape characteristics influence the relationship between bat activity and insect abundance on arable fields. Firstly, bat activity above arable fields was negatively correlated with insect abundance, if landscape characteristics with a positive effect on bat activity were present in the surrounding.



For example, the activity of *P. pipistrellus* decreased with increasing insect abundance on arable fields with a relatively high amount of woody vegetation cover nearby, which seems contradicting. However, if we assume that the insect abundance measured on arable fields reflects an even higher abundance near, e.g., woody vegetation edges due to the accumulation of insects near such structures through wind (Lewis 1969), then our results indicate that *P. pipistrellus* might be drawn from arable fields to edges of woody vegetation in the surrounding landscape. This interpretation is confirmed by results obtained by Treitler et al. (2016) who found less feeding attempts of bats on grasslands further away from forests compared to grasslands close to forests. Secondly, we found that bat activity was positively correlated with insect abundance on arable fields if landscape characteristics were unfavorable in the surrounding. For instance, we observed that the activity of *N. noctula* and *P. pipistrellus* was positively correlated with insect abundance on the arable field if the surrounding was characterized by a relatively high road density and kettle hole density, respectively. Although *N. noctula* is expected to be least affected by the negative effects of roads due to its independence from linear landscape structures during navigation and its feeding high above the ground, it still can be found as roadkill on roads in other regions of the world (Altringham and Kerth 2016). Thus, the negative effect of road density on *N. noctula* found here highlights that this effect might be underestimated for *N. noctula* at least in landscapes dominated by agriculture. *P. pipistrellus* is not known to specifically select aquatic habitats such as kettle holes such as its sibling species *P. pygmaeus* (Lintott et al. 2016). Therefore, one possible explanation for the above-described positive relationship between *N. noctula* and *P. pipistrellus* activity and the insect abundance above the arable field might be that bats avoid unfavorable conditions associated with nearby

landscape characteristics and instead make use of any elevated insect abundance above arable fields. These two patterns potentially point towards a trade-off between the foraging above arable fields, which might offer less prey, and the foraging in other habitats in the surrounding, which probably harbor more prey, but might be associated with increased competition or other risks.

In general, our results underline the flexibility with which bats efficiently use limited resources, such as patches of insects above arable fields. Hereby, the landscape composition and configuration appears to be of importance. Therefore, the potential provisioning of ecosystem services by bats above arable fields might also depend on landscape characteristics.

The level of bat activity above arable fields during summer depends on landscape characteristics

We found that depending on the parameter value (low, medium, or high) and type of landscape characteristics, bat activity either remained on a relatively high level across seasons or decreased to lower levels in summer, which represents the most energy demanding time period of reproduction (Fig. 4, Additional file 10). Our results indicate that landscape elements might be more important during summer than during autumn in defining bat activity. Largely motivated by movements between foraging grounds, bat activity during summer might be more strongly associated with landscape characteristics than bat movements during autumn which include dispersal of young bats and movements related to mating and migration. Our results indicate furthermore that the suitability of arable fields as foraging habitats for bats during summer might depend on the characteristics of the landscape. For instance, during summer, *N. noctula* bats were more active on arable fields with a relatively high water cover in the surrounding, while the activity of *P. nathusii* decreased with an increasing degree of vegetation complexity. To our knowledge, seasonal changes in the importance of landscape elements were rarely investigated. However, Heim et al. (2015) found that the effect of forest cover in a 200-m buffer around grasslands was more important for overall bat activity above grasslands during summer compared to autumn. Furthermore, Kelm et al. (2014) found an indication for such an effect in association with hedgerows in agricultural landscapes. Thus, our results confirm that the importance of landscape elements for bat activity—at least above open fields—can change across seasons. Additionally, this effect appears to represent a general pattern as it occurs in different bat species and is for each species, except *P. pygmaeus*, associated with different types of landscape features. Potentially, this effect is specifically important for bat species which use

predominantly the open space for foraging or are migratory, which is both the case for *N. noctula* and *P. nathusii*.

Relative activity of insectivorous aerial-hawking bat species differs on three levels: habitat use, diet composition, and spatial scale

Based on the type of landscape characteristic which affected the activity of *P. pipistrellus* and *P. pygmaeus* and the direction of the effect, we assume that these two species differ in habitat use preferences. Our results are supported by past studies on the habitat use of these two cryptic bat species (Jung et al. 2012; Nicholls and Racey 2006b; Russ and Montgomery 2002; Vaughan et al. 1997). Even in urban landscapes, the proportion of freshwater had a similar effect on both species (Lintott et al. 2016). Thus, these two cryptic sibling bat species appear to differ in habitat use preferences across different landscape types.

In contrast, *P. nathusii* appears to overlap to some degree with the way both *P. pygmaeus* and *N. noctula* use arable fields. However, the differences in arable field use might be sufficiently high to allow bats to avoid potential competition. For example, our results on the foraging activity of *N. noctula* and *P. nathusii* indicate that both species might differ on the level of the foraging behavior above arable fields. In particular, *P. nathusii* might focus on the overall insect abundance, as these bats foraged most intensively at high insect abundance values irrespective of the crop height (Fig. 6). This interpretation is supported by our finding that the overall abundance of insects was dominated by the order of Diptera (Additional file 11), which was reported to play a major role in the diet of this bat species (Krüger et al. 2014; Smirnov and Vekhnik 2014; Vaughan 1997). In contrast, *N. noctula* foraged most intensively at low insect diversity values above arable fields with the tallest crops (Fig. 6). Interestingly, the lowest third of insect diversity (0–0.22 Shannon's Diversity Index) on fields with the tallest third of crops (>214 cm) was largely associated with insects caught on corn fields in August. Under these conditions we caught slightly less Diptera, but relatively more Lepidoptera, Trichoptera, and Coleoptera (Additional file 14), which represent important prey items for *N. noctula* (Gloor et al. 1995; Kaňuch et al. 2005; Smirnov and Vekhnik 2014; Vaughan 1997). Therefore, we hypothesize that *N. noctula* might focus on specific insects that might be associated with corn. This is a very interesting topic which can serve as a starting point for future investigation, also in the context of ecosystem service.

In addition to differences in landscape characteristic types and foraging activity, also, the scale at which landscape characteristics affected bat activity differed across

bat species. Our expectations regarding the relationship between the scale of landscape characteristics and the bat species' mobility were not entirely met. In the study region, *N. noctula* covered an average distance of 15 to 27 km (Roeleke et al. 2016), while *P. nathusii*, *P. pipistrellus*, and *P. pygmaeus* covered a mean maximum flight range of 7 km (Dietz et al. 2007) and 2 km (Davidson-Watts and Jones 2006), respectively. Based on these values, our expectations were met only for *N. noctula* and *P. pygmaeus*. Although *P. pygmaeus* and *P. pipistrellus* should be similar to their flight ranges (Davidson-Watts and Jones 2006), the activity of *P. pipistrellus* was best explained by landscape characteristics on a larger spatial scale of 3 km as compared to *P. pygmaeus*. However, Nicholls and Racey (2006a) found that the home range size of individual *P. pipistrellus* was three times as large as the home range size of *P. pygmaeus*, which would support our findings on the one hand. On the other hand, the roosts of the radio-tracked *P. pipistrellus* and *P. pygmaeus* in the study of Nicholls and Racey (2006a) were located in very different landscape types. Thus, the home range size differences between both species might be a result of differences in a landscape specific resource distribution and not based on species-specific differences. Furthermore, the activity of *P. nathusii* was expected to be best explained by landscape characteristics on a relatively large spatial scale, as *P. nathusii* covers relatively large distances (Dietz et al. 2007). However, we found that the activity of *P. nathusii* was best explained by landscape characteristics on the spatial scale of 1 km, which is similar to the spatial scale obtained for *P. pygmaeus*. As our results do not completely match the predictions, we assume that the relationship between mobility and the spatial scale of relevant landscape characteristics might be influenced by additional factors such as the distribution of resources in the surroundings of the arable field, or the scale at which a species perceives these resources.

Conclusions

We gained novel insights on how insectivorous aerial-hawking European bat species use large conventionally managed arable fields in a landscape dominated by conventional agriculture. One of the key findings is that landscape characteristics of the surrounding farmland affect the relationship between bat activity and insect abundance. Thus, we would expect that changes in landscape structures around open fields translate into changes in the way bats use the open space above these areas.

The predicted increase in land-use intensity and area of arable fields in the near future could lead to further simplification of the landscape structure. Additionally, the insect abundance and especially the insect diversity

could be further reduced. Already today, the low insect diversity due to the intensification of agricultural management is alarming (Benton et al. 2002; Biesmeijer et al. 2006). As a consequence of landscape structure, homogenization and reduction of arthropod diversity processes like natural pest control might get disrupted (Tschardt et al. 2005) potentially leading to more frequent or severe pest insect outbreaks (Bianchi et al. 2006; Gardiner et al. 2009; Zhao et al. 2015). Therefore, it is important to increase the heterogeneity of agricultural landscapes in order to maintain and increase the control of pest insects by beneficial arthropods and bats.

In addition, we are still far away from understanding resource partitioning dynamics between bat species even in such a relatively simple landscape and bat ensemble structure, although we did observe potential patterns of resource partitioning in this study. Since the predicted continuation of land-use change might lead to increased competition among bat species through further changes in insect community structure and reduced area of refuge habitats, it becomes increasingly important to further investigate the interactions between species.

Based on our results, we recommend increasing the density of woody vegetation patches as well as promoting linear landscape elements to facilitate connectivity, which might be beneficial especially for edge-space bats and bat species from the *Myotis* group which were rarely recorded in this study. Furthermore, conservation measures should aim to preserve wetlands, such as lakes, rivers, and kettle holes, since these appear to be important areas for many aerial-hawking insectivorous bats. Finally, the large-scale increase in arthropod abundance and diversity should be the main aim of conservation efforts in intensively managed agricultural landscapes, as arthropods represent the fundamental source of energy not only for insectivorous bats but also for many other organisms in the agroecosystem.

Additional files

Additional file 1: Percentage of total land area occupied by agriculture and arable fields worldwide in 2011. Data were downloaded from the database of the Statistics Division of the Food and Agriculture Organization of the United Nations (FAO 2015, <http://faostat3.fao.org/compare/E>, date accessed: 05.11.2016) (EPS 972 kb)

Additional file 2: Description of bat species identification from echolocation call recordings. (DOCX 15 kb)

Additional file 3: Reclassification of original landscape element classes into five broader classes. (DOC 32 kb)

Additional file 4: Descriptive statistics for abiotic and biotic factors on a local scale of the site and landscape characteristics for each spatial scale. (DOC 73 kb)

Additional file 5: Summary of the best generalized linear mixed effect models. Models (see model no. in Table 1) were fitted to species-specific relative bat activity (BA_p) and foraging activity (FA_p) using the logit link. A 90% confidence set of models was compiled if no best model was

selected via AICc. We selected the most parsimonious models (in bold letters) if subsets of models from the same spatial scale occurred in the same 90% confidence set. (DOC 48 kb)

Additional file 6: Summary (total number and percentage) of analyzed bat call recordings, 1-min intervals with bat calls (bc), feeding buzzes (fb), and occurrence per night and site (occ). (DOC 44 kb)

Additional file 7: Summary of random effect variances and standard deviances. Values were taken from selected generalized linear mixed effect models fitted to the relative bat activity (BA_p) and foraging activity (FA_p) using the logit link. (DOC 40 kb)

Additional file 8: Seasonal variation in relative activity of *Pipistrellus pygmaeus* above intensively used arable fields from June to September 2012. (EPS 392 kb)

Additional file 9: Results from an ANOVA (type II Wald χ^2 test) show which covariates (all 1 degree of freedom) from the best generalized linear mixed effect models affected relative bat activity. In the case of *Nyctalus noctula*, two models were selected as a 90% confidence set. Interactions between landscape characteristics and either insect abundance (I) or season (S) are indicated by colons. Interactions of vegetation complexity and water cover each with insect abundance as well as the interaction of kettle hole density (small water bodies) and the built-up area each with season were never significant. Also, the vegetation cover and complexity alone were never significant. Interactions which were plotted in graphs are marked in bold. (DOC 52 kb)

Additional file 10: Interaction effect plots. Graphs depict the interaction effect between landscape characteristics and the season. The strength of seasonal variation in bat activity depended on the values (low, medium, high) of landscape characteristics. The spatial scale at which landscape characteristics were relevant is given in parentheses. (EPS 486 kb)

Additional file 11: Overview of insect orders caught simultaneously to bat echolocation call recordings above arable fields. Cited studies identified the listed insect orders as a component in the diet of *Nyctalus noctula* (Nnoc) and *Pipistrellus nathusii* (Pnat). (DOC 40 kb)

Additional file 12: Results from an ANOVA. χ^2 and p values show which covariates (all 1 degree of freedom) from the best generalized linear mixed effect models significantly affected the relative foraging activity of *Nyctalus noctula* and *Pipistrellus nathusii*. The interaction effect of crop height and insect abundance and the interaction of season with crop height, insect abundance, and insect diversity were not significant. Interactions with bold letters are plotted in Fig. 6. (DOC 36 kb)

Additional file 13: European bat species (column 1) which occur in our study region were assigned to functional groups according to their habitat use-related adaptations (column 2). This table is based on Table 1 in the publication of Heim et al. 2016 and was slightly modified. (DOC 36 kb)

Additional file 14: This table describes the composition (mean abundance, %) of the most abundant insect orders (Additional file 11) that were caught under the different conditions that are depicted in Fig. 6a. These conditions are based on the following three combinations of the Shannon Diversity Index (div) and crop height (ch) values: (1) $div \leq 0.22$ and $ch > 213$ cm, (2) $div \leq 0.22$ and $ch \leq 213$ cm, and (3) $div > 0.22$ and $ch \leq 213$ cm. Hereby, combination (1) is based on $n = 14$ recording occasions, while combinations (2) and (3) are based on $n = 60$ recording occasions each. (DOC 33 kb)

Acknowledgements

This work was funded by the Federal Ministry of Science, Research and Culture in Brandenburg, the University of Potsdam, the Leibniz Institute for Zoo and Wildlife Research, and the Deutsche Forschungsgemeinschaft (DFG-GRK 2118/1). We thank the Leibniz Institute for Agricultural Landscape Research (ZALF) for providing a research station and the means for conducting the field work. We want to thank the AgroScapeLabs, in particular, Karin Pirhofer-Walzl and Wiebke Ullmann, for the organizational support. We thank ESRI for providing the ArcGIS software in the framework of the graduate program. We are also thankful for the support of our field-work assistants Anissa Otto, Nadine Hofmeister, Nadja Kath, Jennifer Speyer, and Dennis M. Heim. Furthermore, we would like to thank the representative of the local federal ministry for conservation and the local bat experts

Torsten Blohm and Günter Heise for their advice and help during the field-work. Finally, we cordially thank Alexandre Courtiol for the statistical advice and our reviewers for their constructive comments that further improved this paper.

Authors' contributions

OH, CCV, and JAE designed the study. OH collected and analyzed the data. KJ and SKS collaborated in the fields of echolocation call analysis and landscape analysis as well as statistical analysis, respectively. CCV and JAE supervised and OH co-supervised all students who were involved in this project. CCV and JAE also gave advice regarding the statistical analysis. LL has identified most insect samples. OH wrote the first draft of the manuscript. All coauthors contributed to the final version of the manuscript and read and approved changes before submission.

Competing interests

The authors declare that they have no competing interests.

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Received: 7 February 2017 Accepted: 10 June 2017

Published online: 25 July 2017

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