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Not only hedgerows, but also flower fields can enhance bat activity in intensively used agricultural landscapes

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Abstract

Agri-environment schemes (AES) have become important tools for farmland biodiversity conservation, providing suitable habitats, resources, and connectivity within the agricultural landscapes. Bats are rarely studied in relation to AES effectiveness in contrast to birds, even though their presence and activity as biological control agents on insects, especially pest species, can be important for agricultural crops. While the role of hedgerows for bat occurrence and activity, as well as for their prey's diversity and abundance has been widely studied, the role of other AESs such as flower fields remains unclear. We monitored the activity of the main functional groups (edge, narrow and open space foragers) using ultrasound recorders, as well as potential prey abundances using light traps, across 35 study sites representing different AES in Central Germany from late July to September 2018. The sampled AES consisted of annual flower fields, mixed flower fields (with annual and biennial vegetation), perennial flower fields (sown every 5 years), hedgerows (surrounded by meadows and agricultural fields), and were compared to winter wheat (control) in a balanced design. Bat activity over hedgerows increased threefold for edge space foragers and sevenfold for narrow space foragers compared to wheat fields. Compared to wheat fields, narrow space forager activity increased fourfold over perennial flower fields, threefold over annual and twofold over mixed flower fields. This group's activity over hedgerows also increased almost threefold compared to mixed flower fields. However, the number of feeding buzzes and prey abundance did not differ significantly between AES. We detected foraging group-specific differences in bat activity between the studied AES. Thus, to promote bats in agricultural landscapes and to ensure their biological control services, it is important to establish more AES, such as hedgerows and flower fields, to increase their diversity and connectivity in intensively used agricultural landscapes.

Keywords: Acoustic recording; Habitat complementation; Farmland; Feeding buzz; Insect prey; Habitat type; Vegetation structure; Pest control; Wheat

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Introduction

To mitigate the biodiversity loss from agricultural intensification and to maintain ecosystem services such as pollination and biocontrol in agricultural landscapes (Ekroos *et al.*, 2014), agri-environment schemes (AES) have been implemented in Europe in either different productive areas, such as organic farming or other extensification schemes in orchards, arable crops and grasslands, or in non-productive areas, such as annual and perennial flower fields, and hedgerows (Batáry *et al.*, 2015). Wildflower strips and fields provide important floral resources for insect pollinators and serve as refuge for a great number of arthropods (Geppert *et al.,* 2020; Haaland *et al.*, 2011; Ouvrard & Jacquemart, 2018; Wood *et al.*, 2015). Many of these represent important food sources, explaining why AES are beneficial for many different foraging groups (Boetzl *et al.,* 2021; Baker *et al.*, 2012; Batáry *et al.*, 2010; Bright *et al.*, 2015; Whittingham, 2011). However very few studies have been conducted evaluating the effect of different AES on less obvious predators such as bats (Peter *et al.,* 2021).

Throughout Central Europe, most bat species are still under threat due to severe population declines during the last decades caused by habitat degradation (Racey & Entwistle, 2003), loss of roosting sites and suitable foraging areas, and the use of pesticides causing a decline of insect prey populations (Bontadina *et al.*, 2008;). Bats are highly mobile, adapting their flight and echolocation performance to the clutter conditions (i.e., vegetation) of the habitats where they hunt their prey. According to their foraging behaviour they can be classified as open, narrow and edge space foragers (Schnitzler & Kalko, 2001). As a result, their response to changes in landscape composition and connectivity over larger spatial scales may vary between species and guilds (Frey-Ehrenbold *et al.*, 2013; Heim *et al.*, 2015, 2016, 2017). Insectivorous bats are considered good bioindicators as they are sensitive to habitat degradation, and changes in their abundance may reflect changes in the populations of arthropod prey species (Jones *et al.*, 2009). Bats also provide an important ecosystem service as agricultural pest consumers and therefore may have an economic value for agriculture (Boyles *et al.,* 2011; Cleveland *et al.,* 2006; Puig-Montserrat, *et al.,* 2015, 2020; Russo *et al.,* 2018).

Bats are clearly supported by thriving insect populations within habitat under AES (Heim *et al.,* 2017). So far, the few studies assessing the effectiveness of non-productive AES on the conservation of bats have mostly focused on hedgerows. Bats profit from linear woody structures (i.e., hedgerows, tree lines) that provide orientation, shelter, breeding opportunities, as well as foraging grounds (Boughey *et al.*, 2011; Downs & Racey, 2006; Frey-Ehrenbold *et al.*, 2013; Froidevaux *et al.*, 2019). Indeed, arthropod abundance and diversity tend to be higher along hedgerows (Heim *et al.,* 2017; Kelm *et al.,* 2014), as they provide native plants for the larvae and more niches (Fischer *et al.,* 2013; Maudsley *et al.*, 2002; Weibull & Östman, 2003), shelter from predators and favourable microclimate (Langellotto & Denno, 2004; Maudsley, 2000). At a larger spatial scale, these linear woody elements are key landscape features that serve as stepping stones (Kalda *et al.*, 2015; Manning *et al.*, 2006; Pinaud *et al.*, 2018), interconnecting suitable habitat patches in increasingly homogeneous landscapes (Frey-Ehrenbold *et al.*, 2013). In England, sympathetic hedgerow management improved conditions for three bat taxa of major conservation concern in Western Europe (*Rhinolophus ferrumequinum, R. hipposideros* and *Plecotus* spp.; Froidevaux *et al.*, 2019a, 2019b), as well as increased moth abundance, which are important bat prey (Vaughan, 1997). In other AES, a few studies show that plant diversity in wildflower margins can have a positive effect on bats (McHugh, *et al.,* 2019). Also, bat activity increased above wildflower fields compared to crop fields, suggesting wildflower fields may be adequate foraging habitats for insectivorous bats in agricultural landscapes (Peter *et al.*, 2021). However, although other taxa have been studied extensively, the effect of various types of sown wildflower strips or fields on bats deserves further investigation.

This study assesses the influence of different habitat types under non-productive AES, namely annual, perennial, and mixed flower fields and hedgerows compared to conventionally managed wheat fields as controls on bats and insect prey in Central Germany, while accounting for the potential effect of the surrounding agriculture landscape. Additionally, we assessed the influence of these AES on the abundance of insect prey. (1) We expect that bat activity is higher along hedgerows and perennial flower fields than in conventionally managed wheat fields and annual flower fields, as they provide native vegetation with a higher structure diversity which provide food, shelter, and nesting opportunities for possible bat prey. (2) We expect mixed flower fields to have a higher bat activity than annual flower fields and conventionally managed wheat fields, as they offer a higher structural diversity, which provides longer-lasting vegetation cover, which may promote local invertebrate populations for a longer period of time and offer a higher prey abundance for bats. (3) Annual flower fields are expected to have lower bat activity than the other flower fields, due to the shorter-lived plantings that offer less overwintering habitat and nesting opportunities for prey but will still have higher bat activity than conventionally managed wheat fields. (4) We expect edge and narrow space foragers to prefer habitats with greater structural complexity such as hedgerows, and open space foragers to favour the less structurally complex flower fields. (5) In regard to landscape composition, narrow space foragers are expected to be less active in intensively managed landscapes, as they prefer areas with higher vegetation cover, such as forests, while open space forager activity is expected to be less impacted by intensively managed fields. Edge space foragers are expected to favour greater habitat connectivity and are expected to be more active with increasing amount of woody elements in the surrounding landscape.

Materials and methods

Study area and study design

The study was conducted in the surroundings of the city of Göttingen, in Lower Saxony, Germany (Fig. 1A and B). The region is characterised by forest (ca. 21%) and agricultural land cover (ca. 68%), whose main crops are wheat (ca. 40%), oilseed rape (ca. 15%), maize (ca. 7%), and sugar beet (ca. 6%). We sampled 35 study sites belonging to a range of AES: 21 flower fields (7 annual, 7 mixed and 7 perennial flower fields), 7 hedgerows and 7 winter wheat fields as a control. All flower fields were smaller than 2 ha. Pesticides and fertilizers are prohibited (Lower Saxonian Ministry for Food, Agriculture and Consumer 126 Protection 2017a−c) while the cutting of problematic weeds is allowed by permission.

Annual flower fields are sown once per year with a variable mix of at least 5 out of a list of 29 mainly cultivated plant species (Lower Saxonian Ministry for Food, Agriculture and Consumer Protection, 2017a; Appendix A: Table A1).

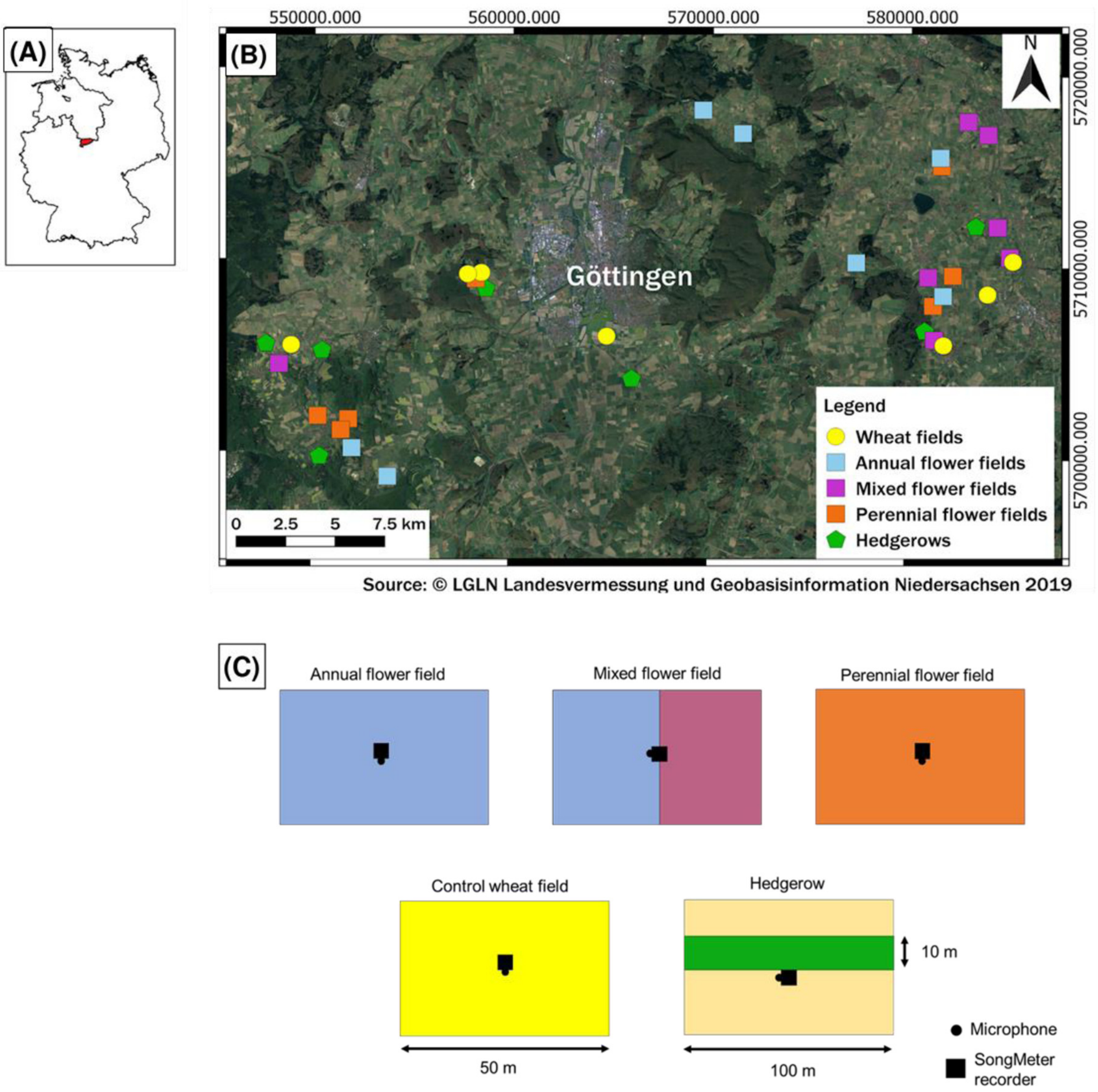

Fig. 1. Map with the location of the study site A) in Lower Saxony, Germany; B) location of the 35 sampling sites (seven of each habitat type) in the district of Göttingen; C) schematic overview of the study design, modified from Piko et al. (2021). Annual flower fields, sown the first year with plants from Appendix A: Table 1 (light blue). Mixed flower fields, sown the first year with the annual plant mix, in winter one section is ploughed (purple) and the other is left intact. The process is repeated the following year, alternating the sown and ploughed sections. Perennial flower fields (orange) are sown with plants from Appendix A: Table 2. Winter wheat fields (yellow); and hedgerows (green) represented as a linear structure growing along agricultural paths, crops, or meadows (beige). Both recorder and microphones were placed in the centre of the flower fields, and at the middle of the length of the hedgerows. Each study site was sampled twice between late July to mid-September 2018.

Mixed flower fields are a subtype of annual flower fields, developed for the conservation of grey partridge (*Perdix perdix*, Gottschalk & Beeke, 2014). In spring 50−70% of the area is sown with a wildflower mix (Appendix A: Table A1), and in winter at least 30% of the vegetation is left unmanaged as overwintering habitat (Fig. 1C). Each year the sown and undisturbed sections of the flower field are interchanged, resulting in the simultaneous growth of annual and biennial vegetation during a 5-year period (Lower Saxonian Ministry for Food, Agriculture and Consumer Protection, 2017b).

Perennial flower fields are sown once with a commercial seed mixture of 32 species from which 70% are regional wild plants with certified origin and 30% cultivated plants (Appendix A: Table A2). The field is left to natural succession for five years, however, the yearly cutting of parts of the flower field is mandatory (Lower Saxonian Ministry for Food, Agriculture and Consumer Protection, 2017c).

The selected hedgerows had a width of 5−15 m and a length of more than 100 m along meadows and crop fields. The most common hedge species found were: *Crataegus monogyna, Prunus espinosa, Rosa canina, Rubus fruticosus, Sambucus nigra* and some tree species such as *Acer* spp.*, Prunus avium and Quercus robur*.

The wheat fields were conventionally managed winter wheat (*Triticum aestivum*), harvested prior to our sampling, due to unusually high temperatures advancing crop ripening. None of our flower fields were harvested or mown within the sampling period.

Acoustic monitoring of bats

Each site was sampled twice for one night during late July to mid-September 2018. We were not able to sample the habitats simultaneously, due to the limited number of recorders available (4) and the great distances between study sites (Appendix B: Table B1). However, we ensured that the unbalanced sampling design and the long sampling period did not bias our results by sampling different habitat types each night, distributing the sampling of each habitat type over the whole sampling period, and incorporating nightly random effects into our statistical models. Bats were recorded with ultrasound recorders (Song Meter SM2Bat + model, Wildlife Acoustics, Inc.). Each recorder had one microphone (Parus open-source microphone; Darras *et al.,* 2021) connected directly to the device and was mounted at 1.5 m above−ground at the core of the sampled flower and wheat fields. For the sampled hedgerows, the recorders were placed on the border of the hedgerow, outside of the woody vegetation, approximately at the middle of the hedgerow length (Appendix B: Fig. B1). The recordings were made in real time (sampling rate: 192 kHz) and triggered by the sound pressure level at a threshold of +6 dB. No sampling was conducted on nights with temperatures lower than 10°C, wind speed higher than 20 km/h, during heavy rain (Appendix C: Fig. C1), or during full moon, as these conditions decrease bat activity (Appel *et al.,* 2019).

We analysed the audio recorded from sunset to midnight, which corresponds to the first bat activity peak of the night and provides a sufficient species coverage (Hayes, 1997). The recordings were imported into the software Audacity (Audacity 2.2.1, Audacity Team 2017) and displayed as spectrograms (FFT window size: 1024). Bat passes were defined as a sequence of at least two consecutive echolocation calls within one second (Thomas & West, 1989). Bat passes were extracted to obtain a precise duration of the pass and eliminate non-bat related sound, such as crickets. Files were then imported into the software BatScope4 (Obrist & Boesch, 2018) for automatic bat species identification. Additionally, the identification of bat calls with a confidence score lower than 70% were verified manually using Raven Lite 2.0 (Cornell lab of ornithology, Ithaca, NY), and compared to published data from Skiba (2009) and Obrist *et al.,* (2004). Detections of questionable species were confirmed by the bat specialist Dr. Martin Obrist. Bat passes were identified to the lowest taxonomic level possible and grouped according to their foraging behaviour, following the classification of Schnitzler & Kalko (2001) and Heim *et al.,* (2016): edge space (genera: *Barbastella* and *Pipistrellus*), narrow space (genera: *Myotis* and *Plecotus*) and open space foragers (genera: *Eptesicus, Nyctalus* and *Vespertilio*). The foraging habitats of these groups are defined by the clutter conditions (i.e., vegetation or the ground) where they hunt their prey (Schnitzler & Kalko, 2001). Open space foragers hunt in uncluttered areas away from vegetation or high above the ground, while narrow space foragers are well adapted to hunt and identify prey in very cluttered environments, such as forest, and possess high manoeuvrability to avoid collision. Edge space foragers forage in semi-cluttered environments and hunt along linear vegetation, vegetation gaps, near the ground or water surfaces.

The total duration of bat passes per foraging group was calculated for each sampled location (hereafter vocalisation activity). However, acoustic recorders detect sound over variable ranges, meaning that sound source frequency, level and the habitat structure in the sampled area can introduce a bias between sampling locations (Darras *et al.,* 2016). To avoid bias, we determined the actual area sampled by the acoustic recorders to standardise our bat activity data. We measured the size of the sound detection space of the recorders (i.e., their detection range) in each sampling location and divided the total duration vocalisation activity per location by the sound detection space area, to obtain activity densities (s/ha) (hereafter activity) that are comparable between sites (Appendix B: Fig. B2). Feeding activity was measured manually by counting the number of feeding buzzes, which is a series of short echolocation calls repeated at a high rate close to prey capture (Griffin et al., 1960; Schnitzler & Kalko, 2001).

Potential prey sampling

We sampled the potential insect prey with one light trap per site on two nights between mid-August and September 2018. The traps consisted of an empty 2.5 L plastic bottle placed upside down and the bottle's cap was modified to attach a 200 ml vial filled with soapy water to break the surface tension. A rectangular opening in the larger bottle allowed the lamp to be attached on the inside and the insects to enter (Appendix D: Fig. D1). Each lamp possessed four small LED lights: green, blue and two UV (ELEKON AG, 2018), with wavelengths of $\lambda_{\max}$ ~530 nm, 465 nm, 340 nm, and 348 nm, and a total illuminance of 5 lx, powered by two AA NiMH batteries (Villarroya-Villalba *et al.,* 2021). Due to logistic constraints, not all sites were sampled for insects and bats simultaneously: 11 of our sites had no light trap during both acoustic sampling nights (2 in wheat fields, 3 in annual and 4 in perennial flower fields, and 2 in hedgerows) and 24 had light traps on one of the acoustic sampling nights (5 in wheat fields, 4 in annual, 7 in mixed and 3 in perennial flower fields, and 5 in hedgerows). To minimise the influence of the light traps on bat activity, the traps were placed at a distance of $>$ 30 m from the recorders. However, our energy-efficient LEDs generate approximately 5 lux of illuminance (Villarroya-Villalba *et al*., 2021), which is superior to the illuminance of common actinic UV lamps which have been shown to have negative effect on the activity of slow flying species (Froidevaux *et al*., 2018), even though the latter also have different light spectrum peaks that are not directly comparable. To avoid biases in bat sampling results, other studies recommend increasing the distance between acoustic recorders and light traps when using lamps with greater intensity (Adams *et al*., 2009; Froidevaux *et al*., 2018; Lumsden & Bennett, 2005; de Oliveira *et al*., 2015; Wolbert *et al*., 2014), so we controlled for the potentially confounding effect of light traps on bat activity in our statistical models with a fixed effect. The caught insects were collected from the traps on the following day and identified to order level.

Landscape analysis

To account for the effect of the surrounding landscape on bats, we measured landscape composition. We used QGIS 3.6 (Development Team, 2019) to set 500 m and 1 km buffer zones around the centre of each field (Piko *et al.,* 2021). These buffer zones were selected based on the home range of species that occur in our study sites (Entwistle et al., 1996; Nicholls & Racey 2006; Roeleke *et al.,* 2016). We used information obtained from land use maps (SLA, 2018) to digitise agricultural fields and landscape elements based on satellite images (Map data ©2019 Google based on GoogleSatellite plugin) and classified five different landscape covers: (1) forest, (2) intensively managed agriculture (i.e. crops and intensively managed grasslands), (3) semi-natural (fallow land, extensively managed grasslands, flower fields and meadow orchards), (4) woody structures (tree rows, groves and hedges), and (5) urban areas within each buffer zone. We calculated the percentage of the landscape covers within each buffer zone.

Statistical analysis

We constructed statistical models to test our hypotheses that bat activity and feeding activity, as well as potential insect prey abundance (flies and moths), are higher in habitats under AES compared to crop fields, while taking landscape and weather effects into account. All statistical analyses were conducted in R 3.6.0 (R Development Core Team, 2019). We took a stepwise approach to model selection, adding variables in order of decreasing importance, as full models with all hypothesized predictors were unstable. We constructed generalised linear models with a negative binomial family using the MASS package (Venables & Ripley, 2002) for each bat foraging group activity, bat feeding activity, and insect prey abundance. We added habitat as a fixed effect to our null models and in the case of bat response variables we also included UV light trap presence as a fixed effect. Landscape predictors at 500 m and 1000 m radius were added to construct all possible models with single landscape predictors (Appendix E: Fig. E1). Weather predictors (mean temperature and mean wind speed) were added as single and combined weather predictors into the best landscape model, as bats and insect prey may be negatively affected by low nightly temperatures and high wind speed (Appendix C: Fig. C1). Lastly, we added random effects due to our study and sampling design: we checked whether the addition of random effects led to converging models using glmer.nb from the lme4 package (Bates & Maechler, 2010). Only converging models with no fit issues (as diagnosed based on simulated residual plots drawn with the DHARMa package (Hartig, 2020) were considered, and the best models were selected based on the lowest Akaike Information Criterion corrected for small sample sizes (hereafter "AICc") (MuMin package). When mixed models were not converging, we used GLMs instead (Appendix E: Fig. E2). To test spatial autocorrelation between recorded sites, we performed a Moran's I test on the residuals of our best model (ape package). To correct for spatial autocorrelation in our model, we constructed a residual autocovariate (RAC) model using the autocov_dist function in the spdep package (Appendix F). To test the effect of the different AES on our response variables, we performed a Tukey post-hoc test (TPH) on all best models using the false discovery rate correction (multcomp package; Hothorn *et al*., 2008). We calculated the variance inflation factor (VIF) to detect any collinearity in our selected models.

Results

Bat foraging group activity

During a total of 140 recording hours in 70 sampling nights, we recorded a total of 3014 bat passes. The highest number of passes was registered over mixed flower fields, with 879 passes, which represented 29% of the total passes, followed by 699 passes (23%) over perennial fields, 690 passes (23%) near hedgerows, 437 passes (14%) over annual fields and 309 passes (10%) over wheat fields. The most common species was *Pipistrellus pipistrellus* with 1726 passes, representing 57% of the total bat passes. We identified 11 species; all were present in mixed and annual flower fields and wheat fields, 10 near hedgerows, and 9 in perennial flower fields (Appendix G: Table G1). We counted a total of 334 feeding buzzes: 96 over hedgerows, 24 over annual, 116 over mixed and 40 over perennial flower fields, and 58 over wheat fields.

All the best models contained a landscape predictor, whose effect was accounted for when testing our main hypotheses about the effect of different AES on bats. The landscape predictor effect size was not different from zero for edge space and open space foragers but was significant for narrow space foragers and feeding activity (Fig. 2).

For edge space forager activity, the stepwise model selection approach yielded a model with semi-natural area within 1000 m and date as a random intercept. For narrow space forager activity, we obtained a model with urban area within 1000 m, mean temperature and wind speed as predictors, with date and plot as random intercepts. For open space forager activity, a very strong outlier (plot BS2.7, date: 2018−08−20, activity: 2546s/ha) precluded convergence on most generalised linear models and on all mixed models, so we excluded it to be able to test our hypotheses. We then obtained a model with forest within 1000 m and mean wind speed as predictors, with plot as random intercept. For feeding activity, we obtained a model with intensive agriculture within 1000 m, no weather predictors, with date and plot as random intercepts.

Statistical results of the GLM and GLMM models of the effect of habitat on bat activity are displayed in Table 1. Edge space forager activity was significantly lower above wheat fields (mean=112.4 s/ha, SE=81.05) compared to hedgerows (mean=280.3 s/ha, SE=93.3, TPH<0.01; Fig. 2); the detectable effect size was a 3.42 fold increase in activity density in hedgerows. Narrow space forager activity was significantly lower above wheat fields (mean=13.4 s/ha, SE=3.6) compared to hedgerows (mean= 64.8 s/ha, SE=16.6, TPH<0.001; Fig. 2), perennial (mean=41.4 s/ha, SE=13.2, TPH<0.001), annual (mean=33.6 s/ha, SE=8.0, TPH<0.01) and mixed (mean= 38.9 s/ha, SE= 8.3, TPH<0.05) flower fields; the latter corresponded to the smallest detectable effect size of 2.45 fold increase in activity. Hedgerows had significantly higher narrow space forager activity compared to mixed flower fields (TPH<0.01). Open space forager activity and the feeding activity were not detectably different between the five different habitats.

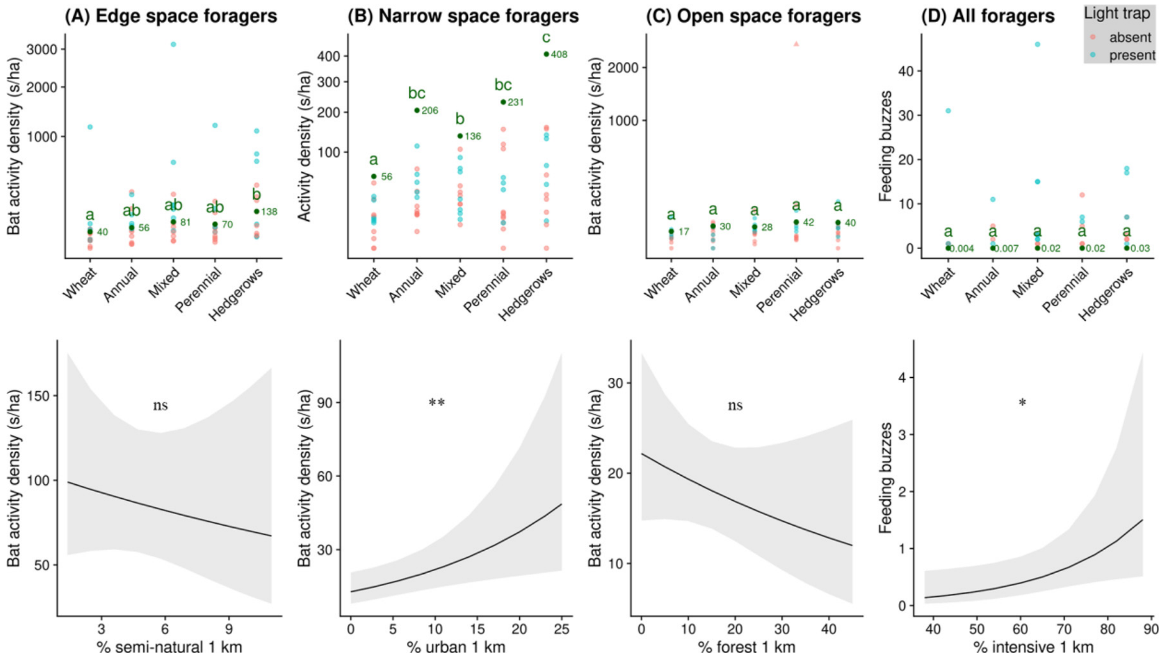

Fig. 2. Bat activity density in winter wheat fields, annual, mixed, and perennial flower strips and hedgerows. The recording duration was from sunset to midnight. Dots represent data points, red dots correspond to recording nights when no light trap was employed and blue dots to nights when light traps were used simultaneously with the recorders. Green dots show habitat effect sizes, their values are indicated with numbers; the green letters identify statistically significant differences ($p < 0.05$) between habitat types. Outlier in Open space forager activity (C) is represented by a triangle. Bat activity densities are square-root transformed for visibility.

The shaded area represents the effect of the percent cover of the main surrounding landscape variables within a radius of 1 km on each of the foraging groups' activity densities. Asterisks indicate the significance ($p<0.01$**, $p<0.05$*) of the retained landscape variable in the best model and "n.s." no statistical significance.

Table 1. Statistical results of the GLMM and GLM models of the effect of habitat type and landscape cover on bat activity, number of feeding buzzes and insect prey abundance. The intercept corresponds to wheat as habitat type and light traps not used during bat monitoring. RAC stands for residual autocovariate.

Response variable	Explanatory variable	Estimate	SE	*Z*-value	*P* > (|Z|)	Tukey Post- Hoc
Edge space forager activity	Intercept	3.695	0.453	8.158	***	a
GLMM AICc: 813.300	Annual	0.323	0.387	0.834	ns	ab
Null model AICc: 852.936	Mixed	0.694	0.395	1.758	.	ab
VIF	Perennial	0.553	0.407	1.359	ns	ab
Habitat: 1.047	Hedgerows	1.230	0.362	3.401	***	b
Light trap: 1.024	Light trap present	1.037	0.427	2.430	*	
% semi-natural 1 km: 1.204	% semi-natural 1 km	-0.040	0.063	-0.638	ns	
Narrow space forager activity	Intercept	4.021	1.400	2.872	**	a
GLMM AICc: 630.928	Annual	1.305	0.364	3.583	***	bc
Null model AICc: 644.806	Mixed	0.894	0.346	2.583	**	b
VIF	Perennial	1.422	0.358	3.969	***	bc
Habitat: 1.043	Hedgerows	1.990	0.373	5.328	***	c
Light trap: 1.026	Light trap present	0.814	0.415	1.959	.	
% urban 1 km: 1.147	% urban 1 km	0.053	0.020	2.659	**	
Mean temperature: 1.140	Mean temperature	-0.223	0.102	-2.184	*	
Mean wind speed: 1.146	Mean wind speed	0.070	0.077	0.916	ns	
Open space forager activity	Intercept	2.853	0.382	7.466	***	a
GLMM AICc: 567.416	Annual	0.544	0.385	1.414	ns	a
Null model AICc: 657.96	Mixed	0.472	0.382	1.233	ns	a
VIF	Perennial	0.881	0.391	2.251	*	a
Habitat: 1.034	Hedgerows	0.847	0.394	2.147	*	a
Light trap: 1.042	Light trap present	0.479	0.235	2.044	*	
% forest 1 km: 1.113	% forest 1 km	-0.014	0.012	-1.187	ns	
Mean wind speed: 1.064	Mean wind speed	-0.094	0.049	-1.893	.	
Feeding activity	Intercept	-5.496	1.758	-3.125	**	a
GLMM AICc: 270.758	Annual	0.515	0.908	0.567	ns	a
Null model AICc: 277.592	Mixed	1.658	0.856	1.938	.	a
VIF	Perennial	1.579	0.877	1.801	.	a
Habitat: 1.009	Hedgerows	1.877	0.871	2.156	*	a
Light trap: 1.022	Light trap present	1.503	0.584	2.572	*	
% intensive 1 km: 1.037	% intensive 1 km	0.048	0.022	2.177	*	
Potential prey abundance	Intercept	2.77	0.416	6.669	***	a
GLM AICc: 488.515	Annual	0.140	0.531	0.263	ns	a
Null model AICc: 488.063	Mixed	0.272	0.511	0.531	ns	a
VIF	Perennial	0.177	0.513	0.345	ns	a
Habitat: 1.013	Hedgerows	0.498	0.512	0.973	ns	a
RAC: 1.055	RAC	1.419	0.319	4.451	***	

ns = not significant; p < 0.05 *; p <0.01 **; p <0.001 ***; p <0.1 .

UV lamp presence significantly increased bat activity three times for edge, two times for narrow, 1.5 times for open space foragers, and four times for feeding activity (Table 1). Narrow space forager activity was positively affected by the percent cover of urban areas within 1000 m (estimate=0.05, $p<0.01$), while the number of feeding buzzes was positively affected by the percent cover of intensive agriculture within 1000 m (estimate=0.04, $p<0.05$). With increasing temperature, narrow space forager activity decreased (estimate=-0.2, $p<0.05$). With increasing wind speed, open space forager activity decreased (estimate=-0.09, $p>0.05$).

Prey abundance

We caught a total of 461 Diptera and 411 Lepidoptera in 70 light trap nights (Appendix H: Table H1). 25% of prey abundance was caught in hedgerows (mean=17.5, SE=7.2), followed by annual flower fields with 21% (mean=13.1, SE=3.9), mixed and perennial flower fields with 19% (mean=11.9, SE=2.8) and 18% (mean=11.4, SE=2.6) respectively, and 17% (mean=10.5, SE=5.6) in wheat fields. We did not detect effects of any tested predictor on prey abundance (Table 1).

Discussion

Effects of habitat type and landscape complexity on bats

We evaluated the influence of different AES (annual, perennial, and mixed flower fields) on bat activity and potential prey abundance, while accounting for the effect of the surrounding landscape and weather. We found a positive effect of hedgerows as linear habitats on all bat groups compared to wheat fields. We did not detect differences in activity of any bat foraging group between perennial flower fields and hedgerows. Perennial flower fields were important for the activity of narrow space foragers and showed a positive trend for open space foragers - the latter are likely to use AES as foraging habitats in agricultural landscapes (Peter *et al*., 2021). Thus, perennial flower fields seem to be particularly important for bat conservation in agricultural landscapes. In our study sites, other predator groups, i.e., birds and spiders, were also more abundant in flower fields with greater structural diversity (mixed and perennial flower fields) (Hass et al., unpublished; Wiedenmann et al., unpublished). Therefore, our study indicates that flower fields can promote bat activity and have similarly positive effects as hedgerows in intensively used agricultural landscapes. However, the number of perennial wildflower strips in Lower Saxony is much lower (N=1449 ha) than that of mixed (N=7075 ha) and annual (N=11,468 ha) wildflower fields (Lower Saxonian Ministry for Food, Agriculture and Consumer Protection 2020). Thus, it is important to promote the establishment of biodiversity-favourable AES such as perennial wildflower fields and hedgerows, that can provide more commuting and foraging areas for bats in the agricultural landscape.

Hedges are known to promote bats in agricultural landscapes (Froideveaux *et al.,* 2019a; Heim *et al.,* 2015) and also in our study they were crucial for enhancing the activity of all foraging groups, especially for edge space and narrow space foragers. Edge space foragers are associated with linear features and structurally complex habitats, hunting, and catching airborne prey found near vegetation, buildings, gaps, or above the ground and water surfaces (Denzinger & Schnitzler 2013). The edge space forager *P. pipistrellus* is the most abundant bat in Europe (least concern in the German Red List; Ludwig *et al.,* 2009) and accounted for 57% of all bat passes recorded in this study. Thus, hedges along fields in agricultural landscapes promote nocturnal predators and must be protected or re-established.

Landscape composition and connectivity can influence bat habitat exploitation (Frey-Ehrenbold *et al*., 2013; Heim *et al*., 2015, 2017); resources are often distributed in patches which may lead bats to increase their home range size to meet their needs (Presley *et al.,* 2019). Additionally, bat activity above flower fields is found to be driven by their suitability as foraging habitats in the agricultural landscape (Peter *et al*., 2021). Contrary to expectations, narrow space forager activity increased with increasing percentage of urban areas, however, these urban areas correspond to rural towns (with the exception of the city of Göttingen) rather than to large cities. Natural or semi-natural habitats, as well as water sources in small urban areas could represent roosting and foraging opportunities for bats (Gallo *et al*., 2018; Laforge *et al.,* 2021; Russo & Ancillotto, 2015). Bat home range size varies between species and bats respond differently to landscape composition and resources within their home range. Less mobile species for example, tend to have smaller home ranges (<0.5 km for *Plecotus auritus* and *Pipistrellus pygmaeus*; Entwistle et al., 1996, Fuentes-Montemayor *et al*., 2013), than more mobile species (3 km for *P. pipistrellus* and *Myotis sp*.; Fuentes-Montemayor *et al.*, 2013, 2017; or 4.2 km for *Nyctalus leisleri*; Waters et al., 1999; or average 6.5 km for *Eptesicus serotinus*; Catto *et al*., 1996). However, home range size decreases in heterogeneous landscapes and forested landscapes also reduce bat daily foraging distance (Laforge *et al.,* 2021). Resources in heterogeneous and interconnected landscapes are widely distributed. Bats as multi-resource users profit from habitat complementation (where bats benefit from having access to different land cover types in proximity to one another, Clake *et al.,* 2022), leading to a dilution effect, where fewer bats may be found over profitable habitats. In homogeneous landscapes, however, more bats may be found foraging over AESs, as they might represent the only resource available within their home range. This could be the reason why we found more feeding buzzes in landscapes with a high percentage of intensively managed agricultural fields. This highlights the importance of the conservation and new establishment of AES especially in intensively used agricultural landscapes (Fuentes-Montemayor *et al*., 2013; Monck-Whipp *et al*., 2018).

Bat and foraging activity over wildflower fields and other AES have been shown to increase with insect abundance, which varies during the season, indicating that the spatio-temporal variation in bat activity is driven by food availability (Kelm *et al*., 2014; Millon *et al*., 2015; Peter *et al*., 2021). We found a positive effect of UV lamp presence on edge space foragers activity, suggesting that bats were more active due to higher numbers of attracted insects. This is supported by the significant positive effect of light traps on the number of feeding buzzes. Studies using passive insect trapping methods should be able to disentangle these effects and to produce more tangible results. Seasonal variation in bat activity in temperate regions depends on the reproductive status of the females (Boughey *et al*., 2011), as they maximise their energy efficiency by exploiting only the most profitable hunting sites in order to build up fat for hibernation and migration (Entwistle et al., 1996; Mackie & Racey, 2007; Shiel *et al*., 1999). Furthermore, the seasonal variation is directly affected by weather conditions such as air temperature influencing food availability (Ciechanowski *et al*., 2007; Kapfer & Aron, 2007; Kelm *et al*., 2014; Mendes *et al*., 2017; Millon *et al*., 2015). We monitored bat activity from late July to September, when maternity colonies dissolve and mating season begins (Skiba, 2009). We recorded an increasing activity of narrow space foragers with decreasing temperatures. This effect might be influenced by shifting the foraging activity of narrow space foragers to profitable agricultural landscapes at the end of the season. We cannot disentangle the temperature and seasonal effect, but other studies also found that bats are hunting in different habitats during different seasons and life stages (Heim *et al.,* 2015, 2016; Kapfer & Aron, 2007; Kelm *et al.,* 2014). However, earlier recordings in the bat season might add more information on all bat life stages.

Effects of habitat type on bat prey

Flower fields and hedgerows offer important resources such as food, shelter from predators, oviposition sites and overwintering habitats to pollinators and natural enemies of crop pests (Albrecht *et al.,* 2020; Holland *et al*., 2016; Kremen *et al*., 2019; Tschumi *et al*., 2015). Wildflower cover can increase insect abundance in wildflower fields (Peter *et al*., 2021), while plant diversity and flower strip age may be important drivers of arthropod diversity benefiting ecosystem service provision (Albrecht *et al.,* 2020). In our study, habitat had no effect on prey abundance, suggesting that light traps attract insects from the surroundings (i.e., woody structures) regardless of the habitat the traps were placed in.

Nearly half of the insects caught were dipterans and 40% were lepidopterans, both of which are important food components of the bats in the agricultural landscapes (Vaughan, 1997). Other arthropod taxa such as spiders, weevils, and planthoppers, studied in our flower fields were found to benefit from perennial and mixed flower fields (Hass et al., unpublished), while pollinator abundance was highest in annual flower fields (Piko *et al*., 2021). Thus, the studied AES are still expected to provide reasonable food for insectivores, however, future studies should consider the use of passive sampling methods such as Malaise traps (Peter *et al*., 2021) to sample bat prey.

Conclusions

In this study we showed that bat activity was higher above hedgerows, perennial, mixed and annual flower fields, indicating that those AES promote bat activity in agricultural landscapes. Structurally diverse flower fields, i.e., perennial, and mixed, had similarly positive effects as hedgerows. Our results help to understand the potential role of different AES for bat species hunting in agricultural landscapes. In intensively used agricultural landscapes, bats may profit most from AES. Therefore, to promote bats in agricultural landscapes and to ensure their biological control services, it is important to increase the heterogeneity and establish new AES, especially in intensively used agricultural landscapes.

Data availability

Representative bat call sequences for each species are publicly available in the bat call library on ecoSound-web (Darras *et al*., 2020). All data associated with this manuscript will be available via the Dryad Digital Repository https://doi.org" https://doi.org.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.05.002.

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