



# How Bats Escape the Competitive Exclusion Principle—Seasonal Shift From Intraspecific to Interspecific Competition Drives Space Use in a Bat Ensemble

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Predators that depend on patchily distributed prey face the problem of finding food patches where they can successfully compete for prey. While the competitive exclusion principle suggests that species can only coexist if their ecological niches show considerable differences, newer theory proposes that local coexistence can be facilitated by so-called stabilizing and equalizing mechanisms. A prerequisite to identify such mechanisms is the understanding of the strength and the nature of competition (i.e., interference or exploitation). We studied the interaction between two open-space foraging bats by testing if common noctule bats *Nyctalus noctula* shift their space use in response to simulated aggregations of conspecifics or heterospecific *Pipistrellus nathusii*. When confronted with playbacks of heterospecifics, *N. noctula* increased their activity in early summer, but decreased activity in late summer. This pattern was accompanied by a decrease in the proportion of large insects in late summer, suggesting a more intense competition for food in late summer compared to early summer. When confronted with playbacks of conspecifics, *N. noctula* did not change their activity, irrespective of season. Our results indicate that in early summer, intraspecific competition is more severe than interspecific competition for insectivorous bats. Likely, conspecifics engage in interference competition for flight space, and may suffer from reduced prey detectability as echolocation calls of conspecifics interfere with each other. During insect rich times, interspecific competition on the other hand may be mediated by fine scale vertical partitioning and the use non-interfering echolocation frequencies. In contrast, when food is scarce in late summer, bats may engage in exploitation competition. Our data suggests that *N. noctula* avoid aggregations of more agile bats like *P. nathusii*, probably due to impeded hunting success. Yet, as fast and efficient fliers, *N. noctula* may be able to escape this disadvantage by exploiting more distant foraging patches.

**Keywords:** aerial, biodiversity, coexistence, flight, insectivore, movement, *Nyctalus noctula*, playback

## INTRODUCTION

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

competing species alter their movements and thus their space use in such a way that they avoid aggregations of strong competitors (Jeltsch et al., 2013; Schlaegel in review).

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

However, seasonal as well as possibly anthropogenically driven changes in insect availability might violate our assumption of constant, unlimited food resources for aerial hawking bats. Recent studies show that in Central Europe insect abundance is decreasing toward late summer (Anthony et al., 1981; Hallmann et al., 2017; Heim et al., 2017), which coincides with the time when several bat species face a trade-off between spending their time for feeding, mating, and either finding a winter roost or migrating southwards. Given that foraging time as well as prey availability can be limited in late summer, competition might then change toward the exploitation of resources, which will

bring an advantage to the smaller and more maneuverable fliers (Norberg and Rayner, 1987) that might be more successful in catching a limited number of prey items within short time. Yet, the question remains whether larger and faster species can mitigate this increase in interspecific competition by exploiting more distant but possibly less rich and yet unoccupied prey patches to equalize this potential disadvantage.

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

## MATERIALS AND METHODS

### Study Sites

In 2016, we conducted playback experiments directed toward *N. noctula* during the non-migratory breeding season (mid-June to mid-August, hereafter referred to as early season) and during its mating and potentially migratory season (beginning of September until beginning of October, hereafter referred to as late season). Playback experiments took place in Northeastern Germany, i.e., in northern parts of the federal country Brandenburg, called Uckermark. The Uckermark is dominated by agricultural fields, but includes many waterbodies, ranging from small kettle holes to relatively large lakes. We aimed at conducting playback experiments at the shores of 23 of these limnic habitats. Although there are only few forest remnants, and roosting opportunities in the area are thus expected to be scarce, we knew from previous GPS studies (Roeleke et al., 2016; Roeleke et al. unpublished data) that *N. noctula* colonies in the Uckermark preferentially forage above waterbodies within

distances of at least 7 km from their roost. The 23 playback locations were distributed over an area of ~60,000 ha. During each experimental night, we conducted playback experiments at two sites simultaneously. Distance between the paired playback locations ranged from 1 to 5 km. Since we conducted the experiments roughly at the same time, it is unlikely that we broadcasted playbacks to the same individuals at the different sites during a given night. We further aimed at conducting playbacks twice at each site—once during the early and once during the late season (see section Playback Experiments). However, due to spatial and temporal variation in bat activity, we could not always achieve this for all sites. To avoid pseudo-replication, we only visited each site once per season.

### Playback Preparation

At each site, we broadcasted three different playback types toward foraging *N. noctula*; feeding buzzes of *N. noctula*, feeding buzzes of *P. nathusii*, and a sine tone between 20 and 40 kHz as a control (Supplement Material 1). Feeding buzzes are specialized bat calls that are designed for the terminal phase of prey capture, and which are unambiguously identifiable. The single playback trials were 3 min long and consisted of three phases; (i) 1 min of silence (baseline), in order to record the acoustic baseline activity of *N. noctula* at the respective site, (ii) 1 min of broadcasting the respective playback (playback), and (iii) 1 min of silence again (post), in order to see potential post-playback effects (cf. Übernickel et al., 2013; Voigt-Heucke et al., 2016).

### Playback Experiments

We started the playback trials as soon as we observed foraging activity of one or more *N. noctula* via the recording setup. After each trial, we waited at least 3 min and checked again for acoustic foraging activity before we broadcasted the next playback. In most nights, we conducted the experiments shortly after sunset when the first *N. noctula* arrived. However, in case all bats left the area during the playbacks, we tried to conduct a second round of playback experiments later on when *N. noctula* activity over the area was more stable. At around midnight, *N. noctula* activity always declined to low levels. If we did not manage to conduct our experiment until midnight, we stopped the experiments to ensure that all bats within our study were confronted with playbacks in a similar situation, i.e., during their first foraging bout of the night. During some experimental trials, we also noticed *P. nathusii* foraging close to the shoreline and thus close to our experimental setup. However, since the natural *P. nathusii* activity was low compared to the broadcasted stimuli, we are certain that their potential effect was negligible. We did not evaluate potential effects of the playbacks on *P. nathusii* since the playbacks were not directed toward them, and we thus could not assure consistent baseline activity of *P. nathusii* before broadcasting.

We only performed experiments at wind speeds  $\leq 3$  m/s during nights without rainfall. Please see Supplement Material 1 for a detailed description of playback preparation and the experimental setup.

## Acoustic Analysis

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

## Insect Trapping and Analyses

At each playback site, we trapped flying insects with a custom built ultra-violet (UV) light trap (light source of about 365 nm wavelength). When insects were approaching the light, they collided with a smooth plastic surface in front of the lamp and subsequently slipped into a bottle filled with 95% ethanol. We placed the traps at the shore of the respective waterbodies, ~5 m from the playback setup, at 3 m height. As soon as we noticed the first *N. noctula* with our recording setup, we switched on the UV light of the trap and attached the bottle with the ethanol for 1 h. Thus, we ensured that insects were not attracted to the UV light before the onset of the playback experiment.

To derive the most important prey measurements from a bats point of view, we sorted and counted insects by para-taxonomic groups reflecting a combination of order and size (Table 1). We dried the sorted samples for 72 h at 50°C and measured dry mass with an electronic balance (ME5, Sartorius, Germany, 0.001 mg resolution).

## Data Management and Statistical Analysis

Our acoustic analysis showed that sometimes bat activity stopped for a longer time during any of the three phases of our experiment (i.e., baseline, playback, post). We excluded these trials from further analysis since we could not be sure if the focus animals were really foraging in such cases. Please see Supplement Material 2 for a detailed description of the estimation of the experimental area and the subsequent data cleaning.

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

$$\frac{\text{calls playback phase} - \text{calls pre phase}}{(\text{calls playback phase} + \text{calls pre phase})/2} \quad (1)$$

We then modeled the relative difference with a linear mixed effect model (R package lme4, Bates et al., 2015). As predictor variables we used the three-fold interaction of playback type (i.e., conspecifics, heterospecifics, control), baseline activity (number of *N. noctula* calls during the pre-phase), and season. As random effect we included experimental trial nested within site. To test whether the effects of the playback would last longer than the broadcasting of the playback itself, we ran a similar model with the relative difference between pre- and post-phase as dependent variable. We ensured normal distribution of modeled residuals by visually checking quantile plots of the

models. We calculated pseudo-R-squared values with the R package MuMIn (Barton, 2014) and effect sizes of the predictor variables with the R package effects (Fox, 2003). We assumed statistical significant effects of predictor variables when the 95% confidence intervals did not span 0. After confirming with Kolmogorov-Smirnov-Tests that numbers and masses from the different insect groups were not normally distributed, we used paired Mann-Whitney-*U*-Tests to test whether there was an effect of season on mass or number of caught insects, or on the relative number of the different size classes within each sample. We used all samples for this test, including those from location and season combinations where we did not obtain data from the playback experiments. All data handling and analyses were done with R 3.3.2 (R Core Team, 2016). Review and approval of the experiments was not required by national guidelines, since no animals were caught, handled, or physically manipulated.

## RESULTS

### Bat Activity at Waterbodies

We sampled 30 different waterbodies in the study area for *N. noctula* activity. More waterbodies were used by foraging *N. noctula* in the early than in the late season (Chi<sup>2</sup>-Test, Chi<sup>2</sup> = 4.65, *N* = 30, *p* = 0.03). At sites where *N. noctula* was present in both seasons, the level of *N. noctula* activity did not differ between seasons (Mann-Whitney-*U*-Test, *W* = 124, *N* = 28, *p* = 0.21) (Table 1).

### Insect Trapping

Most caught insects were of rather small size. Number and dry mass of caught insects varied largely between the sampled sites (Table 1). Although there seemed to be a slight shift from large (body length >9 mm) to small insects (body length < 6 mm) from the early to the late season, we did not detect any significant differences for number and mass of the different insect size classes (paired Mann-Whitney-*U*-tests, *N* = 46, Figure 1). Yet, paired Mann-Whitney-*U*-tests (*N* = 46) showed that the relative number of large insects was significantly higher in the early season (*V* = 132, *p* = 0.045), while the relative number of small insects was higher in the late season (*V* = 57, *p* = 0.025). Please see Supplement Material 3 for a site specific presentation of abundances and masses of the different insect classes.

### Playback Experiments

*N. noctula* did not change their activity when confronted with our control treatment, a sine tone between 20 and 40 kHz. In general, *N. noctula* showed less shifts in activity when their initial density (i.e., number of calls recorded during the pre-phase) was comparably high. However, when including activity during the pre-phase not as an interaction term but only as a main effect in the model, it turned out that *N. noctula* generally responded negatively toward playbacks when the initial density of conspecifics was high (i.e., around 500 calls per minute during the pre-phase, see Supplement Material 3 for the effect plot). Our full model with the three-fold interaction between initial

**TABLE 1** | Presence and continuous foraging activity of *N. noctula* and total number and mass of insects at sampled sites.

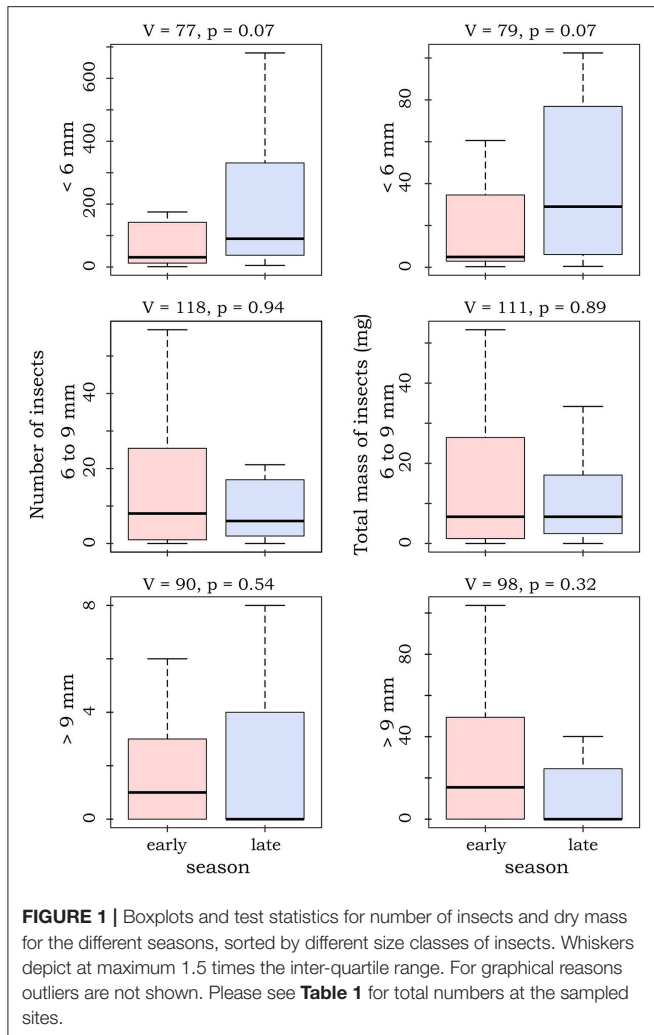
Site	Early season				Late season			
	<i>N. noctula</i> present	Continuous foraging	No. of insects	Mass of insects (mg)	<i>N. noctula</i> present	Continuous foraging	No. of insects	Mass of insects (mg)
1-1	Yes	Yes	23.0	4.6	No	No	260.0	82.1
1-2	Yes	Yes	56.0	19.2	Yes	Yes	252.0	129.7
2-1	No	No	39.0	11.6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

density, season, and playback type had a pseudo  $R^2$ -value of 0.42. This model revealed that *N. noctula* did not react toward the hunting calls of heterospecific *P. nathusii*. Further, there was only a slight positive response toward hunting calls of conspecifics at rather low initial densities (**Figure 2A**). However, this turned into a clear avoidance of conspecifics in the late season when the initial density was low to medium. At the same time, at least at low initial densities, *N. noctula* activity increased when we broadcasted heterospecific playbacks in the late season. Only at high initial densities, *N. noctula* started to avoid the experimental area during the *P. nathusii* playbacks (**Figure 2B**).

Irrespective of playback type and season, the number of calls during the pre-phase and the post-phase of the playback did not differ significantly, i.e., the relative difference was fluctuating around 0 (**Figures 2C,D**).

## DISCUSSION

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



studied insectivorous bats experienced stronger intraspecific than interspecific competition during the early season, whereas the opposite was true during the late season.

## Seasonal Shifts of Habitat Use

During late summer, foraging *N. noctula* used fewer waterbodies in our study area than during the early summer. This seems to be counter-intuitive at first glance, since one would expect higher abundances of foraging bats during the late season, due to the by then weaned offspring. Further, migrating bats from northern and north-eastern countries are arriving around late August to late October in Central Europe, including our study area (Ahlén et al., 2009; Furmankiewicz and Kucharska, 2009; Ciechanowski et al., 2010). The influx of migrating *N. noctula* is probably the reasons why Heim et al. (2016) found an increase of *N. noctula* activity above agricultural fields in the study area in late summer. We suggest that the observed decrease in use of our sampled waterbodies was not due to an overall reduced activity in the area, but rather due to a shift of habitat use from limnic to terrestrial foraging grounds. This is in concordance with isotopic analyses by Voigt et al. (2016) who found that

*N. noctula* feeds less on aquatic insect during late summer than during early summer. The shift in habitat use may partially result from the need to mate in the late season. Male bats have to establish and defend solitary roosts, while females search for these so-called mating roost. Thus, males may have to feed nearby their roost, and females may save time when feeding opportunistically during their search for mating roosts rather than at designated foraging areas such as waterbodies. A recent tracking study suggests such a strategy, at least for females, by showing that female *N. noctula* cover large areas and focus less on single waterbodies for foraging in late summer (Roeleke et al., 2016).

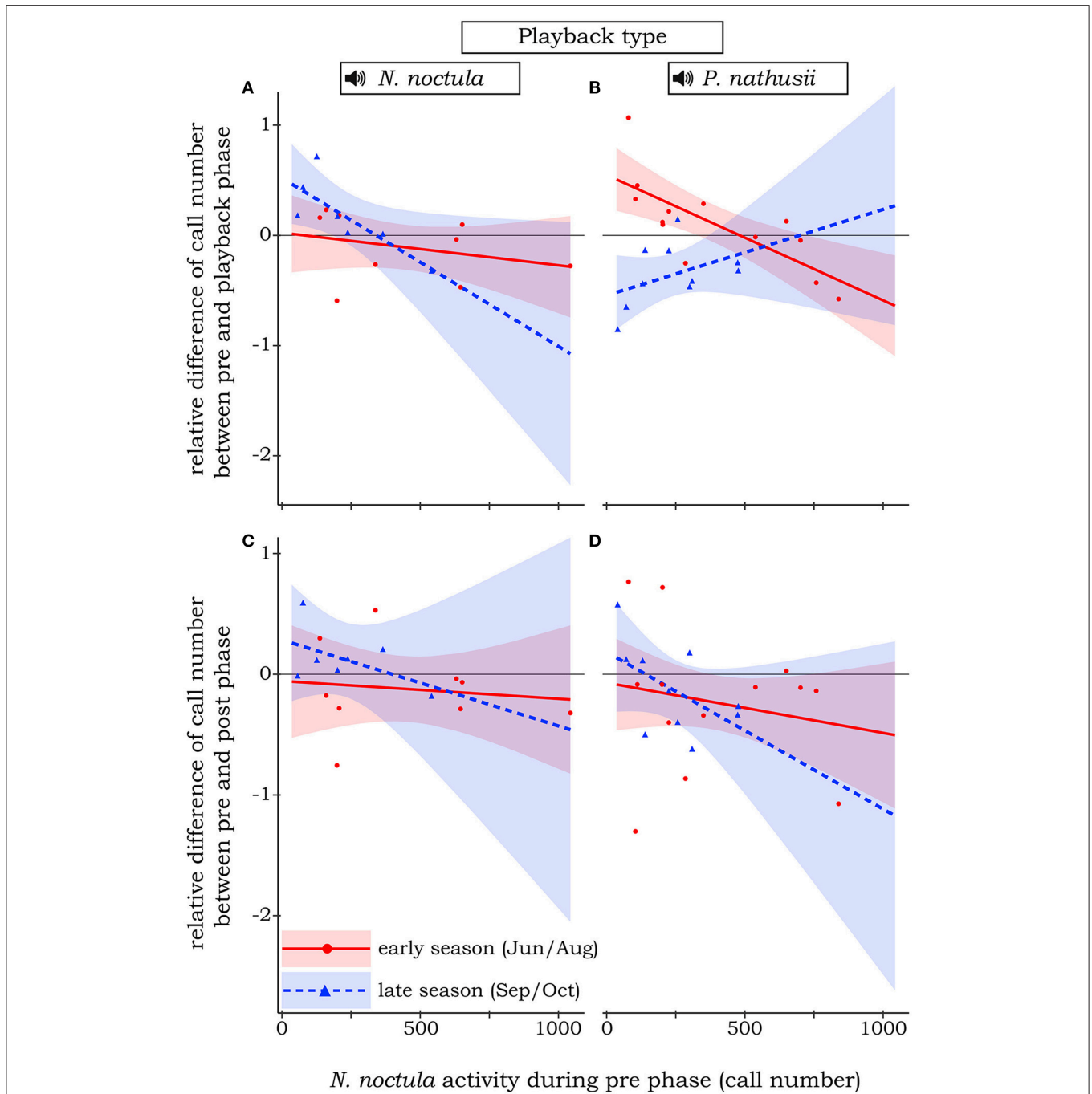
## Seasonal Shifts of Prey Availability

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

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

## Playback Experiments—Post Effect and Density Dependent Response

We did not detect any significant effects of the experimental treatment in the post playback phase, i.e., the bat activity almost instantly went back to the baseline activity level after the broadcasting of playbacks. This shows that *N. noctula* conceives



**FIGURE 2 |** Relative difference of *N. noctula* activity between pre-phase and playback phase (A,B) or the pre-phase and post phase (C,D) of the experiment, depending on *N. noctula* activity during the pre -phase, the different playback types, and the season. Raw data is depicted by circles and triangles. Lines show the estimated effect, shaded areas show the corresponding 95% confidence intervals. Solid red line and red circles: early season. Dashed blue line and blue triangles: late season. For simplicity, insignificant effects toward the control treatment (sine tone) are not shown.

new competitive situations very quickly, and adjusts its space use likewise quickly and dynamically.

*N. noctula* only reacted toward our playbacks when the baseline activity was low to medium (i.e., less than 500 calls per minute). Possibly, *N. noctula* perceived acoustic information

from actual present conspecifics more reliable than our playback. However, feeding buzzes are naturally fainter than search calls (Holderied et al., 2005), and high acoustic search call activity may hinder the acoustic detection of feeding con- or heterospecifics in experimental as well as natural situations. However, it may

also be that the space that could be efficiently used for foraging was already saturated with individuals. Using densely occupied foraging patches can be ineffective (Amichai et al., 2015), which may result in an individual partitioning of foraging space (cf Beauchamp and Fernández-Juricic, 2005).

## Playback Experiments—Seasonal Changes of Competition

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

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

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

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

## CONCLUSIONS

We found that the aerial hawking open space foraging bat *N. noctula* actively seeks heterospecific *P. nathusii* during foraging bouts in early summer, but avoids patches occupied by foraging heterospecifics in late summer. *N. noctula* did not respond to foraging conspecifics in early summer, but showed a slight positive response to conspecifics in late summer. We conclude that the number of aerial hawking open space foragers at a food patch is limited by intraspecific interference competition for flight space and soundspace in early summer,



but that interspecific exploitation competition for insect prey is limiting the number of bats in late summer. High intraspecific competition may thus act stabilizing on insectivorous bat ensembles when food resources are plentiful. During probably lower prey availability in late summer, aerial hawkers that are specialized for fast flight in uncluttered habitats may suffer from inferior capture rate compared to more maneuverable bats like *P. nathusii*. Water bodies were used less during this time. We speculate that fast flying aerial hawkers can use farther away or less rich hunting grounds, since their specialized wing morphology allows them to fly large distances at low energetic costs (Winter and von Helversen, 1998). This adaptation to fast yet cheap flight may equalize fitness disadvantages toward superior foragers. One could even speculate that habitats which are suboptimal from a foraging perspective may support the diversity of bats by offering refuges from interspecific competition.

## DATA AVAILABILITY

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

## AUTHOR CONTRIBUTIONS

CV and MR conceptualized the study. CV supervised the students. MR and LJ performed the experiments. LJ analyzed the

acoustic recordings. MR did the statistical analysis. MR and CV wrote the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2018.00101/full#supplementary-material>

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