Foraging flight strategy varies with species identity of co-occurring individuals in bats

Montaine Delmotte[1,2,3], Alice Baudouin[4], Anaïs Pessato[1,2], Andréas Ravache[1,2], Martin Thibault[1,2,5], Fabien Verniest[1,2], Kévin Barré[1,2,6]

[1] Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP 135, 57 rue Cuvier, 75005 Paris, France

[2] Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Station de Biologie Marine, 1 place de la Croix, 29900 Concarneau, France

[3] INRAE, UR1115, Plantes et Systèmes de culture Horticoles, 84000, Avignon, France

[4] Ligue pour la Protection des Oiseaux Auvergne-Rhône-Alpes, 18 place génissieu, 26120, Chabeuil, France

[5] UMR ENTROPIE (UR-IRD-IFREMER-CNRS-UNC), Labex-CORAIL, 98800 Nouméa, New Caledonia.

[6] Faculty of Science, Technology and Medicine, University of Luxembourg, Esch-sur-Alzette, Luxembourg

Corresponding author:

Kévin Barré (ORCID: 0000-0001-5368-4053)

Station Marine de Concarneau, 1 place de la Croix, 29900 Concarneau, France

kevin.barre@mnhn.fr

+33 2 98 50 99 28

Running title: Bat foraging flight strategy

Abstract

Foraging is a key function in the animal kingdom. Foraging in group drives food patch discovery through social information transfer that maximizes individual’s foraging success through either cooperation or competition in response to congener presence. Understanding how congener presence affects the foraging strategy is especially challenging as it requires close monitoring of animal movements, foraging success and competitive interactions. The consequences of congener presence on foraging flight strategy of bats, a highly social taxa with strong behavioural plasticity in response to resource ephemerality, remains little tested. Through a three-dimensional acoustic tracking of individual echolocation calls, we assessed to which extent foraging flight strategy of bats varied in response to conspecific and heterospecific presence. We found that flight speed, the main lever for adjusting energy balance during foraging (i.e. slowing down to capture prey and speeding up to find new prey patches), is no longer used in presence of intra-guild heterospecifics. Also, the overall foraging level increased regardless of co-occurring species, through a facilitation and/or a higher prey availability. The study shows that bats integrate species identity in making decisions about their foraging flight strategy, with a stronger tolerance towards conspecifics with which social relations are most important, e.g. because they share the same roost. This might have important implications in understanding consequences of interactions, especially in relation to anthropogenic pressures that rearrange bat communities and their prey in time and space, which could exacerbate natural competition.

Key words

Chiroptera; competition; facilitation; foraging flight behaviour; inter-individual interactions; 3D acoustic tracking

1. Introduction

Foraging is a key function that directly determines individuals' fitness and population dynamics in animals (Snijders et al. 2018). The optimal foraging theory suggests that animals evolve to maximize the balance between net energy intake per unit of time and foraging costs (Charnov, 1976). However, the efficiency of foraging strategies varies with both environmental conditions and biotic interactions which are often hardly predictable. The selective value of a particular foraging strategy is therefore fluctuant and animals sharing the same resources display a variety of intra and inter-specific strategies to maximize their foraging success (Bell 2010). Coping with environmental stochasticity in the search for an optimal foraging strategy calls for plasticity in behavioural responses such as movements (O'brien et al. 1990) and social interactions (Caraco & Giraldea 1991). Foraging in group, also referred to as social foraging, is a widespread strategy in animal kingdom, including complex benefits and costs that remain challenging for the comprehension of the foraging success of individuals (Giraldeau and Caraco 2000).

The presence of other foragers can benefit to individuals through social information transfer that increases the discovery rate of food patches (Giraldeau and Caraco 2000). However, the presence of other foragers can also cost individuals by reducing their foraging efficiency, for instance through resource depletion or interferences (Clark and Mangel 1986; Beauchamp and Fernández-Juricic 2005; Silk 2007). As a consequence, by gathering information about food resources from the other foragers (Danchin et al. 2004; Dall et al. 2005), individuals adapt their behaviour to maximize their foraging output through either cooperation or competition (Giraldeau and Caraco 2000; Kelt et al. 2019). Social foraging has been well documented in birds, mammals, fishes and invertebrates (e.g. Deygout et al. 2010 & Monier 2024; Smith and Holekamp 2023; Ryer and Olla 1995, Bilde et al. 2007; respectively).

It is overall expected that the benefits and costs of the presence of other foragers on foraging individuals should be greater between individuals belonging to the same species as they share similar foraging strategy and niche (Cornell 1983; Jiang et al., 2015). Interspecific interactions can also influence foraging individuals, and this is especially true for species with a close foraging niche such as intra-guild species. However, this form of interaction is scare and more variable, given that it is highly context-dependent (Kelt et al., 2019).

Empirical explorations of social foraging determinants, especially interindividual interactions, are difficult to carry out. Indeed, they require close monitoring of animal movements, foraging success and competitive interactions (Cvikel et al. 2015). For this reason, most studies have until recently focused on species that are easy to monitor, such as diurnal, large birds (e.g. raptors; Flemming et al. 1992; Buckley 1997; Deygout et al. 2010) and mammals (e.g. whales and canids; Creel and Creel 1995; Allen et al. 2024). Recent advances in acoustic signal treatment allows to automatically track and decode behaviour of species otherwise difficult to monitor, such as bats. This enables to collect a large amount of quantitative data on interactions between individuals sharing a single patch (Fraser et al. 2020). Biological and ecological traits of insectivorous bats make this taxon very relevant in expending current knowledge on interindividual interactions. Indeed, bats exploit ephemeral resources (Salinas-Ramos et al. 2020) and use social information to adapt their foraging strategy in response to resource availability (Gager 2019). Thus, individuals have to cope with the trade-off between the cooperation by information transfer and the drawback of the presence of others foragers at the same time.

Insectivorous bats emit echolocation calls to orientate themselves in space, communicate with each other (Fenton 2003; Jones and Siemers 2011), and to locate, pursue and capture preys while foraging (Griffin 1958; Griffin et al. 1960; Schnitzler et al. 2003). To capture preys, bats emit feeding buzzes characterized by a reduced duration and increased repetition rate of echolocation calls just before capture attempts (see Fig. 1a). Bats can eavesdrop on these congener feeding buzzes (Gillam 2007; Chaverri et al. 2018) to detect favourable foraging areas more easily (Dechmann et al. 2009; Egert-Berg et al. 2018). While these cues can facilitate and enhance individual foraging efficiency, they can also lead to competitive interactions in a context of low resource availability (Dechmann et al. 2009), and even cause acoustic interferences pushing individuals to change their behaviour (e.g. by increasing their call intensity) to remain efficient (Amichai et al., 2015). Benefits from eavesdropping may also vary depending on whether it was emitted by a conspecific or an heterospecific (Ridley et al 2013). To our knowledge, no study has yet assessed the consequences of such interactions on bat foraging flight strategy while accounting for the presence of other individuals and species identity. Here, we explored the effect of co-occurrence on the foraging strategy of bats under two scenarios: i) in presence of conspecifics (i.e. individuals from the same species), and ii) in presence of intra-guild heterospecifics (individuals from another species with closely related ecological niches).

Bats use a foraging flight strategy which consists in flying fast to maximize contact with potential prey and slowing down when they detect one to increase manoeuvrability for capture, with most species emitting a feeding buzz right before the capture (Fig. 1a; Jones and Rayner 1988; Schnitzler and Kalko 2001; Grodzinski et al. 2009; Barré et al. 2024). Thus, existing literature has demonstrated a clear negative relationship between foraging intensity and flight speed across several species from different guilds (Holderied and Jones 2009). In other words, when bats forage intensely (as measured by the probability of feeding buzz emission), they fly at lower speeds (as measured by the flight speed). According to aerodynamic models, this strategy optimizes energy balance, likely enhancing individual fitness, which aligns with the principles of the optimal foraging theory (Grodzinski et al. 2009; Troxell et al. 2019; McGuire and Boyles 2024). The relationship between these two metrics is thus considered a reliable proxy of the bat foraging flight strategy. As such, foraging efficiency can be inferred by examining the relationship between the feeding buzz score and the flight speed.

Finally, we assessed to which extent foraging flight strategy of bats varied in response to the presence of other individuals (hereafter referred to as co-occurrence). The foraging flight strategy without co-occurrence was considered as the reference individual strategy. In line with the social foraging theory, three potential responses to the presence of other foraging bats were predicted. Firstly, we expected that co-occurrence may result in interindividual competition, which would affect individual foraging flight strategy by weakening the relationship between foraging probability and flight speed (Hypothesis 1, Fig. 1b). This behavioural change in response to the presence of competitors could be due to either a reduced foraging probability for a given flight speed, or faster or slower flight speed than expected depending on the foraging probability. Indeed, ecological and acoustic niche overlap between individuals belonging the same guild should exacerbate the consequences of interferences and resource depletion (Gager 2019). Alternatively, co-occurrence could induce an increase in foraging probability whatever flight speed through facilitation and/or resource increase (Hypothesis 2, Fig. 1c) as bats can eavesdrop on other individuals feeding buzzes. Thus, individuals may increase their foraging behaviour after hearing other individuals foraging, or simply because the prey density, and consequently the density of other bats, has increased. Lastly, co-occurrence may have no effect on individuals' foraging strategy (Hypothesis 3, Fig. 1b). Such a neutral response could occur in case of constantly no limiting resource and constant foraging level between individuals, or insufficient co-occurrence events to generate resource depletion or interferences. Further, we expect competition to occur more towards conspecifics due to ecological and acoustic niche overlaps that should exacerbate the consequences of resource depletion and interferences (Gager 2019), while facilitation could occur towards both cons- and heterospecifics given that individuals are able to be attentive to the foraging behaviour of all species (Gager 2019; Lewanzik et al. 2019).

2. Material and methods

2.1. Study area

For the study we used data from Barré et al. (2023; 2024) from 16 sites along the Rhône Valley in the Auvergne-Rhône-Alpes region in France (Fig. S1). This area is characterized by a high activity of several *Pipistrellus* genus bat species: *Pipistrellus nathusii*, *Pipistrellus kuhlii* and *Pipistrellus pygmaeus* (Bas et al. 2023). These sites were initially monitored to assess flight and feeding behaviour responses of insectivorous bats to ground-mounted solar farms (Barré et al. 2024), and we only retained control sites (i.e. 100 to 500 m away from solar farms) for our study.

Sampling sites were located in open space (233 ± 192 m from river banks and 39 ± 15m from woody edges) in old industrial sites or embankments resulting from the Rhône canalization. Sampling sites were selected within landscapes made of approx. 50% farmland, 35% woodland, and 15% impervious surfaces. They exhibited comparable distances to nearest woody edge and water body, and proportions of woodland (Table S1). At a local scale, sampling stations presented a homogeneous habitat cover (low herbaceous vegetation) throughout the recorder's detection volume (~30 m radius; see section 2.2 for more details) to ensure an optimal and standardized bat call detectability (Table S1).

2.2. Bat acoustic tracking and trajectory reconstruction

Nine nights with favourable weather conditions for bats (average temperature during the sampling period: 11.4–20°C; wind speed: 0–5.3 $m.s^{-1}$; no rain) were sampled in 2022 from September 21st to 30th. Each night, bat echolocation calls were recorded at one or two sites simultaneously during the three first hours after sunset to, at least, monitor the first bat activity peak period (Mariton et al. 2023). Each site was only sampled once.

We computed three-dimensional (3D) positions from echolocation calls using the Trajecto V1 system from Suva-tech (Phnom-Penh, Cambodia; https://www.suva-tech.com/), and following the methodology described in Barré et al. (2020; 2021; 2024). This system consists in an arrangement of four microphones (FG 23329, Knowles Acoustics, Itasca, IL USA) forming a microphone array in the shape of a horizontal equilateral triangle with a side length of approximately two meters, and with one microphone set in the middle and others in corners (Fig. 1c). Microphones recorded sound frequencies from 1 to 250 kHz in a detection range of roughly 30 m radius, including all bat echolocation calls, in half-second sound files. The reception delay of bat echolocation calls between the synchronized microphones is used to compute bat 3D positions (Ing et al. 2016; Koblitz 2018).

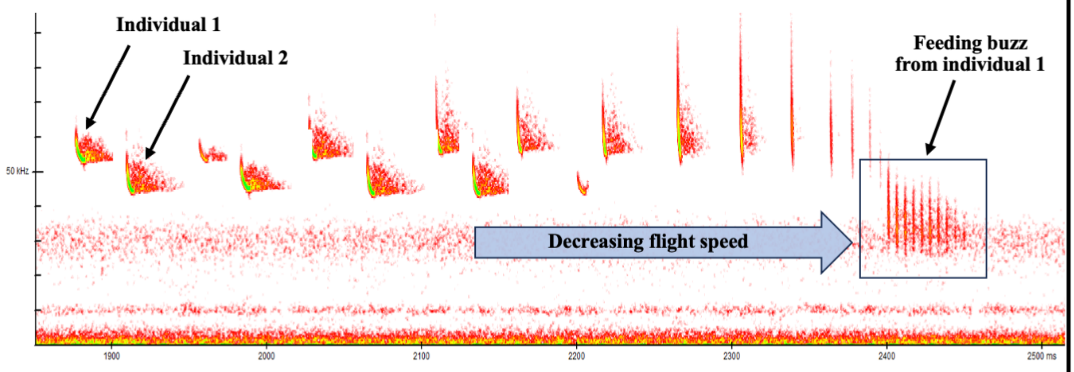
From 3D positions, we reconstructed complete bat 3D flight trajectories following the approach described by Barré et al. (2020, 2021). This approach uses differences in call frequency, flight speed, time, and distance between positions as criteria to group positions that are most likely to belong to a single trajectory.

A total of 710 mid-range echolocators flight trajectories was reconstructed from 6,477 3D positions. *P. nathusii* was the dominant species with 291 trajectories (41 %), followed by *P. pygmaeus* with 214 trajectories (30 %), *P. kuhlii* with 122 trajectories (17 %), *P. pipistrellus* with 77 trajectories (11 %) and *Hypsugo savii* with 6 trajectories (0.8 %) (Table S2). Bat trajectories contained on average 9.1 positions.

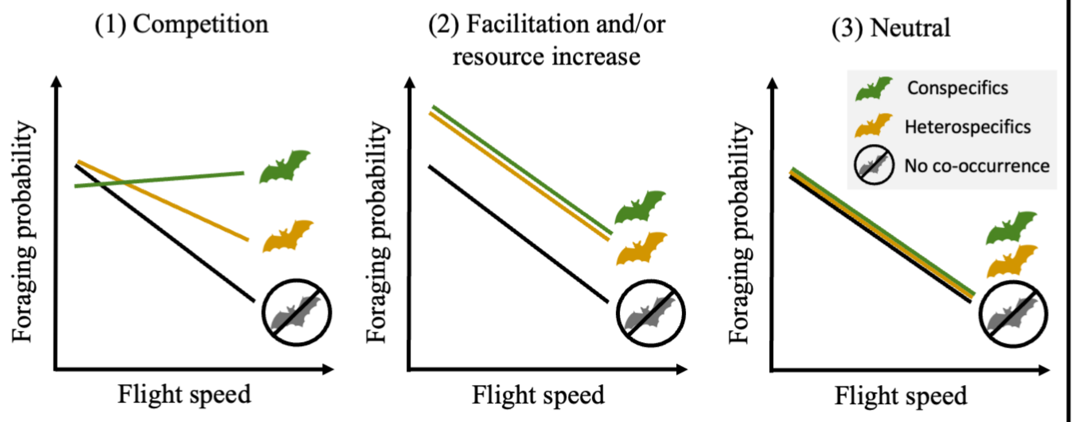
2.3. Assigning species and foraging probability to trajectories

To classify bat trajectories (i.e. bat calls) at the most precise taxonomic level, we ran the Tadarida software (Bas et al. 2017) on half-second sound files in which they were included. Then, we also ran a sonotype classifier to calculate and assign to each trajectory a probability of feeding buzz emission, indicating prey capture attempts (Roemer et al. 2021, Fig. 1). Species identity and feeding buzz score were then assigned to each trajectory. As echolocation calls from a single trajectory can be included in several consecutive half-second sound files, the trajectory can contain several species identifications. In that case, we selected the most represented species with the highest automated identification score.

(A) Spectrogram example of two co-occuring bat trajectories



(B) Hypotheses



(C) Experimental set-up and data preparation steps

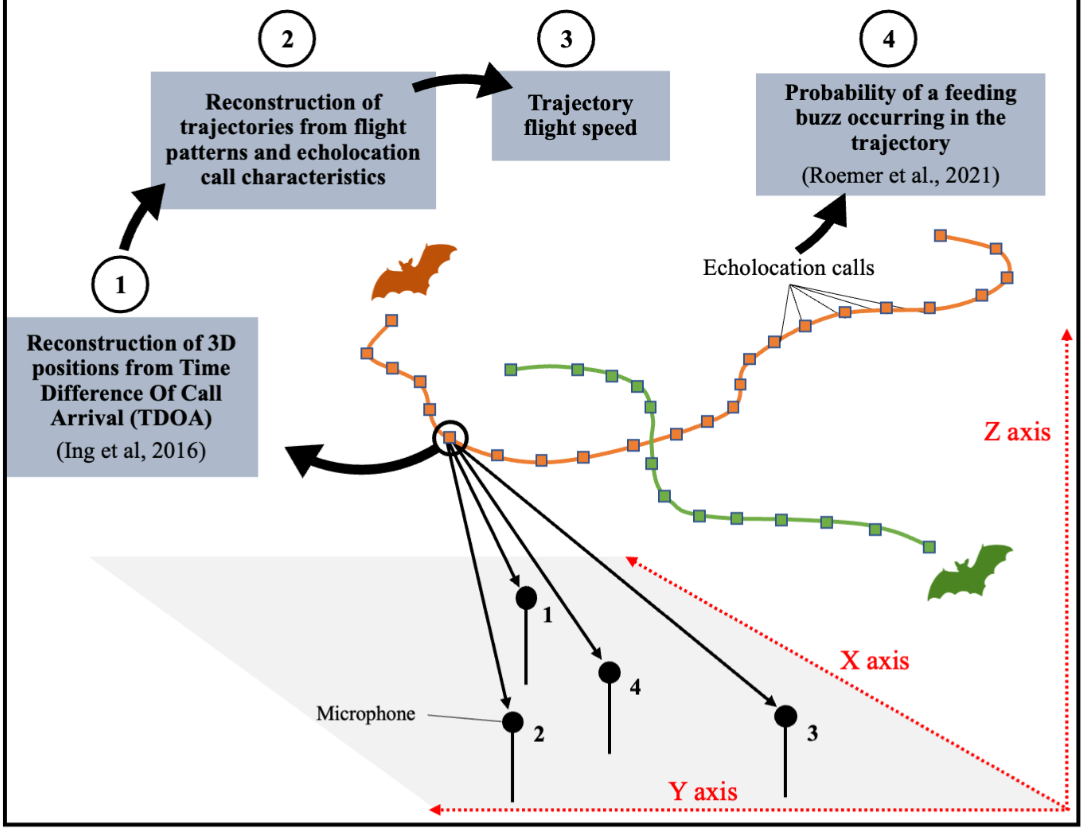


Figure 1. Schematic overview of a spectrogram example of co-occurring bats with a foraging buzz event (A), tested hypotheses (C), and the set-up used to reconstruct bat trajectories and compute the behavioural metric from echolocation calls (B). In panel B, situations without co-occurrence are shown in black while intra-guild co-occurrence is depicted in green for conspecifics and in yellow for heterospecifics.

Finally, we focused our analyses on the mid-range echolocators functional guild, which comprises in our dataset five species (*P. nathusii*, *P. pygmaeus*, *P. kuhlii*, *Pipistrellus pipistrellus* and *Hypsugo savii*) sharing similar call structure (Frequency Modulated downward – Quasi-Constant Frequency, FMd-QCF), foraging strategies (edge-space foragers) (Denzinger and Schnitzler 2013), and dietary niche (Vaughan 1997). This guild is the one that most frequently emits feeding buzzes, and the only one for which we recorded a sufficient number of trajectories to conduct analyses (Table S2).

2.4. Computing flight behaviour metrics

From 3D positions of each bat trajectory, we computed flight speed (V_i) between two 3D positions using the following expression (Equation 1):

$$V_i = \frac{\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2 + (z_i - z_j)^2}}{t_i - t_j} \qquad (1)$$

with *x, y* and *z* the distances to microphone 1 (Fig. 1c) for each of the 3D axes, *t* the time of call arrival to the microphone array of a given position *i* and its previous position *j*.

We filtered out flight speeds > 11 $m.s^{-1}$ (1.4% of bat trajectories) as these speeds are unlikely (Grodzinsky et al. 2009). Then, we selected the minimum flight speed of the trajectory instead of average flight speed, as this metric is expected to be more sensitive to the occurrence at a precise moment of a foraging behaviour within the trajectory than the average value (Barré et al. 2024).

Finally, since several feeding buzz scores can occur in a single trajectory if it extends over several sound files on which the feeding buzz classifier worked, we retained the maximum value of feeding buzz score contained in each trajectory as a robust indicator of bat feeding probability (Barré et al., 2024), for the same reason as explained above.

2.5. Computing co-occurrence number

To test the influence of co-occurrence events (i.e. the simultaneous presence of other individuals) on individual bat behaviour, we computed for each trajectory the number of conspecifics and heterospecifics present at the same time in the detection volume (i.e. between the start and end time of the trajectory). Since the microphone array records bats only up to a distance around 30 m, a recorded individual could have been in contact with other individuals already present in the detection volume before our first detection. Therefore, we applied a temporal buffer anterior to the start time of the trajectory to compute conspecifics and heterospecifics number. Because mid-range echolocators bats can perceive echolocation calls from other mid-range echolocators individuals from about 50 m away (Stilz and Schnitzler 2012), we applied a temporal buffer of 11.36 s, which corresponds to the time it would take an mid-range echolocator bat to cover 50 m at its average flight speed (4.4 $m.s^{-1}$ in our data). Since the number of other bats (either conspecifics or heterospecifics) could be low (Fig. S2), we discretized these two variables into categorial variables defined as presence/absence of conspecifics and presence/absence of heterospecifics. Finally, for heterospecifics, we restricted the calculation of co-occurrences to intra-guild interactions due to the extremely low number of inter-guild co-occurrences (Fig. S2). Since the aim of the study was to compare responses to conspecifics and heterospecifics independently, we excluded (i) trajectories showing both conspecific and heterospecific presence, (ii) trajectories showing a conspecific absence but heterospecfic presence for the study of conspecific effects, and trajectories showing a heterospecific absence but conspecific presence for the study of heterospecific absence.

We detected the simultaneous presence of at least one conspecific or intra-guild heterospecific for respectively 43 % and 20 % of trajectories (Fig. S2). For simultaneous presence events of conspecifics, 55 % of them exhibited one conspecific, 30 % two conspecifics, 13 % three conspecifics, 2 % four conspecifics (Fig. S2). For simultaneous presence events of intra-guild heterospecifics, 57 % of them exhibited one heterospecific, 32 % two heterospecifics, 8 % three heterospecifics, and 3 % four heterospecifics (Fig. S2).

2.6. Statistical analyses

To test how the presence of conspecifics and heterospecifics affected the foraging strategy of bats (i.e. their tendency to slow down to capture prey using feeding buzzes), we built generalized linear mixed models (GLMMs) using the *glmmTMB* R package (Brooks et al., 2017), including the maximum feeding buzz score of the trajectory as the response variable. To respect the application conditions of the models (i.e. a distribution close to a normal distribution and a homoscedasticity of the residuals, no dispersion or outlier issue; Fig. S3), we normalized the feeding buzz score using the *orderNorm* transformation from the *bestNormalize* R package (Peterson, 2021; Peterson & Cavanaugh, 2020) as its distribution was strongly skewed towards very small values (Fig. S4), and we used a Gaussian distribution in the models. We also chose to model the normalized response variable with a Gaussian distribution instead of an unnormalized one with a binomial distribution, because the latter produced residuals of very poor quality (Fig. S5). Then, to assess if the conspecifics or heterospecifics presence induced a modification of bat foraging strategy, we included in models as fixed explanatory variables the presence/absence of co-occurrence (i.e. either conspecifics or intra-guild heterospecifics, each modelled separately), the minimum flight speed of the trajectory, and an interaction term between them. Site identity was included as a random intercept in both models to control for pseudo-replication and inter-site variation sources. We did not include the date as random effect because it was highly redundant with the site identifier since we sampled one or two sites only per night. Yet, the site identifier was already capturing all the variability, and a random effect on the date alone did not produce an Akaike information criterion (AIC) smaller than that of the site, and the AIC was higher when the two were combined. Finally, species identity of the targeted individual was also included as a random effect in order to account for different activity level among the species of the mid-range echolocators guild. We therefore constructed two different models as follows:

Feeding buzz score ~ Conspecifics presence/absence * Minimum flight speed + (1|Site) + (1|Species), family = gaussian

Feeding buzz score ~ Heterospecifics presence/absence * Minimum flight speed + (1|Site) + (1|Species), family = gaussian

We used the *emtrend* and *emmeans* functions from the *emmeans* R package (Lenth, 2024) to test whether the regression coefficient of the minimum flight speed differed significantly in the absence and presence of co-occurrence, and to test whether the feeding buzz score significantly differed in presence of co-occurrence. These functions allow for robust and statistically rigorous post-hoc comparisons of adjusted marginal means, making it easier to test specific effects and differences between groups. Then, we checked the residuals of each model using the *DHARMa* R package (Hartig F, 2022; see Fig. S3).

Finally, we tested the difference in minimum flight speed between the presence/absence of conspecifics and heterospecifics in two distinct models. For that we built models with the same structure than presented above, using the minimum flight speed normalized with the *orderNorm* transformation as response variable, and the presence/absence of co-occurrence as fixed explanatory variable.

All statistical analyses were performed with R software 4.3.3 (R Core Team, 2024) using RStudio. The significance threshold was set at an alpha value of 0.05.

3. Results

3.1. Bat foraging flight strategy without co-occurrence

As expected, in absence of congeners, higher foraging probabilities in mid-range echolocators bats were associated with slower trajectories. Specifically, we found a significant negative relationship between the minimum flight speed and the maximum feeding buzz score of trajectories (Fig. 2; Tables 1 & S3).

3.2. Bat foraging flight strategy with co-occurrence

The feeding buzz score was significantly higher in presence of conspecifics than in absence regardless of the flight speed (Fig. 2), as shown by the significant post-hoc comparison between conspecific absence and presence (Table S3). The negative slope of the relationship between the feeding buzz score and the flight speed remained similar in presence and absence of conspecifics (Tables 1 & S3; Fig. 2A).

In presence of intra-guild heterospecifics, the feeding buzz score was also significantly higher in average than in absence (Fig. 2), as shown by the significant post-hoc comparison between heterospecific absence and presence (Table S3). However, here, we found a significant interaction between heterospecific presence/absence and the flight speed (Table 1), with a strong change in the foraging flight strategy in presence of heterospecifics (Fig. 2). Specifically, heterospecific presence cancelled the negative relationship otherwise observed between the feeding buzz score and the flight speed, as demonstrated in post-hoc tests showing a significant negative slope in absence of heterospecifics which became non-significant in presence of heterospecifics (Table S3; Fig. 2).

Finally, minimum flight speed of individuals did not differ between situations with and without co-occurrence of conspecifics and intra-guild heterospecifics (Table S4).

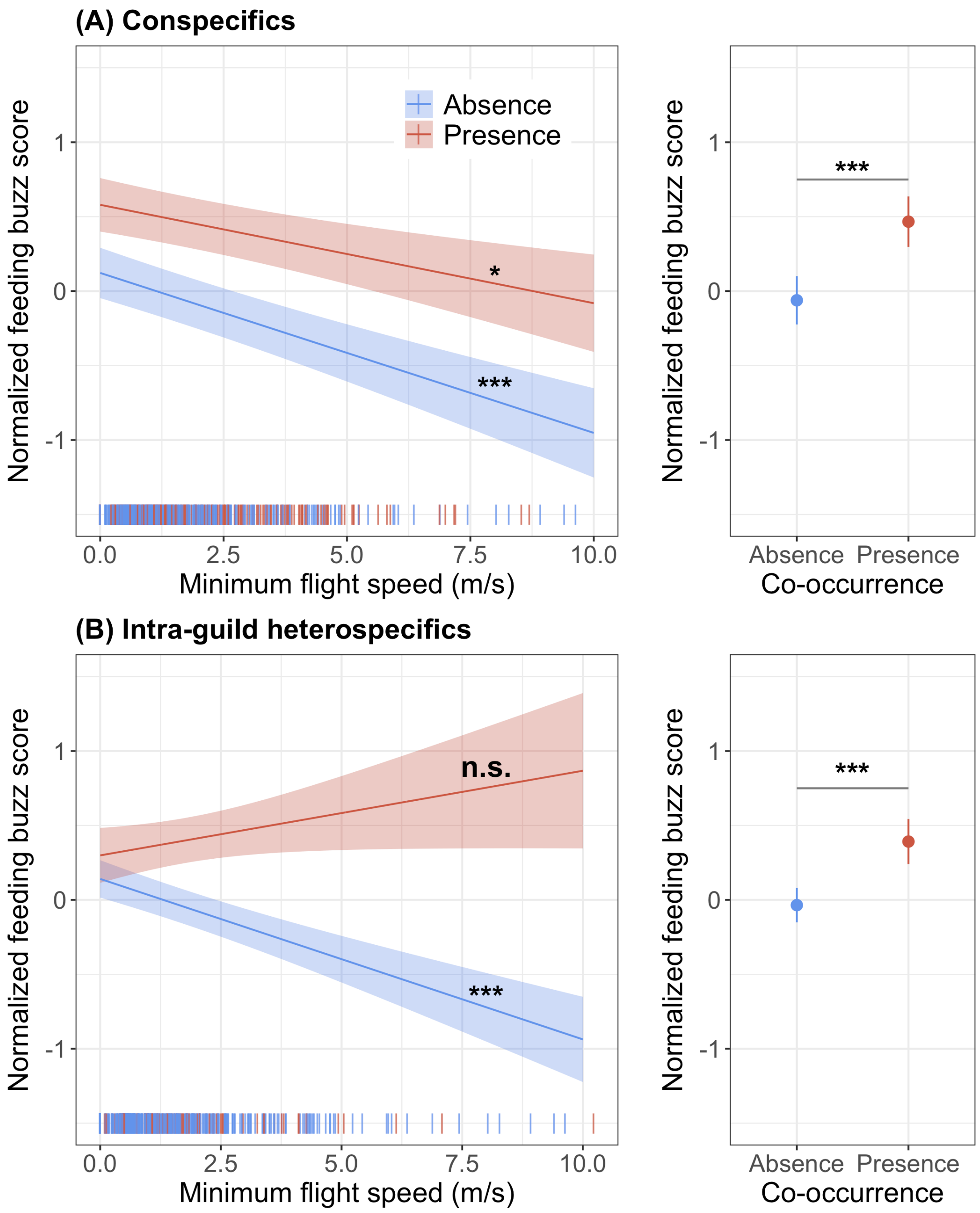


Figure 2. Predicted values from GLMMs of the relationship between the normalized maximum feeding buzz score and the minimum flight speed of mid-range echolocators bats in absence and presence of conspecifics (A) and intra-guild heterospecifics (B). Stars depict significant relationships and *n.s.* annotations depict non-significant ones, from post-hoc tests presented in table S3.

Table 1. Estimates, standard errors, z values and P-values from GLMMs testing the relationship between the feeding buzz score and the minimum flight speed of the trajectory while accounting for the presence/absence of conspecific and intra-guild heterospecific. The delta AIC (Akaike Information Criterion) exhibits the difference in AIC value of the models with the null model, when positive models are considered as better than the null model.

Variable	**Estimate**	**SE**	**z value**	**P-value**	**delta AIC**
Conspecifics model					
Intercept	0.122	0.169	0.723	0.470	50.642
Conspecific presence	0.458	0.112	4.084	**< 0.001*****	
Minimum flight speed	-0.107	0.030	-3.599	**< 0.001*****	
Conspecific presence : Minimum flight speed	0.041	0.045	0.917	0.359	
Intra-guild heterospecifics model					
Intercept	0.141	0.125	1.123	0.261	18.748
Heterospecific presence	0.158	0.168	0.939	0.348	
Minimum flight speed	-0.108	0.031	-3.459	**< 0.001*****	
Heterospecific presence : Minimum flight speed	0.165	0.068	2.426	**0.015***	

4. Discussion

In this study, we provide results that contribute to a better understanding of social foraging at low bat density, by showing that flight strategy of bats differs according to the species identity of co-occurring individuals with which they interact. We specifically found that in presence of individuals belonging the same species, bats kept their optimal foraging flight strategy which consisted to slow down when trying to capture preys, while increasing their capture attempts. However, when bats were exposed to individuals belonging to a different species from the same guild, they no longer adapted their flight speed to their foraging intensity. The study thus shows that inter-individual interactions can affect the foraging strategy of bats, and that they integrate species identity in making decisions about the flight strategy to adopt. Results might have important implications for the understanding of consequences of interactions on individuals.

4.1. Bat foraging flight strategy

When foraging alone, individuals were slowing down to attempt capturing prey, then speeded up when they were not foraging. This is highly consistent with literature which demonstrates a clear negative relationship between foraging intensity and flight speed across several species from different guilds (Holderied and Jones 2009). Aerodynamic models suggest that this strategy optimizes energy balance of insectivorous echolocating bats, likely enhancing individual fitness (Grodzinski et al. 2009; Troxell et al. 2019; McGuire and Boyles 2024).

4.2. *Effects of co-occurrence on bat foraging flight strategy*

In the presence of individuals belonging to the same species, bats did not change their foraging flight strategy, but exhibited higher levels of capture attempts. This result may reflect either facilitation, e.g. by information transfer about prey location between individuals (e.g. by eavesdropping to feeding buzzes emitted by other foragers); a naturally high prey availability attracting more foraging individuals, or a combination of both mechanisms (Dechmann et al. 2009; Gager 2019; Lewanzik et al. 2019). Here we are unable to conclusively determine which exact mechanism is at play, as monitoring variations in prey availability was not possible.

In presence of individuals belonging to a different species from the same guild, bats strongly changed their flight strategy since they no longer adapted their flight speed to their foraging intensity. This behaviour change could suggest a direct competition for food. Indeed, since our results indicate that flight speed of individuals did not differ between the absence and presence of other bats, we can suggest that competitive situations force bats to no longer use flight speed as a lever to facilitate foraging, probably leading to suboptimal flight speeds. This could potentially lead to a sub-optimal prey capture strategy, but it may also be the only way to continue foraging without having to change patches too often. This explanation appears to be consistent with studies showing that individuals may deliberately choose to compete with other foragers by chasing the same prey rather than leaving the area for another (Racey and Swift 1985; Chiu et al. 2010; Corcoran 2022). Another hypothesis could be that in a close acoustic niche context, feeding buzzes and more generally echolocation calls could be used by individuals not only to locate flying targets and obstacles, but also to disturb co-occurring individuals by preventing them to sense and capture preys, and to try to force them to leave the food patch (Amarasekare 2002; Corcoran and Conner 2014; Corcoran 2022). Alternatively, bats could change their flight strategy to adopt a territorial and aggressive behaviour in presence of congeners to defend foraging patches (Hillen et al. 2009; Stone et al. 2015), which could constitute an energetically more beneficial strategy than acoustic interferences (Cvikel et al. 2015; Corcoran 2022). Finally, as for the presence of other individuals belonging the same species, the overall foraging level increases in the presence of individuals belonging to another species. Hence, the competition is probably not the only mechanism at play, and others could occur such as facilitation by information transfer between individuals about prey location, and/or a higher prey availability attracting more foraging individuals.

Then, of the fact that individuals only shifted their flight behaviour in presence of a different species suggests a tolerance towards individuals belonging the same species. Although the acoustic niche overlap is lower towards different species, individuals nevertheless share similar foraging strategies inherent to the mid-range echolocators guild, making competition very likely. One explanation could be that individuals have a greater interest in cooperating with individuals of the same species given their extremely gregarious nature and social cohesion in colonies.

The results are especially important as anthropogenic pressures such as artificial light at night deeply rearrange the composition of bat communities and their prey in time and space (Jägerbrand and Spoelstra 2023), which therefore potentially exacerbate natural competition through indirect effects on inter-individual interactions.

4.3. Prospects and limitations

We highlighted a potential alteration of optimal flight strategy in mid-range echolocators bats due the presence of individuals. Future studies could go further by coupling 3D trajectory data with morphological, energetic and prey availability data to assess to which extent this alteration reflects a suboptimal shift on a physiological point of view.

In addition, we recorded a limited number of bat flight trajectories, potentially due to the period of sampling (fall, in late September), and sites offering a limited amount of prey (located in old industrial sites or embankments resulting from the Rhône canalization). This probably resulted in a loss of statistical power and prevented us to study inter-guild and species-specific relationships. Instead of testing a presence/absence of other individuals, it would be interesting to collect more data with high variations in the number of co-occurring individuals to explore density-dependence mechanisms such as the optimal foraging group size, as recently shown by Krivoruchko et al. (2024) in relation to conspecifics for *Molossus nigricans* in Mexico. Indeed, benefits from social information sharing, either intentional or not, have been shown to be dependent on the group size. Studies suggested the existence of an optimal foraging group size that maximizes the efficiency of foraging while minimizing local competition or social interference (Clark and Mangel 1986; Giraldeau and Caraco 2000; Beauchamp and Fernández-Juricic 2005; Silk 2007). Understanding how group size affects the foraging success is therefore likely to provide crucial information on how species use habitats in space and time at both individual and population levels (Michelena et al. 2009).

Finally, in this study we used the bat feeding buzz score as a proxy of prey capture attempts. However, future studies could measure and use the post-buzz pause duration, i.e. the silence time between the last buzz emission and the beginning of a new echolocation call sequence, as a proxy capture attempt success, as suggested by several studies (Britton and Jones 1999; Mizuguchi et al. 2022; Stidsholt et al. 2023). The post-buzz pause duration indeed increases in case of a successful capture attempt due to the prey handling time between capture and chewing.

Acknowledgments

This work was supported by the Office Français de la Biodiversité (OFB), the Compagnie nationale du Rhône (CNR), and the Agence de la transition écologique (ADEME). The equipment was funded by the Muséum national d'Histoire naturelle (MNHN) through the Actions Thématiques du Muséum (ATM) and the Ligue pour la Protection des Oiseaux (LPO) Auvergne-Rhône-Alpes. We thank Christian Kerbiriou for its comments on the manuscript and Ros-Kiri Ing for its technical support regarding the equipment. Finally, we thank the two anonymous reviewers for their constructive comments.

Data availability

Analyses reported in this article can be reproduced using the data provided by Barré (2025).

Authors' contribution

K.B. designed the study and the methodological approach, with the support of M.D. K.B. and A.B. collected the data. K.B. created the workflow for data preparation and processing. K.B. and M.D. conducted the analyses, and all authors contributed to result interpretations. M.D. and K.B. led the writing of the manuscript with the input of A.P., A.R., M.T. and F.V.

Conflict of interest

None to declare.

5. References

Allen JA, Cade DE, Casey CB, Weindorf S, Johnston DW, Linsky JMJ, Goldbogen JA, Nowacek DP, Friedlaender AS. 2024. Evidence of sociality and group foraging in Antarctic minke whales (Balaenoptera bonaerensis). Behav Ecol Sociobiol. 78(5):61. https://doi.org/10.1007/s00265-024-03481-4.

Amarasekare P. 2002. Interference competition and species coexistence. Proceedings of the Royal Society of London Series B: Biological Sciences. 269(1509):2541–2550. https://doi.org/10.1098/rspb.2002.2181.

Amichai E, Blumrosen G, Yovel Y. 2015. Calling louder and longer: how bats use biosonar under severe acoustic interference from other bats. Proc Biol Sci. 282(1821):20152064. https://doi.org/10.1098/rspb.2015.2064.

Barré, K. 2025. Data from: Foraging flight strategy varies with species identity of co-occurring individuals in bats. Behavioral Ecology. https://doi.org/10.5061/dryad.6q573n6b0

Barré K., Baudouin A., Froidevaux J. S. P., Chartendrault V., & Kerbiriou C. 2023. Data from: Insectivorous bats alter their flight and feeding behaviour at ground-mounted solar farms. Journal of Applied Ecology. Zenodo https://doi.org/10.5281/zenodo.10149959.

Barré K, Baudouin A, Froidevaux JSP, Chartendrault V, Kerbiriou C. 2024. Insectivorous bats alter their flight and feeding behaviour at ground-mounted solar farms. Journal of Applied Ecology. 61(2):328–339. https://doi.org/10.1111/1365-2664.14555.

Barré K, Kerbiriou C, Ing R-K, Bas Y, Azam C, Le Viol I, Spoelstra K. 2021. Bats seek refuge in cluttered environment when exposed to white and red lights at night. Movement Ecology. 9(1):3. https://doi.org/10.1186/s40462-020-00238-2.

Barré K, Spoelstra K, Bas Y, Challéat S, Kiri Ing R, Azam C, Zissis G, Lapostolle D, Kerbiriou C, Le Viol I. 2020. Artificial light may change flight patterns of bats near bridges along urban waterways. Animal Conservation. 24(2):259–267. https://doi.org/10.1111/acv.12635.

Bas Y, Bas D, Julien J-F. 2017. Tadarida: A Toolbox for Animal Detection on Acoustic Recordings. 5(1):6. https://doi.org/10.5334/jors.154.

Bas Y, Kerbiriou C, Julien JF, Roemer C. 2023. Maps predicted activity. Team-Chiro. https://croemer3.wixsite.com/teamchiro/maps-predicted-activity?lang=fr.

Beauchamp G, Fernández-Juricic E. 2005. The group-size paradox: effects of learning and patch departure rules. Behavioral Ecology. 16(2):352–357. https://doi.org/10.1093/beheco/arh169.

Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1537), 87-97. https://doi-org /10.1098/rstb.2009.0150.

Britton ARC, Jones G. 1999. Echolocation behaviour and prey-capture success in foraging bats: laboratory and field experiments on Myotis daubentonii. Journal of Experimental Biology. 202(13):1793–1801. https://doi.org/10.1242/jeb.202.13.1793.

Buckley NJ. 1997. Experimental tests of the information-center hypothesis with black vultures (Coragypsatratus) and turkey vultures (Cathartesaura). Behav Ecol Sociobiol. 41(4):267–279. https://doi.org/10.1007/s002650050388.

Caraco T., & Giraldea L. A. 1991. Social foraging: producing and scrounging in a stochastic environment. Journal of Theoretical Biology, 153(4), 559-583. https://doi.org/10.1016/S0022-5193(05)80156-0.

Charnov E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology, 9(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Chaverri G, Ancillotto L, Russo D. 2018. Social communication in bats. Biological Reviews. 93(4):1938–1954. https://doi.org/10.1111/brv.12427.

Chiu C, Reddy PV, Xian W, Krishnaprasad PS, Moss CF. 2010. Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, Eptesicus fuscus. Journal of Experimental Biology. 213(19):3348–3356. https://doi.org/10.1242/jeb.044818.

Clark CW, Mangel M. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology. 30(1):45–75. https://doi.org/10.1016/0040-5809(86)90024-9.

Corcoran AJ. 2022. Sing or Jam? Density-Dependent Food Competition Strategies in Mexican Free-Tailed Bats (Tadarida brasiliensis). Frontiers in Ecology and Evolution. 10. https://www.frontiersin.org/articles/10.3389/fevo.2022.877579.

Corcoran AJ, Conner WE. 2014. Bats jamming bats: Food competition through sonar interference. Science. 346(6210):745–747. https://doi.org/10.1126/science.1259512.

Connell, J. H. (1983). On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments. *The American Naturalist*, *122*(5), 661–696. https://doi.org/10.1086/284165

Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour. 50(5):1325–1339. https://doi.org/10.1016/0003-3472(95)80048-4.

Cvikel N, Egert Berg K, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y. 2015. Bats Aggregate to Improve Prey Search but Might Be Impaired when Their Density Becomes Too High. Current Biology. 25(2):206–211. https://doi.org/10.1016/j.cub.2014.11.010.

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution. 20(4):187–193. https://doi.org/10.1016/j.tree.2005.01.010.

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH. 2004. Public Information: From Nosy Neighbors to Cultural Evolution. Science. 305(5683):487–491. https://doi.org/10.1126/science.1098254.

Dechmann DKN, Heucke SL, Giuggioli L, Safi K, Voigt CC, Wikelski M. 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. Proceedings of the Royal Society B: Biological Sciences. 276(1668):2721–2728. https://doi.org/10.1098/rspb.2009.0473.

Denzinger A, Schnitzler H. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in physiology. 4:164. https://doi.org/10.3389/fphys.2013.00164.

Deygout C, Gault A, Duriez O, Sarrazin F, Bessa-Gomes C. 2010. Impact of food predictability on social facilitation by foraging scavengers. Behavioral Ecology. 21(6):1131–1139. https://doi.org/10.1093/beheco/arq120.

Egert-Berg K, Hurme ER, Greif S, Goldstein A, Harten L, M LGH, Flores-Martínez JJ, Valdés AT, Johnston DS, Eitan O, et al. 2018. Resource Ephemerality Drives Social Foraging in Bats. Current Biology. 28(22):3667-3673.e5. https://doi.org/10.1016/j.cub.2018.09.064.

Fraser et al., eds. 2020. Bat Echolocation Research: A handbook for planning andconducting acoustic studies. Second Edition. Bat Conservation International.Austin, Texas, USA. https://hdl.handle.net/1959.11/61281.

Fenton MB. 2003. Eavesdropping on the echolocation and social calls of bats. Mammal Review. 33(3–4):193–204. https://doi.org/10.1046/j.1365-2907.2003.00019.x.

Flemming SP, Smith PC, Seymour NR, Bancroft RP. 1992. Ospreys Use Local Enhancement and Flock Foraging to Locate Prey. The Auk. 109(3):649–654. https://doi.org/10.1093/auk/109.3.649.

Gager Y. 2019. Information transfer about food as a reason for sociality in bats. Mammal Review. 49(2):113–120. https://doi.org/10.1111/mam.12146.

Gillam EH. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. Can J Zool. 85(7):795–801. https://doi.org/10.1139/Z07-060.

Giraldeau L-A, Caraco T. 2000. Social Foraging Theory. Princeton University Press.

Griffin DR. 1958. Listening in the dark: The acoustic orientation of bats and men. Oxford, England: Yale Univer. Press (Listening in the dark: The acoustic orientation of bats and men).

Griffin DR, Webster FA, Michael CR. 1960. The echolocation of flying insects by bats. Animal Behaviour. 8(3):141–154. https://doi.org/10.1016/0003-3472(60)90022-1.

Grodzinski U, Spiegel O, Korine C, Holderied MW. 2009. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii? Journal of Animal Ecology. 78(3):540–548. https://doi.org/10.1111/j.1365-2656.2009.01526.x.

Hartig F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6.1, https://github.com/florianhartig/dharma.

Hillen J., Kiefer A., Veith M, 2009. Foraging site fidelity shapes the spatial organisation of a population of female western barbastelle bats. Biological Conservation, 142(4), 817-823. https://doi.org/10.1016/j.biocon.2008.12.017.

Holderied M, Jones G. 2009. Flight Dynamics. In: T.H. K, Parsons S, editors. Ecological and Behavioral Methods for the Study of Bats. Johns Hopkins University Press. p. 459–475.

Ing RK, Colombo R, Gembu G-C, Bas Y, Julien J-F, Gager Y, Hassanin A. 2016. Echolocation Calls and Flight Behaviour of the Elusive Pied Butterfly Bat (Glauconycteris superba), and New Data on Its Morphology and Ecology. Acta Chiropterologica. 18(2):477–488. https://doi.org/10.3161/15081109ACC2016.18.2.014.

Jägerbrand AK, Spoelstra K. 2023. Effects of anthropogenic light on species and ecosystems. Science. 380(6650):1125–1130. https://doi.org/10.1126/science.adg3173.

Jiang, G., Liu, J., Xu, L., Yan, C., He, H., & Zhang, Z. (2015). Intra- and interspecific interactions and environmental factors determine spatial–temporal species assemblages of rodents in arid grasslands. *Landscape Ecology*, *30*(9), 1643–1655. https://doi.org/10.1007/s10980-014-0039-6

Jones G, Rayner JMV. 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats Myotis daubentoni (Chiroptera: Vespertilionidae). Journal of Zoology. 215(1):113–132. https://doi.org/10.1111/j.1469-7998.1988.tb04888.x.

Jones G, Siemers BM. 2011. The communicative potential of bat echolocation pulses. J Comp Physiol A. 197(5):447–457. https://doi.org/10.1007/s00359-010-0565-x.

Kelt DA, Heske EJ, Lambin X, Oli MK, Orrock JL, Ozgul A, Pauli JN, Prugh LR, Sollmann R, Sommer

S. 2019. Advances in population ecology and species interactions in mammals. Journal of Mammalogy. 100(3):965–1007. https://doi.org/10.1093/jmammal/gyz017.

Koblitz JC. 2018. Arrayvolution: using microphone arrays to study bats in the field. Can J Zool. 96(9):933–938. https://doi.org/10.1139/cjz-2017-0187.

Krivoruchko K., Koblitz J. C., Goldshtein A., Biljman K., Guillén-Servent A., & Yovel Y. 2024. A social foraging trade-off in echolocating bats reveals that they benefit from some conspecifics but are impaired when many are around. Proceedings of the National Academy of Sciences, 121(30), e2321724121. https://doi.org/10.1073/pnas.2321724121.

Lenth R., Singmann H., Love J., Buerkner P., & Herve M. (2018). Package “Emmeans”. R Package Version 4.0-3. http://cran.r-project.org/package=emmeans.

Lewanzik D, Sundaramurthy AK, Goerlitz HR. 2019. Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate cost–benefit ratio of interactions. Journal of Animal Ecology. 88(10):1462–1473. https://doi.org/10.1111/1365-2656.12989.

Mariton L, Le Viol I, Bas Y, Kerbiriou C. 2023. Characterising diel activity patterns to design conservation measures: Case study of European bat species. Biological Conservation. 277:109852. https://doi.org/10.1016/j.biocon.2022.109852.

McGuire LP, Boyles JG. 2024. Chapter 10 - Energetics of foraging bats. In: Russo D, Fenton B, editors. A Natural History of Bat Foraging. Academic Press. p. 173–198. https://www.sciencedirect.com/science/article/pii/B9780323918206000127.

Mizuguchi Y, Fujioka E, Heim O, Fukui D, Hiryu S. 2022. Discriminating predation attempt outcomes during natural foraging using the post-buzz pause in the Japanese large-footed bat, Myotis macrodactylus. Journal of Experimental Biology. 225(7):jeb243402. https://doi.org/10.1242/jeb.243402.

Monier SA. 2024. Social interactions and information use by foraging seabirds. Biological Reviews. 99(5): 1717–1735. https://doi.org/10.1111/brv.13089.

O’brien W. J., Browman H. I., & Evans B. I. 1990. Search strategies of foraging animals. American Scientist, 78(2), 152-160.

R Core Team 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Racey PA, Swift SM. 1985. Feeding Ecology of Pipistrellus pipistrellus (Chiroptera: Vespertilionidae) during Pregnancy and Lactation. I. Foraging Behaviour. Journal of Animal Ecology. 54(1):205–215. https://doi.org/10.2307/4631.

Roeleke M, Schlägel UE, Gallagher C, Pufelski J, Blohm T, Nathan R, Toledo S, Jeltsch F, Voigt CC. 2022. Insectivorous bats form mobile sensory networks to optimize prey localization: The case of the common noctule bat. Proceedings of the National Academy of Sciences. 119(33):e2203663119. https://doi.org/10.1073/pnas.2203663119.

Roemer C, Julien J-F, Ahoudji PP, Chassot J-M, Genta M, Colombo R, Botto G, Negreira CA, Djossa BA, Ing RK, et al. 2021. An automatic classifier of bat sonotypes around the world. Methods in Ecology and Evolution. 12(12):2432–2444. https://doi.org/10.1111/2041-210X.13721.

Ridley A. R., Wiley E. M., & Thompson A. M. 2013. The ecological benefits of interceptive eavesdropping. Functional Ecology, 28(1), 197-205. https://doi-org.inee.bib.cnrs.fr/10.1111/1365-2435.12153.

Ryer CH, Olla BL. 1995. Influences of food distribution on fish foraging behaviour. Animal Behaviour. 49(2):411–418. https://doi.org/10.1006/anbe.1995.0054.

Salinas-Ramos VB, Ancillotto L, Bosso L, Sánchez-Cordero V, Russo D. 2020. Interspecific competition in bats: state of knowledge and research challenges. Mammal Review. 50(1):68–81. https://doi.org/10.1111/mam.12180.

Schnitzler H-U, Kalko EKV. 2001. Echolocation by Insect-Eating Bats.BioScience. 51(7):557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2.

Schnitzler H-U, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology & Evolution. 18(8):386–394. https://doi.org/10.1016/S0169-5347(03)00185-X.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B: Biological Sciences. 362(1480):539–559. https://doi.org/10.1098/rstb.2006.1994.

Smith JE, Holekamp KE. 2023. Hunting Success in the Spotted Hyena: Morphological Adaptations and Behavioral Strategies. In: Srinivasan M, Würsig B, editors. Social Strategies of Carnivorous Mammalian Predators: Hunting and Surviving as Families. Cham: Springer International Publishing. p. 139–175. https://doi.org/10.1007/978-3-031-29803-5_5.

Snijders L., Kurvers R. H., Krause S., Ramnarine I. W., & Krause J. 2018. Individual-and population-level drivers of consistent foraging success across environments. Nature Ecology & Evolution, 2(10), 1610-1618. https://doi.org/10.1038/s41559-018-0658-4.

Stidsholt L, Hubancheva A, Greif S, Goerlitz HR, Johnson M, Yovel Y, Madsen PT. 2023. Echolocating bats prefer a high risk-high gain foraging strategy to increase prey profitability. Watanabe YY, Weigel D, Watanabe YY, Fenton B, editors. eLife. 12:e84190. https://doi.org/10.7554/eLife.84190.

Stilz W-P, Schnitzler H-U. 2012. Estimation of the acoustic range of bat echolocation for extended targets. The Journal of the Acoustical Society of America. 132(3):1765–1775. https://doi.org/10.1121/1.4733537.

Stone E, Zeale MRK, Newson SE, Browne WJ, Harris S, Jones G. 2015. Managing Conflict between Bats and Humans: The Response of Soprano Pipistrelles (Pipistrellus pygmaeus) to Exclusion from Roosts in Houses. PLoS ONE 10(8): e0131825. https://doi.org/10.1371/journal.pone.0131825.

Troxell S. A., Holderied M. W., Pētersons G., & Voigt C. C. 2019. Nathusius' bats optimize long-distance migration by flying at maximum range speed. Journal of Experimental Biology, 222(4). https://doi.org/10.1242/jeb.176396.

Vaughan, N. 1997. The diets of British bats (Chiroptera). Mammal Review, 27(2), 77–94. https://doi.org/10.1111/j.1365-2907.1997.tb00373.x.