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Original Article

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

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Foraging is a key function in the animal kingdom. Foraging in groups drives food patch discovery through social information transfer that maximizes an 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 the foraging flight strategy of bats, a highly social taxon with strong behavioral plasticity in response to resource ephemerality, remain little tested. Through a 3D 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 (ie slowing down to capture prey and speeding up to find new prey patches), is no longer used in the 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 toward conspecifics with which social relations are most important, eg because they share the same roost. This might have important implications in understanding the 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.

Keywords: 3D acoustic tracking; chiroptera; competition; facilitation; foraging flight behavior; interindividual interactions.

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 interspecific strategies to maximize their foraging success (Bell 2010). Coping with environmental stochasticity in the search for an optimal foraging strategy calls for plasticity in behavioral responses such as movements (O'Brien et al. 1990) and social interactions (Caraco and Giraldea 1991). Foraging in groups also referred to as social foraging, is a widespread strategy in the 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 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 interference (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 behavior 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 (eg Ryer and Olla 1995; Deygout et al. 2010; Smith and Holekamp 2023; Monier 2024, 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

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similar foraging strategy and niche (Connell 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 scarce 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 (eg raptors; Flemming et al. 1992; Buckley 1997; Deygout et al. 2010) and mammals (eg whales and canids; Creel and Creel 1995; Allen et al. 2024). Recent advances in acoustic signal treatment allow for to automatic tracking and decoding behavior of species otherwise difficult to monitor, such as bats. This enables to collection of 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 expanding 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 through information transfer and the drawback of the presence of other foragers at the same time.

Insectivorous bats emit echolocation calls to orient themselves in space, communicate with each other (Fenton 2003; Jones and Siemers 2011), and to locate, pursue, and capture prey while foraging (Griffin 1958; Griffin et al. 1960; Schnitzler et al. 2003). To capture prey, 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 favorable 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 behavior (eg 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 a 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 2 scenarios: (1) in the presence of conspecifics (ie individuals from the same species), and (2) in the 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 maneuverability 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 2 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 the reference individual strategy. In line with the social foraging theory, 3 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 behavioral 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 to the same guild should exacerbate the consequences of interference 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 behavior 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 the case of constant non-limiting resources and constant foraging level between individuals, or insufficient co-occurrence events to generate resource depletion or interference. Further, we expect competition to occur more toward conspecifics due to ecological and acoustic niche overlaps that should exacerbate the consequences of resource depletion and interferences (Gager 2019), while facilitation could occur toward both cons- and heterospecifics given that individuals are able to be attentive to the foraging behavior of all species (Gager 2019; Lewanzik et al. 2019).

Materials and methods

Study area

For the study, we used data from Barré et al. (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 behavior responses of insectivorous bats to ground-mounted solar farms (Barré et al. 2024), and we only retained control sites (ie 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 ± 15 m from woody edges) in old industrial sites or embankments resulting from the Rhône canalization. Sampling sites were selected within landscapes made of ~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,

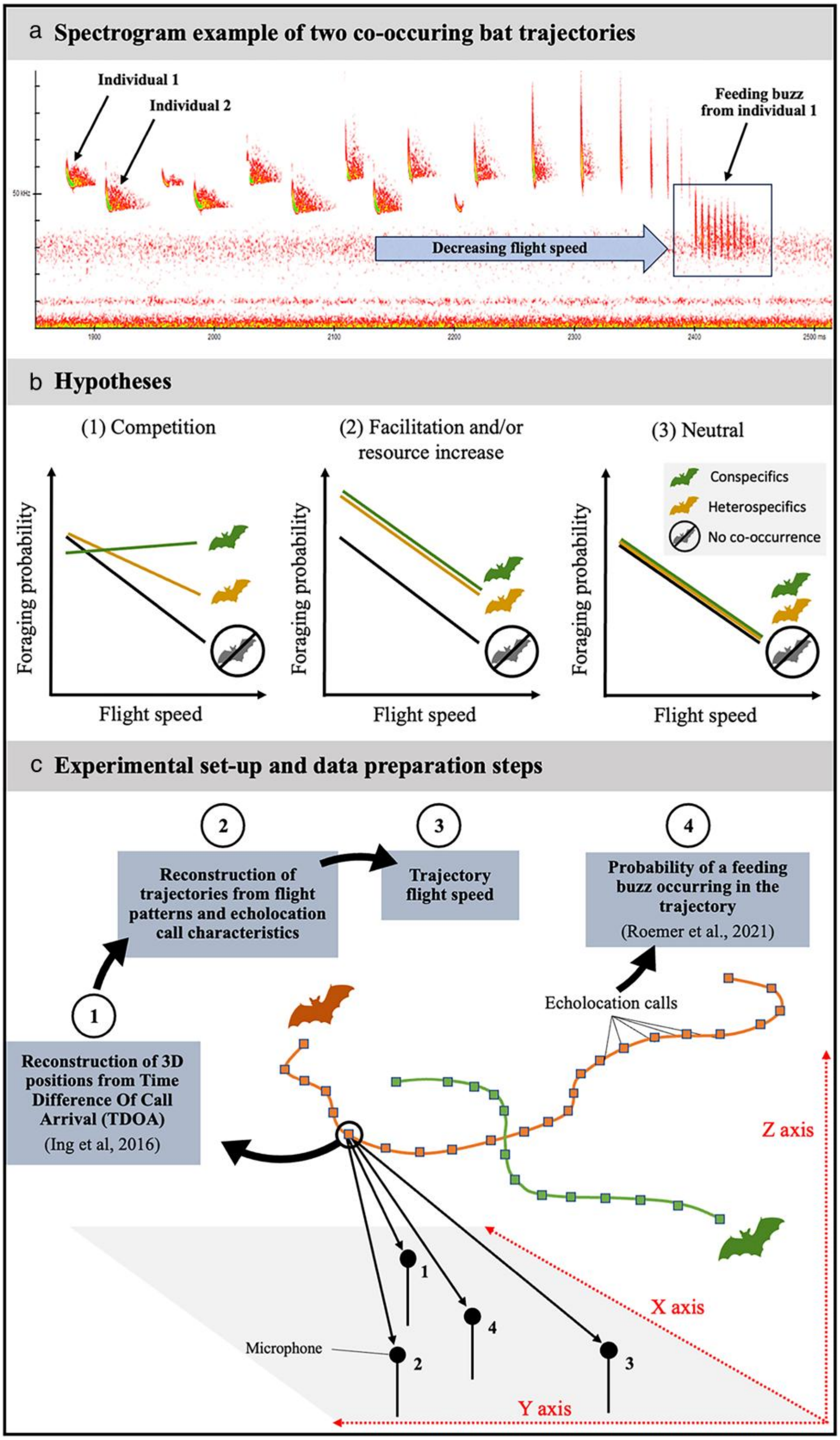

Fig. 1. Schematic overview of a spectrogram example of co-occurring bats with a foraging buzz event a), tested hypotheses c), and the setup used to reconstruct bat trajectories and compute the behavioral metric from echolocation calls b). In b), situations without co-occurrence are shown in black while intra-guild co-occurrence is depicted in green for conspecifics and in yellow for heterospecifics.

sampling stations presented a homogeneous habitat cover (low herbaceous vegetation) throughout the recorder's detection volume (~30-m radius; see section "Bat acoustic tracking and trajectory reconstruction" for more details) to ensure an optimal and standardized bat call detectability (Table S1).

Bat acoustic tracking and trajectory reconstruction

Nine nights with favorable weather conditions for bats (average temperature during the sampling period: 11.4 to 20 °C; wind speed: 0 to 5.3 m s^{-1}; no rain) were sampled in 2022 from 21 to 30 September. Each night, bat echolocation calls were recorded at 1 or 2 sites simultaneously during the first 3 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 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. (2021a, 2021b, 2024). This system consists in an arrangement of 4 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 ~2 m, and with 1 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. (2021a, 2021b). 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 were 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%), *Pipistrellus pipistrellus* with 77 trajectories (11%) and *Hypsugo savii* with 6 trajectories (0.8%) (Table S2). Bat trajectories contained on average 9.1 positions.

Assigning species and foraging probability to trajectories

To classify bat trajectories (ie 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.

Finally, we focused our analyses on the mid-range echolocators functional guild, which comprises in our dataset 5 species (*P. nathusii*, *P. pygmaeus*, *P. kuhlii*, *P. pipistrellus*, and *H. 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 1 that most frequently emits feeding buzzes, and the only 1 for which we recorded a sufficient number of trajectories to conduct analyses (Table S2).

Computing flight behavior metrics

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

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

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 (Grodzinski et al. 2009). Then, we selected the minimum flight speed of the trajectory instead of the average flight speed, as this metric is expected to be more sensitive to the occurrence at a precise moment of a foraging behavior 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.

Computing co-occurrence number

To test the influence of co-occurrence events (ie the simultaneous presence of other individuals) on individual bat behavior, we computed for each trajectory the number of conspecifics and heterospecifics present at the same time in the detection volume (ie between the start and end time of the trajectory). Since the microphone array records bats only up to a distance of 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. Because mid-range echolocating bats can perceive echolocation calls from other mid-range echolocator 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 a 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 2 variables into categorical 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 (1) trajectories showing both conspecific and heterospecific presence, (2) trajectories showing a conspecific absence but heterospecific 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 1 conspecific or intra-guild heterospecific for respectively 43% and 20% of trajectories (Fig. S2). For simultaneous presence events of conspecifics, 55% of them exhibited 1 conspecific, 30% 2 conspecifics, 13% 3 conspecifics, 2% 4 conspecifics (Fig. S2). For simultaneous presence events of intra-guild heterospecifics, 57% of them exhibited 1 heterospecific, 32% 2 heterospecifics, 8% 3 heterospecifics, and 3% 4 heterospecifics (Fig. S2).

Statistical analyses

To test how the presence of conspecifics and heterospecifics affected the foraging strategy of bats (ie their tendency to slow down to capture prey using feeding buzzes), we built generalized linear mixed models (GLMMs) using the *glmmTMB* R package, including the maximum feeding buzz score of the trajectory as the response variable. To respect the application conditions of the models (ie 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 as its distribution was strongly skewed toward 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 (ie either conspecifics or intra-guild heterospecifics, each modeled 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 1 or 2 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 2 were combined. Finally, species identity of the targeted individual was also included as a random effect in order to account for different activity levels among the species of the mid-range echolocators guild. We therefore constructed 2 different models as follows:

$$\text{Feeding buzz score} \sim \text{Conspecifics presence/absence} \times \text{Minimum flight speed} + (1|\text{Site}) + (1|\text{Species}), \text{family} = \text{Gaussian}$$

$$\text{Feeding buzz score} \sim \text{Heterospecifics presence/absence} \times \text{Minimum flight speed} + (1|\text{Site}) + (1|\text{Species}), \text{family} = \text{Gaussian}$$

We used the *emtrend* and *emmeans* functions from the *emmeans* R package (Lenth et al. 2018) 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 the 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 2022; see Fig. S3).

Finally, we tested the difference in minimum flight speed between the presence/absence of conspecifics and heterospecifics in 2 distinct models. For that, we built models with the same structure as presented above, using the minimum flight speed normalized with the *orderNorm* transformation as the response variable, and the presence/absence of co-occurrence as a 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.

Results

Bat foraging flight strategy without co-occurrence

As expected, in the absence of congeners, higher foraging probabilities in mid-range echolocating 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 and S3).

Bat foraging flight strategy with co-occurrence

The feeding buzz score was significantly higher in the presence of conspecifics than in the 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 the presence and absence of conspecifics (Fig. 2a; Tables 1 and S3).

In the presence of intra-guild heterospecifics, the feeding buzz score was also significantly higher on average than in its 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 canceled 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 (Fig. 2; Table S3).

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

Discussion

In this study, we provide results that contribute to a better understanding of social foraging at low bat density, by showing that the flight strategy of bats differs according to the species identity of co-occurring individuals with which they interact. We specifically found that in the presence of individuals belonging to the same species, bats kept their optimal foraging flight strategy, which consisted of slowing down when trying to capture prey, 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 the consequences of interactions on individuals.

Bat foraging flight strategy

When foraging alone, individuals slowed down to attempt capturing prey, then sped up when they were not foraging. This is highly consistent with the literature, which demonstrates a clear negative relationship between foraging intensity and flight speed

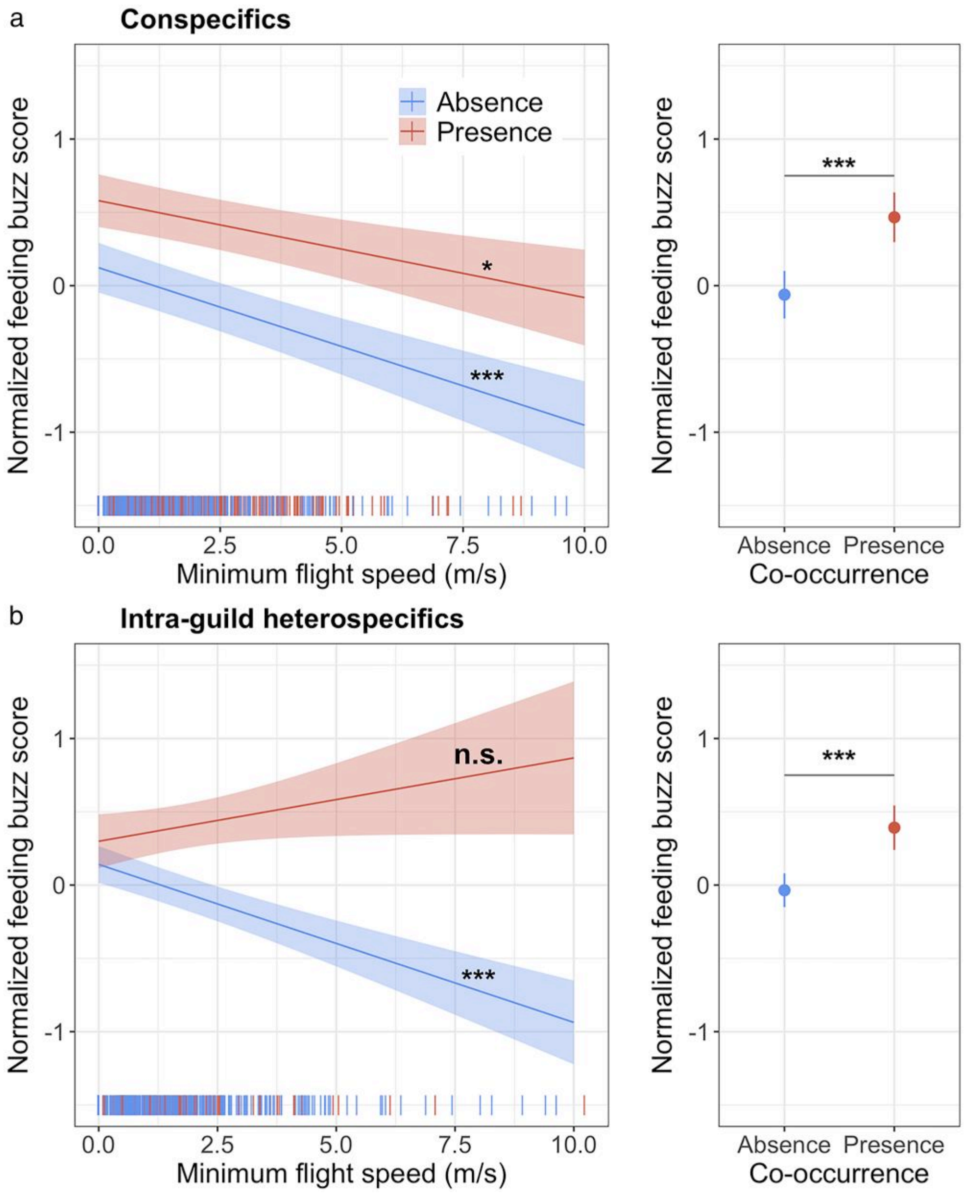

Fig. 2. Predicted values from GLMMs of the relationship between the normalized maximum feeding buzz score and the minimum flight speed of mid-range echolocating bats in the absence and presence of conspecifics a) and intra-guild heterospecifics b). Stars depict significant relationships and *n.s.* Annotations 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.

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***	

The delta AIC exhibits the difference in AIC value of the models with the null model, when positive models are considered as better than the null model. Significant effects are shown in bold (***$P < 0.001$, *$P < 0.05$).

across several species from different guilds (Holderied and Jones 2009). Aerodynamic models suggest that this strategy optimizes the energy balance of insectivorous echolocating bats, likely enhancing individual fitness (Grodzinski et al. 2009; Troxell et al. 2019; McGuire and Boyles 2024).

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 facilitation, eg by information transfer about prey location between individuals (eg 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 the 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 behavior change could suggest a direct competition for food. Indeed, since our results indicate that the 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 suboptimal 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 behavior in the 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 to 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, the fact that individuals only shifted their flight behavior in the presence of a different species suggests a tolerance toward individuals belonging to the same species. Although the acoustic niche overlap is lower toward 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.

Prospects and limitations

We highlighted a potential alteration of optimal flight strategy in mid-range echolocating bats due to the presence of individuals. Future studies could go further by coupling 3D trajectory data with morphological, energetic, and prey availability data to assess the extent to which this alteration reflects a suboptimal shift from 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 from studying inter-guild and species-specific relationships. Instead of testing the 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-dependent 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.

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, ie the silence time between the last buzz emission and the beginning of a new echolocation call sequence, as a proxy for 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 the case of a successful capture attempt due to the prey handling time between capture and chewing.

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Author contributions

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Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Conflicts of interest

None declared.

Data availability

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

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