



A social foraging trade-off in echolocating bats reveals that they benefit from some conspecifics but are impaired when many are around

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Social foraging is very common in the animal kingdom. Numerous studies have documented collective foraging in various species and many reported the attraction of various species to foraging conspecifics. It is nonetheless difficult to quantify the benefits and costs of collective foraging, especially in the wild. We examined the benefits and costs of social foraging using on-board microphones mounted on freely foraging *Molossus nigricans* bats. This allowed us to quantify the bats' attacks on prey and to assess their success as a function of conspecific density. We found that the bats spent most of their time foraging at low conspecific densities, during which their attacks were most successful in terms of prey items captured per time unit. Notably, their capture rate dropped when conspecific density became either too high or too low. Our findings thus demonstrate a clear social foraging trade-off in which the presence of a few conspecifics probably improves foraging success, whereas the presence of too many impairs it.

Animal sociality is shaped by contradicting forces: On the one hand, individuals can benefit from being around their own kind; while on the other hand, high conspecific densities might have disadvantages such as increased competition over resources (1, 2). When and why do the benefits of behaving in a group outweigh the drawbacks constitute major questions in the field of animal behavior (1, 3). The benefits of sociality might arise through various mechanisms and might be relevant on various temporal and spatial scales—from the gradual learning of long migratory routes from experienced individuals (4) to immediate collective sensing of the environment in search of food or to avoid predators (3, 5, 6).

Group sensing is one of the most suggested social benefits and probably one of the most ancient ones, used even by bacteria, which implement collective sensing in order to exploit environmental gradients (7). However, in addition to posing increased competition, group foraging could also impose difficulties on the process of collective sensing itself, which might deteriorate at increased conspecific densities, e.g., due to sensory interference (8).

Consequently, a social foraging trade-off has been suggested, in which the presence of conspecifics up to a certain threshold improves the overall success of the individual, but beyond which the success rate declines (9, 10).

Multiple studies have documented collective foraging in various species, and many animals have been shown to be attracted to foraging conspecifics (11–16). However, very few of these studies have directly quantified the social foraging trade-off described above, and even fewer did so in the wild, due to the difficulty in tracking the interactions between many individuals while also monitoring their foraging success (9, 16–21). Examining this trade-off in wild bats was the goal of this study.

Many bat species are highly social, exhibiting various levels of sociality, from roosting in large populations to foraging with many nearby conspecifics (10, 17, 22–26). The bats' use of echolocation to intercept prey provides public information about their foraging attempts. Specifically, whenever a bat attempts to catch a prey item, it emits a typical echolocation sequence, known as a feeding-buzz (27, 28). Due to the physics of sound waves spreading, these sequences of calls can be detected by other bats from distances that are much greater than the bats' own echolocation-based prey-detection range. Thus, feeding-buzzes can serve as a nonintentional advertisement of finding prey, which could lead bats to search in a group or attract individuals to join other foraging bats at a profitable patch. Indeed, both a mathematical framework and live bat tracking have indicated how in cases of patchily distributed ephemeral resources, bats can benefit from collective search due to these acoustic benefits (10, 18, 29). High bat densities, however, might also impair foraging due to spatial and sensory interference (8, 30). When foraging in the vicinity of conspecifics, bats must also avoid collisions and contend with the loud acoustic interference created by conspecific calls. Consequently, we hypothesized that bats would be most successful when foraging in the vicinity of conspecifics

Significance

Many animals aggregate during foraging. While this behavior has often been suggested to contribute to foraging success, it might also come at a cost. Quantifying the trade-off between the benefits and costs of social foraging is extremely difficult in wild animals and specifically so in bats. We hypothesized that bats would benefit from the presence of some conspecifics but would struggle at high conspecific densities. We used miniature on-board microphones mounted on small insectivorous bats, which enabled us to detect conspecifics in the bats' vicinity and to assess the bats' foraging success by documenting their chewing sounds. Our findings confirmed the above-noted trade-off and offer valuable insight into the ecological and evolutionary drivers of sociality.

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but that their performance would deteriorate when conspecific density became too high.

Echolocating bats offer a unique opportunity to study the social foraging trade-off in the wild, because they continuously emit sounds that enable us to follow their foraging while also monitoring the presence of conspecifics using sound recordings. Indeed, several previous studies that employed individual-tracking or acoustic playbacks have reported that bats intentionally aggregate when searching for prey (10, 22, 23), and other studies have reported on bats' foraging strategies with nearby conspecifics (8, 18, 31, 32).

In this study, we report the results of using an on-board microphone that enabled us to record sound continuously while the bats were foraging. These recordings were used to directly quantify individual foraging attempts based on the echolocation emissions of attack sequences and to assess foraging success as reflected in the chewing sounds recorded immediately following the echolocation attack sequences (see *SI Appendix, Supplementary File 1* for such a recording and *SI Appendix, Fig. S1* that show chewing sounds recorded in the hand).

We were able to detect the presence of conspecifics from up to ~50 m [almost as far as the bat's hearing detection range (10)], which enabled us to assess conspecific density during flight. Parallel acceleration recordings performed with the same device enabled the determination of when the bats were flying. Notably, the use of the on-board microphones allowed us to monitor both the presence of conspecifics, as well as the bats' foraging success (via chewing), and thus to examine the relation between the two.

We used this system to study the social foraging trade-off in black mastiff bats (*Molossus nigricans*) that forage on ephemeral prey that are typically patchily distributed. Black mastiff bats emerge a little before dusk from their small communal roosts, which comprise a few dozen individuals (33, 34). They typically perform short foraging bouts (<1 h) and are aerial hawkers and specialized beetle-eating foragers (large pleurostict scarab beetles, hydrophilid beetles, and flying ants have been reported in their diet, along with a conspicuous scarcity of moths) (34, 35). We chose to examine this species because current theory suggests that animals that rely on a patchily distributed ephemeral food resources would benefit most from a foraging strategy that combines individual exploration with social learning (36, 37).

Results

We analyzed the audio and acceleration recordings of 10 black mastiff bats. The bats typically left their colony twice a day for short foraging bouts of $\sim 36 \pm 10$ min at sunset and at dawn which are typical for

Table 1. Captured bats' data

Bat	Bat mass on tagging [g]	Sex	Tag mass [g]	Percent of body mass [%]	Tag schedule (local time)	Flight start	Flight end	Flight duration	Number of attacks	Max number of attacks per 5 s	Number of successful attacks	Percent of successful attacks [%]
1	44.25	f	4.34	9.8	5:30–7:00	6:25:29	6:42:21	0:16:52	76	2	64	84
2	44.18	f	4.33	9.8	5:30–7:00	5:54:42	6:38:09	0:43:27	259	4	175	68
3	40.8	f	4.28	10.5	5:30–7:00	5:56:16	6:42:48	0:46:32	255	3	219	86
4	37.77	f	4.27	11.3	5:30–7:00	5:56:50	6:39:51	0:43:01	157	3	121	77
5	41	f	4.63	11.3	20:00–21:30	20:33:13	21:06:18	0:33:05	90	2	65	72
6	37.12	f	4.29	11.6	20:00–21:30	20:33:24	21:05:20	0:31:56	81	3	61	75
7	38.02	f	4.28	11.3	20:00–21:30	20:33:38	21:00:41	0:27:03	110	3	71	65
8	46.56	m	4.58	9.8	20:00–21:30	20:29:35	21:20:08	0:50:33	139	3	87	63
9	40.8	f	4.61	11.3	20:00–21:30	20:33:26	21:05:51	0:32:25	77	2	66	86
10	38.63	f	4.33	11.2	20:00–21:30	20:30:02	21:05:09	0:35:07	110	3	77	70

this species (38) (Mean \pm SD for all bats). Because we could not record audio continuously from sunset to dawn, we recorded either the evening or morning activity bout of the bat. We found no differences between the patterns of the morning and evening bouts and therefore we analyzed them together (*Methods*). During these bouts, the bats performed an average of 135.4 ± 69.4 attacks (i.e., 3.73 ± 1.26 per minute, Mean \pm SD, see Table 1, with a maximum of four attacks in a 5-s window). Their average success rate was $74.5 \pm 8.6\%$. Attacks began immediately after leaving the roost and were fairly uniformly distributed across the foraging bouts (Fig. 1 *A* and *B*).

Clustering based on the acoustic parameters of the conspecific calls suggests that the number of conspecific calls is a good proxy for the number of nearby conspecifics (*SI Appendix, Fig. S2 A and B*). Thus, in all further analyses, the number of conspecific calls per 5 s was used as an estimate for conspecific density. Attacks and successful attacks were also counted in 5-s windows. Conspecific echolocation calls were nearly always searching calls while conspecific attack and feeding-buzzes were very rare. Note that the bin defined as "0" conspecifics might have contained some conspecifics that were not detected by our microphone but were detected by the bats (which are more sensitive to sound than our microphone).

Our results support the social foraging trade-off hypothesis. On the one hand, the overall attack rate (attacks per minute) showed significant positive correlation with the density of nearby conspecifics, continuously increasing up to 75 conspecifics by an average of 0.034 attacks per conspecific call (Fig. 2*C*, $P < 0.0024$, Mixed Effect GLM—generalized linear mixed-effects (GLMM)—with the total attack rate set as the explained parameter, the conspecific density as a fixed factor, and bat ID as a random effect, assuming a Poisson distribution, see Table 2 and *Methods* for full statistics). On the other hand, the overall *successful* attack rate (successful attacks per minute) rose from a density of 0 conspecifics to that of 1 to 25 conspecifics, but above that number it showed a very strong negative correlation with the density of conspecifics, decreasing by an average of ~ 0.02 successful attacks per additional conspecific call (Fig. 2*C*, $P < 1.0e-22$, GLMM with the successful attack rate set as the explained parameter, and the rest as above—see Table 2). The percentage of successful attacks (i.e., how many of the attacks were successful out of the total number) was also negatively correlated with conspecific density (Fig. 2*D*, $P < 1.9e-08$, GLMM with the proportion of successful attacks out of all attacks per minute set as the explained parameter, and the rest as above, but with the logit link function, and see Table 2). Success dropped below 50% at conspecific densities higher than 75 calls per 5 s, likely making foraging at such high conspecific densities inefficient.

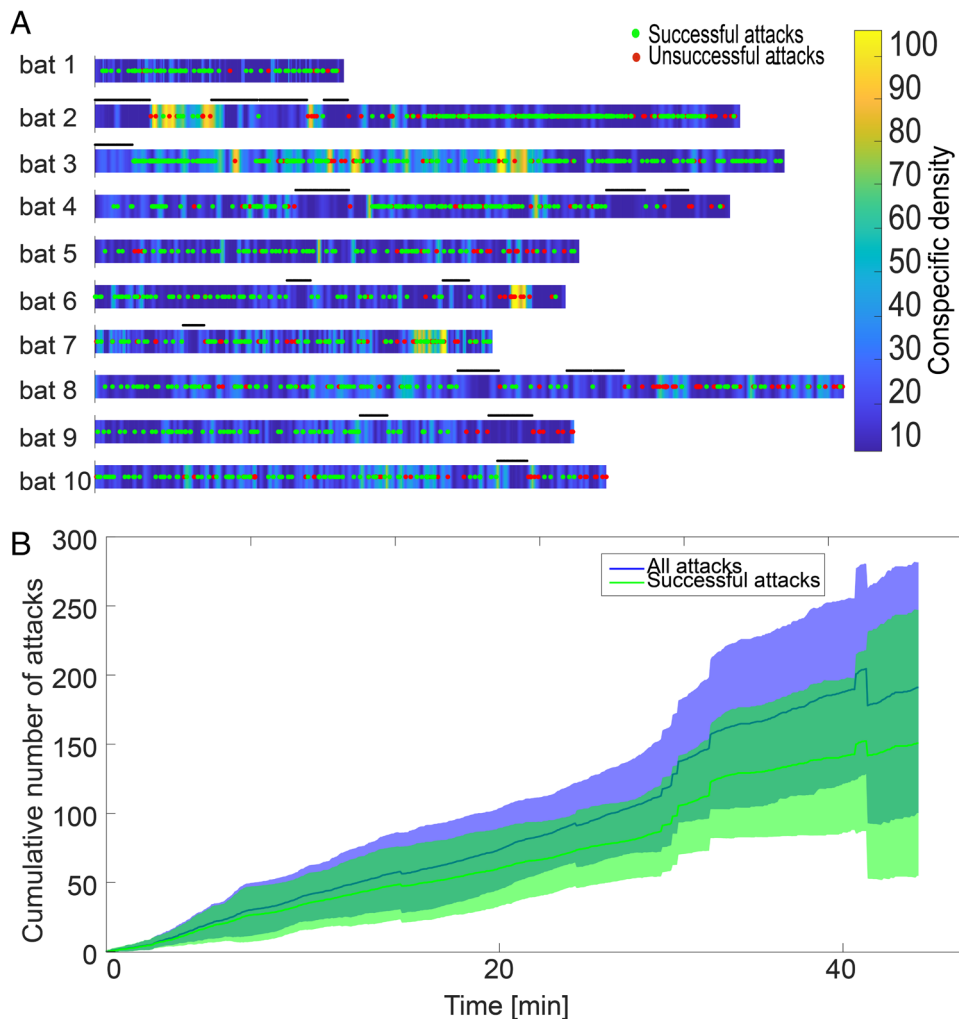


Fig. 1. Complete description of bat foraging. (A) Successful (green dots) and unsuccessful (red dots) attacks throughout the entire recording period for all 10 bats. The levels of conspecific density are color-coded. Black horizontal lines depict flights with no attacks for more than 1.5 min—the longest time periods without attacks that were observed at least once for almost every bat (except bats 6 and 10)—and were identified by us as commute episodes. (B) The cumulative number of total/successful attacks from the beginning of the flight. The average of all 10 bats is presented. Shaded area represents the SD.

Furthermore, when the conspecifics' call intensity was included in the analysis as a proxy for the closeness of nearby conspecifics, both the attack and success rates were negatively correlated to conspecific call intensity, suggesting that nearby conspecifics hinder foraging success more than more distant conspecifics ($P < 0.002$ and $P < 0.004$ respectively; GLMM with a Poisson distribution with the total/successful attack rate set as the explained parameter and conspecific density and the maximal call intensity in 5-s intervals as fixed factors, and bat ID as a random effect).

In addition to successful attacks, we examined the abundance of aborted attacks, i.e., attacks that were halted before completion and found that their propensity was positively and significantly correlated with the conspecific density, suggesting that more attacks are stopped in the middle when there are more nearby conspecifics ($P < 2.1 \times 10^{-125}$ with a Poisson distribution with the disrupted attack rate set as the explained parameter, the conspecific density as a fixed factor, and bat ID as a random effect). Moreover, we found that conspecific calls are significantly more intense during aborted attacks than during completed attacks, suggesting that conspecifics are closer during aborted attacks and are likely the cause for abstaining from attacking (SI Appendix, Fig. S4).

The above findings suggest that at higher conspecific densities, foraging success deteriorates. In order to demonstrate the existence

of a social foraging trade-off, we examined whether bats nonetheless benefited from the presence of conspecifics: that is, whether they obtained more prey with some conspecifics around (1 to 25 per 5 s) than with no conspecifics at all (i.e., we compared the first two bins in Fig. 2C). The total and successful attack rate was significantly higher with some conspecifics around than with none present. The increase was of 8.1% from 3.46 to 3.77 total attacks and of 11.7% from 2.64 to 2.99 successful attacks on average per minute, with 0 vs. 1 to 25 conspecific calls, respectively ($P < 0.0007/P < 0.016$; GLMM with a Poisson distribution with the total/successful attack rate set as the explained parameter, the conspecific density as a fixed factor, and bat ID as a random effect, and every 5-s bin considered as a separate trial).

To assess the most profitable conspecific density, it is necessary to take into account both the rate of successful attacks and the time spent at each conspecific density. To this end, we estimated the proportion of successful and overall attacks that were performed (for the entire night) at each conspecific density. The proportion of attacks and successful attacks (of all attacks) was significantly higher in the presence of some conspecifics than without any ($P < 0.004$ and $P < 0.003$ for attacks and successful attacks respectively, GLMM with a logit link function with the total/successful attack proportion set as the explained parameter, the conspecific density as a fixed factor, and with bat ID as a

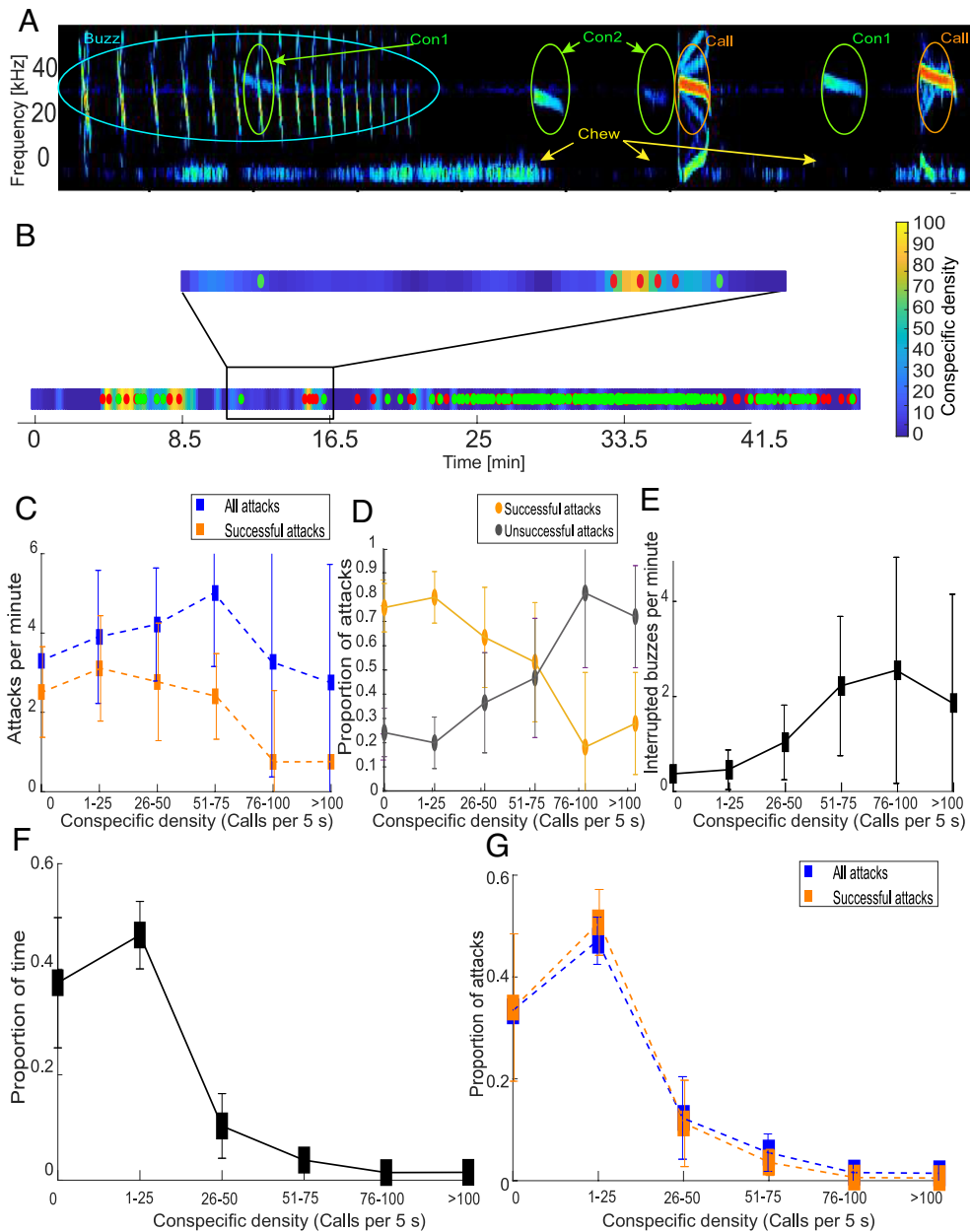


Fig. 2. Bats detect more prey when flying with conspecifics, but catching success lessens at high conspecific densities. (A) Spectrogram of a successful attack. The beginning of the attack echolocation sequence is labeled “buzz” and marked by a blue circle; conspecific calls are marked with green circles and labeled “con”; the first chewing sound is marked with a yellow arrow and labeled “chew.” (B) The complete foraging bout of one bat. Background colors depict conspecific density (the bins are 5-s long), green dots depict successful attacks, red dots depict unsuccessful attacks. See Fig. 1A for the behavior of all bats. In panels C–E, the Mean ± SD of 10 bats is presented. X-label on the *Bottom* is relevant for all panels. Conspecific density in these panels represents the number of conspecific calls per 5 s. (C) The number of attacks (successful and overall) per minute as a function of conspecific density. (D) The proportion of successful and unsuccessful attacks per conspecific density. The values of the two sum to 1. (E) Number of aborted attack sequences per minute as a function of conspecific density. (F) The proportion of flight time spent at each conspecific density. (G) The proportion of successful/attacks per minute out of successful/all attacks per minute during the entire flight at each conspecific density. The values of each line sum to 1. This graph takes into account both the attack rate (C) and the time spent at each conspecific density (F).

random effect and with the sum of the attacks per density considered as a separate trial).

Finally, we sought to examine whether bats intentionally aggregated when searching rather than aggregating passively at the foraging sites as a result of high prey density. To this end, we examined the flight segments without attacks that occurred between the periods of foraging (i.e., attacking), assuming that these segments represent searching flight intervals (between foraging sites, see black horizontal lines in Fig. 1A). We then examined whether there were nearby conspecifics during these search bouts, assuming that if the bats aggregated by chance at foraging

sites, rather than searched as a group, they would fly alone during these search bouts (i.e., with 0 conspecifics around). Our findings showed otherwise: Bats performed search flights nearly equally at 0 or at 1–25 conspecific densities (Fig. 1A), alternating frequently between these two conspecific densities. On average, the bats spent ~49% near 0 conspecifics, ~43% near 1 to 25 conspecifics, and the remaining 8% near more than 25 conspecifics during these zero attacks bouts of flight. Considering that bats emerge from a small colony (with circa 20 to 30 bats) and were shown to return to the roost individually (38), they are not expected to be present around conspecifics so often by chance. We suggest that the bats

Table 2. Statistical analyses parameters

Analysis	<i>P</i> -value	Effect size	Log-likelihood	AIC	BIC	SE	Degrees of freedom	Sample size	Fixed effect	Random effect	Number of bats
Overall attack rate per minute	0.002	0.002	-7404.8	14,816	14,832	0.0006	1,709	1,711	Conspecific density (0-75)	Bat	10
Successful attack rate per minute	1.04E-22	-0.006	-8392.6	16,791	16,808	0.00056	1,786	1,788	Conspecific density (0->100)	Bat	10
Proportion of successful attacks out of all attacks at each trial	1.95E-08	-0.015	-1652.2	3,312.4	3,331	0.00269	759	761	Conspecific density (0->100)	Bat	10
Overall attacks per 5 s windows	0.002	0.013	-2648.9	5,305.9	5,327	0.0043	1,321	1,324	Conspecific density and maximum call intensity	Bat	9
Successful attacks per 5 s windows	0.004	0.014	-2816.9	5,641.8	5,663	0.0047	1,321	1,324	Conspecific density and maximum call intensity	Bat	9
Disrupted attack sequences	2.13E-125	0.02	-9744.9	19,496	19,512	0.0008	1,786	1,788	Conspecific density (0->100)	Bat	10
Attacks rate	7.00E-04	0.006	-7263	14,532	14,551	0.0025	3,558	3,560	Conspecific density (0-25) in 5 s window	Bat	10
Successful attacks rate	1.60E-02	0.007	-7680.8	15,368	15,386	0.0029	3,558	3,560	Conspecific density (0-25) in 5 s window	Bat	10
Proportion of attacks per density out of all attacks	0.004	0.023	-9.95	27.9	31.88	0.004	18	20	Conspecific density (0-25)	Bat	10
Proportion of successful attacks per density out of all successful attacks	0.003	0.028	-12.36	32.72	36.7	0.008	18	20	Conspecific density (0-25)	Bat	10

tend to intentionally stay in the vicinity of conspecifics also during search/commute flights.

Discussion

Many mechanisms by which animals benefit from the presence of conspecifics during foraging have been suggested in the socio-biology literature. Krebs et al. (39) suggested several possible foraging advantages that might lead to social foraging, such as increasing the availability of the food (e.g., when animals flush the prey out of the tree canopy while moving); decreasing the probability of searching an already depleted areas; and learning about the adversity and palatability of various food sources.

If the food source is ephemeral, patchily distributed, and non-depletable, as in the case of some of the insectivorous bats that forage on large swarms of insects, social foraging can tremendously benefit the animals via collective searching. Even though insect swarms can be detected from as far as 8 m [as opposed to ~2 m

for an individual insect (40)], conspecific calls can be detected from much greater distance [sometimes up to 120 m (18)]. Here, we show that the bats' foraging performance deteriorates when there are too many conspecifics around—supporting the social foraging trade-off hypothesis. Based on previous work, we suggest that the benefit gained from group foraging is mainly a result of collective searching in which the bats move with nearby individuals and eavesdrop on their echolocation attack signals in order to improve the search for prey (15, 16). Our data also suggest that aggregating is an active choice for these bats, since they emerge from small colonies with circa 20 to 30 bats and are thus not expected to fly with other bats by chance. However, the studied bats were almost always found in the presence of some conspecifics, even when flying for several minutes without attacking, in what seemed like searching bouts.

In a previous study, we have already argued and modeled the benefits bats gain from searching collectively (10). However, the current study moved us several steps forward in understanding

the social trade-off. Thanks to our much more sensitive microphone, we were able to quantify both the presence of conspecifics and the foraging success (via chewing) simultaneously and continuously, which was not possible previously. This allowed us to explore the effects of conspecifics on actual prey capture and not only on prey-detection as we did before, and indeed, we found that these two measurements exhibit different dependencies on conspecific density.

Black mastiff bats probably forage on ephemeral and patchily distributed prey (33, 34), which are suitable for collective searching because the location of such prey is hard to predict and hard to find when searching alone; but, once found, there is enough prey for many individuals. Note too that the zero conspecifics sometimes detected on our devices does not necessarily mean zero conspecifics from the bat's perspective, as its hearing sensitivity is higher. This means that our findings were probably somewhat conservative and that we would have observed an even stronger pattern if our microphone had been as sensitive as the bats' aural system.

We further suggest that the deterioration of foraging performance at high conspecific densities is mainly a result of interrupted movement and only to a lesser degree the result of sensory interference, as recently suggested by a foraging model (8). In this latter study, it was shown that when bats forage together at a foraging site, the need to avoid collisions with other bats and the occasional competition over the same prey item will reduce the feeding rate as a function of the density of conspecifics (even if there are enough prey for all bats). The model showed that sensory interference also plays a role in such situations, but its effect is secondary to that of the interrupted movement. In fact, the rate of disturbance described by Mazar and Yovel (2020) per 20 conspecifics is quite similar to the rate that we found here at similar conspecific densities. The latter study reported a circa 100% decrease in catches per time unit with a 10-fold increase in conspecific density, which is similar to what we observed (Fig. 1C). Since black mastiff bats forage in open areas, their behavior is mainly affected by prey and conspecific density rather than by environmental obstacles. However, further research combining acoustic and tracking information is required in order to clearly test this.

Our findings also suggest that bats adjust their behavior to match the social foraging trade-off and spend more time at conspecific densities that are beneficial for foraging. A similar trend was also found by Roeleke et al. (18), who tracked the movement of a bat species with a similar foraging style.

Moreover, several previous studies have shown that bats respond to conspecific echolocation calls (41–46) and can be attracted by artificial playbacks of conspecific calls in the field (47). Roeleke et al. (48) showed that *Nyctalus noctula* bats reacted to both con- and heterospecific playbacks in a season-dependent manner. Interestingly, the bats were attracted to conspecific playbacks of up to ~250 calls per minute, which is consistent with our finding that *M. nigricans* bats spent most of their time foraging at the densities of 1 to 25 calls per 5 s. However, it is noteworthy that most playback studies used playback of feeding-buzzes to attract foraging bats, whereas in the wild, if bats search collectively, they must also be attracted to the searching calls of other bats, as has been shown for ephemeral foragers (10, 22). Based on our recordings too, that vast majority of conspecific calls that the bats encountered were search calls (while conspecific feeding-buzzes were very rare).

In conclusion, due to their reliance on sound, echolocating bats offer a unique opportunity to study fundamental questions in sociobiology in a quantitative manner. Specifically, recording sound allowed us to infer the density of conspecifics including an estimation of their distance, to assess the probability of prey-detection

(attacks) and their success (chewing). It is extremely difficult to continuously assess all these parameters in freely moving wild animals over full foraging bouts. Future work should deepen our understanding of social foraging trade-offs, for example, by looking into interindividual differences and their effects on foraging success.

Methods

Ethics. Capturing and handling of bats were performed under license FAUT-0145 from the Secretaría de Medio Ambiente y Recursos Naturales of the Mexican Government to A.G.-S. Bats were treated according to the 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (49).

Animals. Fifty *M. nigricans* bats were caught as they emerged from their tree roost near the village of La Mancha, Actopan Municipality, State of Veracruz, Mexico, using nylon mist-nests 38 mm mesh and 75/2 denier/ply. Each bat was immediately mounted with a miniature microphone + accelerometer device, which weighed 4.44 ± 0.2 g, equaling $10.8 \pm 0.7\%$ of their body mass. Devices were mounted using surgical cement (Permatype), and the bats were released (see full procedures in ref. 22). Mounting such a weight has been shown in the past to have minimal to negligible influence on the bats' natural behavior (30).

The devices' microphones were calibrated using a calibrated GRASS 40DP microphone, and the maximum detection distance of a conspecific calls was estimated to be ~50 m for an emission level of 130 dB SPL re 10 cm, which is typical for aerial insectivorous bats in their body size range (30).

The bats were recorded continuously for 90 min, either starting immediately upon release (four females) or at 5:30 AM (one male + six females). In total, we retrieved data from 10 bats (Table 1). The acceleration and the audio recordings enabled the detection of the flight bouts and their segmentation for further analysis.

Audio Analysis. The recordings were analyzed semiautomatically using our in-house BATALEF (Matlab) software (50), and bats' and their neighboring conspecifics' calls were manually corrected following the automatic detection. All the chewing sounds were manually recognized and marked in the recordings for further analysis. The buzzes (attacks) were identified by detecting series of calls with short (shorter than 0.04 s) interpulse intervals. A series was considered a buzz when it contained more than five calls (with such intervals) in it. Recognizing chewing sounds (after the buzzes) was performed manually and enabled us to assess how many of the attacks were successful and culminated in catching the prey.

Further analysis was performed using custom-written scripts in MATLAB. Conspecific density was estimated as the number of conspecific calls within 5-s bins (51). The number of attacks (and successful attacks) was also assessed in 5-s bins, but the results are presented per 1 min for easier reading. The mean number of attacks (and successful attacks) was estimated for each bat at each conspecific density and then averaged per bat and for all bats.

Statistics. In order to examine the correlation between the number of conspecific calls and the number of conspecifics, we analyzed the spectra of all conspecific calls for some of the bats (six bats and a total duration of 16 min). To this end, we clustered all conspecific signals detected in 1-s time bins in a three-dimensional space of features comprising the calls' terminal frequency, peak frequency, and duration (SI Appendix, Fig. S2). Clustering was performed using the clusterdata function in MATLAB for all the time bins containing more than two conspecific calls. Clusters were then screened and evaluated between 0.2 and 2 cutoff values and the optimal number of clusters was selected per each second accordingly. The number of clusters in each second was then summed to represent 5-s windows as in the rest of the analyses. Assuming that each cluster represents a conspecific, we next examined the correlation between the number of clusters and the number of conspecific calls and found that the two strongly correlated (SI Appendix, Fig. S2A).

Average change in attacks/successful attacks per conspecific call was calculated by dividing the difference between attacks/successful attacks in maximum and minimum conspecific densities by the range of conspecific density values.

We ran a GLMM model in Matlab to analyze the effect of conspecific density on the rate of attacks and on successful attacks. Because each bat attacked many times throughout the night, often minutes apart, we used multiple 5-s bins from the same individual in the analysis. To this end, we first segmented the flight into bins according to conspecific density (all adjacent 5-s bins with the same density were combined into longer bins). This analysis thus refers to each segment with a certain conspecific density as an independent time period, with the bat's ID set as a random effect. The attack and successful attack numbers were then normalized per one min. We used the normalized attacks per minute rate as the explained variable, a conspecific density per 5-s window and for some analyses a conspecific maximal call intensity (Table 2) as a fixed variable, and a bat as a random variable. Maximal call intensity was used as a proxy not only for the number but also for the proximity of the surrounding conspecifics.

We also used a GLMM to compare the foraging performance with (1 to 25 conspecifics per 5 s) and without conspecifics (0). In this case, we used every

5-s window as an independent trial. We used conspecific density in each time window as a fixed variable and a bat as a random variable. GLMM with the same variables but logit link was used to compare the proportion of attacks/successful attacks out of all attacks during a flight. For this, the number of attacks/successful attacks in each window out of the total number of the attacks/successful attacks was calculated for each bat.

Data, Materials, and Software Availability. Frequency table data have been deposited in this article—dataset, Mendeley Data, V1 <https://data.mendeley.com/datasets/h7krh54zxc/1> (10.17632/h7krh54zxc.1) (51).

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