

Report

Bats Aggregate to Improve Prey Search but Might Be Impaired when Their Density Becomes Too High

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Summary

Social foraging is a very common yet extremely complex behavior [1]. Numerous studies attempted to model it [2–7] with little supporting evidence. Studying it in the wild is difficult because it requires monitoring the animal's movement, its foraging success, and its interactions with conspecifics. We present a novel system that enables full night ultrasonic recording of freely foraging bats, in addition to GPS tracking. As they rely on echolocation, audio recordings of bats allow tapping into their sensory acquisition of the world [8]. Rapid changes in echolocation allowed us to reveal the bats' dynamic reactions in response to prey or conspecifics—two key behaviors that are extremely difficult to assess in most animals. We found that bats actively aggregate and forage as a group. However, we also found that when the group became too dense, bats were forced to devote sensory attention to conspecifics that frequently entered their biosonar “field of view,” impairing the bats' prey detection performance. Why then did bats fly in such high densities? By emitting echolocation calls, bats constantly provide public information about their detection of prey. Bats could therefore benefit from intentionally flying at a distance that enables eavesdropping on conspecifics. Group foraging, therefore, probably allowed bats to effectively operate as an array of sensors, increasing their searching efficiency [4, 6]. We suggest that two opposing forces are at play in determining the efficient foraging density: on the one hand, higher densities improve prey detection, but on the other hand, they increase conspecific interference.

Results and Discussion

Various models have attempted to explain animal group foraging [9, 10]. Some emphasized the disadvantages of increasing conspecific density (e.g., increased competition [2, 9, 11]), while others pointed out possible advantages (e.g., decreased predation risk [12, 13] or collective sensing [5, 14]). To study group foraging in the field, researchers must not only follow individuals' movement but also monitor their foraging and their interactions with conspecifics. Even with modern GPS technology, it is almost impossible to

acquire this data for most animals because tracking the animal's movement does not provide direct information about its foraging or its interactions with conspecifics.

The constant reliance of bats on sound emission for sensory perception enabled us to monitor all of the above processes by recording their echolocation signals. Over 60 years of laboratory and field studies allowed us to reliably infer behavior from bat echolocation [8]. Moreover, because bats rapidly adjust their signals in a task-dependent manner, one can detect their immediate response to various events, such as the presence of a conspecific. We therefore developed a miniature GPS device that allows simultaneous ultrasonic recording.

We mounted these devices on *Rhinopoma microphyllum* bats, social insectivorous bats that typically roost in (segregated female or male) colonies of hundreds to thousands of individuals and have been observed foraging in groups [15, 16]. When approaching prey, *R. microphyllum* bats emit an unmistakable attack sequence of echolocation calls [8, 17] (Figure 1A, lower box). We used these sequences to quantify bats' attacks on prey. Moreover, because all bats constantly emit echolocation calls, the system allowed us to determine any time a conspecific came near our tagged bats (Figure 1A, upper box). We recorded more than 1,100 interactions between tagged bats and conspecifics. We analyzed the bats' echolocation response to examine several fundamental questions. Were less or more attacks performed in the presence of conspecifics? Did the bats ever compete with a conspecific over a prey item? Was there vocal communication between the bats? Our results suggest that bats intentionally aggregate to improve prey finding but that they should maintain an intermediate conspecific density to ensure efficient prey detection.

We monitored the movement of 12 bats and the echolocation behavior of nine of these bats (seven females and two males). Overall, individuals exhibited large interindividual variation in their movement and their number of attacks (Table 1). We could not determine whether attacks were successful; however, this was irrelevant for this study, as we focused on the effects of group foraging on finding prey. All bats flew nonstop, with one individual flying continuously for over 5 hr and another flying more than 90 km. All bats spent a substantial proportion of their time in high conspecific density. We estimated that bats spent at least $41\% \pm 14\%$ of their foraging at <150 m from a conspecific and $8\% \pm 2\%$ at <12 m from a conspecific (Figure 1B, blue line; Table 1). Due to the limited recording range of our microphone, this is only a lower bound of the real density, which was probably considerably higher (Supplemental Experimental Procedures available online). Many theories predict that a high density should be detrimental for foraging [18]. At such proximity, competition over prey increases, and it has been suggested that bats might suffer from sensory interference, often termed jamming [19–21]. Because conspecifics emit echolocation calls with similar frequencies, the loud calls emitted by a nearby conspecific could mask the faint echoes returning from an insect, impairing the bat's detection abilities.

We tested whether the local high density at the foraging sites was detrimental for prey detection and found that the probability to attack prey was significantly lower in higher conspecific

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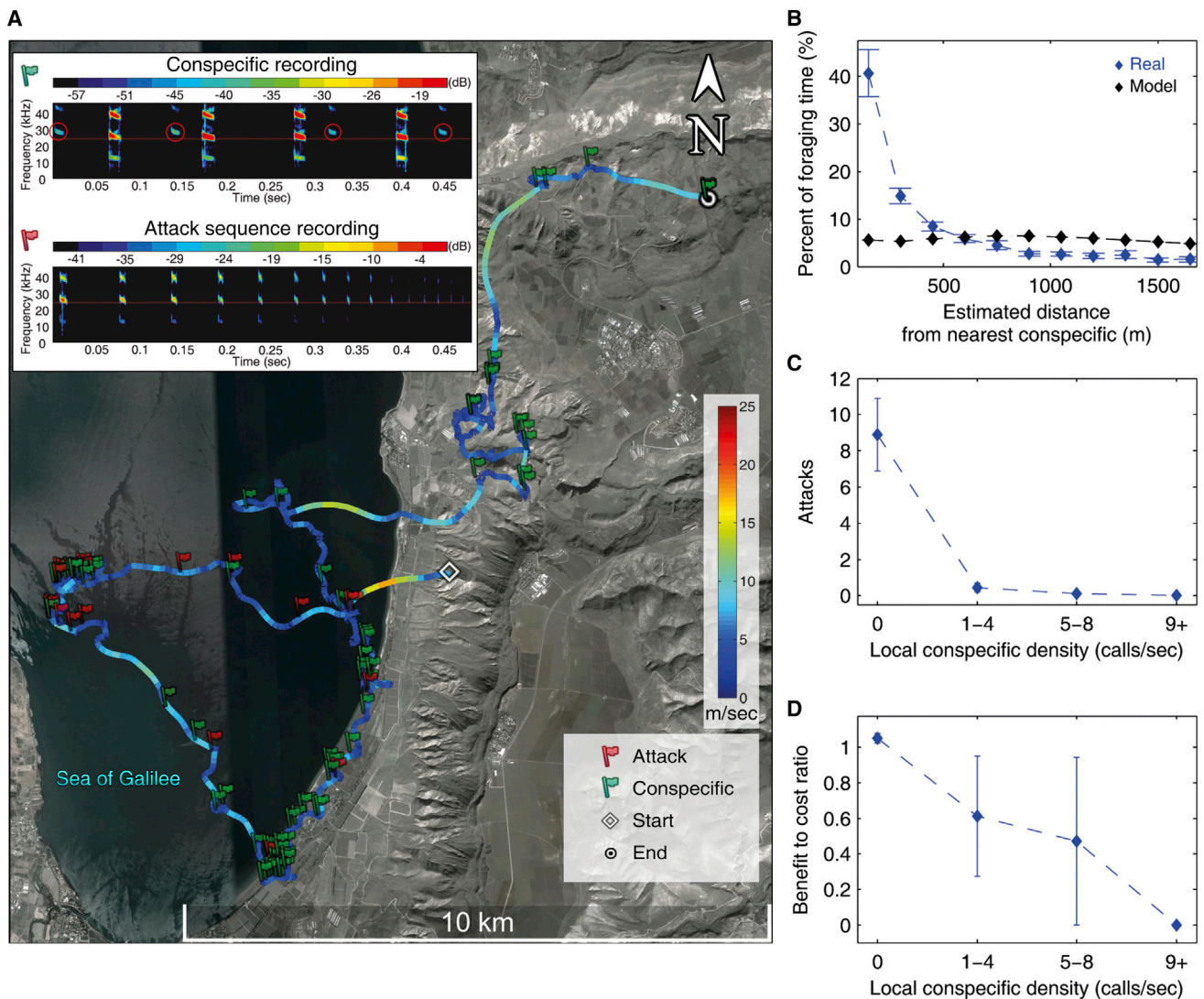


Figure 1. *R. microphyllum* Bats Spend a Substantial Part of Their Night Foraging Near Conspecifics

(A) Full night trajectory for one bat (bat 1), including its attempts to attack prey and encounters with conspecifics (red and green flags, respectively). Bat's speed is depicted by color coding the trajectory. Top spectrogram shows conspecific calls (red circles) between the tagged bat's echolocation calls. Bottom spectrogram presents an attack of the tagged bat.

(B) Blue indicates the estimated percent of time each bat spent at different distances from the nearest conspecific. Black indicates the estimated results for a model of bats moving independently of each other (Supplemental Experimental Procedures).

(C) Number of attacks as a function of conspecific density (within 12 m from the tagged bat). In panels (B)–(D), the mean and SEs for all bats are presented (SEs in C are very small). For the model (B), the mean + SE of 100 simulations are presented.

(D) Benefit-to-cost ratio as a function of conspecific density. The benefit-to-cost ratio was defined as the following ratio: percent of attacks to percent of time spent at each conspecific density. A value of more than 1 suggests efficient foraging at this conspecific density, whereas values of less than 1 suggest inefficient foraging.

The large SEs in the 1–4 and 5–8 density bins were a result of two bats performing two attacks (each).

densities, suggesting some sort of interference (Figures 1C and 1D; Kruskal-Wallis, $p = 0.01$, and post hoc Tukey test, $n = 9$). Was this conspecific interference a result of direct competition? Due to the short insect detection range of bat echolocation, when competing over the same item, bats had to be extremely close to each other (<10 m [22]) so that a simultaneous attack on prey (by a tagged bat and a conspecific) could be recorded by our microphone. In more than 1,100 conspecific encounters, we never recorded an attack performed by a conspecific. This suggests that both the tagged bat and the nearby conspecific suffered from interference. The reduction in attack rate was probably not a result of prey

depletion in the foraging site. The interference we describe was local in space and in time (temporary); bats seized attacking (near conspecifics) and then resumed attacking prey as little as 5 s later. Forty-seven percent of the attacks were performed within 60 s after encountering a conspecific. Bats repeated this behavior of seizing and resuming attacks again and again within the same foraging site (Figure 2A). We therefore argue that although prey might have been depleted, causing bats to change foraging sites, we describe an additional sort of local interference.

What then was the reason for the reduction in attacks near conspecifics? Bats' echolocation response to conspecifics

Table 1. The Foraging Activity of Individual Bats during a Full Night

Bat Number	Flight Time (min)	Estimated Flight Distance (km)	Foraging (% of Time)	Foraging—Number of Attacks (Estimated)	Estimated Time Spent within 150 m from a Conspecific (% of Time)	Time Spent within 12 m from a Conspecific (% of Time)
1	262	60	81	25 (125)	40	4
2	146	37	83	13 (65)	32	6
3	283	92	82	7 (35)	26	7
4	109	28	86	5 (25)	37	9
5	319	68	97	7 (35)	59	12
6	86	22	86	7 (35)	60	10
7	139	54	73	3 (15)	37	8
8	65	32	59	6 (30)	20	8
9	172	46	82	13 (65)	57	7

See [Supplemental Experimental Procedures](#) for a description of how the number of attacks and the time within 12 or 150 m from a conspecific were estimated. Flight distance is an underestimation due to our limited GPS sampling rate.

strongly implied that they were not jammed but rather responded as if the conspecifics were nearby objects entering their biosonar “field of view.” Bats decreased call duration and decreased intercall interval, as is typical for bats that are approaching objects [17, 23]. Although bats are known to swarm in very high densities, any animal is likely to attend a nearby moving object that enters its sensory field of view [24]. The average conspecific distance in over 1,100 documented encounters was 6 ± 2 m. Moreover, in approximately 19% of these encounters, more than one conspecific was present ([Supplemental Experimental Procedures](#)). Such dense situations would probably require sensory attention, making the detection of tiny insects difficult for short periods. In fact, even the changes observed in the echolocation signals near a conspecific (i.e., shortening the calls [23]) should have reduced the prey detection range. We therefore hypothesize that the decrease in attack rate at high local conspecific density reflects a sensory trade-off, where a bat shifts its sensory attention to nearby moving conspecifics at the expense of detecting prey. This trade-off is probably relevant to other animals that forage in groups, which must momentarily devote attention to a conspecific entering their sensory field of view.

We next examined why bats flew in such high densities, possibly impairing their detection of prey. As fast-flying bats that forage in open spaces, *R. microphyllum* have no real predators when foraging; therefore, reducing predation risk is probably not the explanation [25]. Was it merely a result of the prey distribution [26] that brought bats together? We used modeling to test whether independently searching the foraging area (i.e., with no intention of aggregating) could explain the density we observed. We ran simulations mimicking the estimated global bat density in the entire foraging area. The simulated bats moved like the real bats in terms of speed and turning angles but with no attraction or repulsion ([Supplemental Experimental Procedures](#)). All models tested predicted much lower local bat densities (at least eight times lower) than we observed, strongly implying that the real bats actively aggregated (Kolmogorov-Smirnov test, $p = 0$; [Figures 2B and 2C](#)). Moreover, the models predicted a rather uniform distribution (very different from that observed) and predicted that bats should hardly ever ($0.7\% \pm 0.01\%$) enter the 12 m range of another bat, which in reality occurred 8% of the time.

Our models assumed that bats could not predict the locations of prey patches within the foraging area. Bats’ behavior strongly implied this. Our bats almost completely covered the convex hull of their activity within only 1–2 nights of

searching (75%; [Figure 2D](#)). This intensive coverage of the entire foraging area, along with the fact that bats did not return to the same sites night after night, revealed an exhaustive search. The average distance between the centers of activity of an individual bat on consecutive nights was very large: 8.7 ± 4.5 km ([Supplemental Experimental Procedures](#)). The bats’ movement patterns within the night ([Figures 1A and S1](#)) also implied constant searching without ballistic flights, which would suggest movements toward known patches.

Finally, field playback experiments in which we played search echolocation calls (of bats that had not yet detected prey) confirmed that bats were significantly attracted to searching conspecifics (binomial test, $p = 0.01$; [Figure S2](#)). This further establishes that bats were intentionally aggregating during search of prey. Bats were also significantly attracted to playbacks of attack sequences emitted by conspecifics [14, 27–30] (binomial test, $p = 0.01$; [Figure S2](#)). However, the possibility that bats independently searched the area and aggregated at patches that were found by conspecifics is unlikely when taking into account the limited range (see below) from which a conspecific can be detected within such a large foraging area.

If the aggregation did not result from the distribution of prey, why then did bats forage in such high densities? Bats’ flight trajectories portrayed an exhaustive search covering very long distances, often with little success ([Table 1](#); [Figures 1A and S1](#)). Interestingly, there was no correlation between foraging time or distance and prey detection (Spearman correlation, $p = 0.18$ or $p = 0.43$, for time or distance, respectively; $n = 9$). For example, bat 5 flew more than twice as long as bat 2 but found about the same amount of prey. Because echolocation provides a very limited insect detection range (<10 m [22]), searching a 3D volume individually is extremely inefficient. For instance, a full search of a 2D 1×1 km area (much smaller than the areas covered by our bats) would take approximately 6 hr when flying at 5 m/s (as bats did). This is more than the longest activity period of all monitored bats. This theoretic duration would further increase dramatically in the case of a 3D search ([Figure S1](#)).

In contrast to their limited prey detection range, bats can eavesdrop on a conspecific’s attack from much longer distances (up to 160 m; [Supplemental Experimental Procedures](#)). We hypothesized that due to this large difference (<10 m versus >100 m), bats improve their searching efficiency by maintaining a distance that allows eavesdropping on conspecifics, enabling the group to effectively operate as an array with dozens to hundreds of sensors [31, 32]. Indeed,

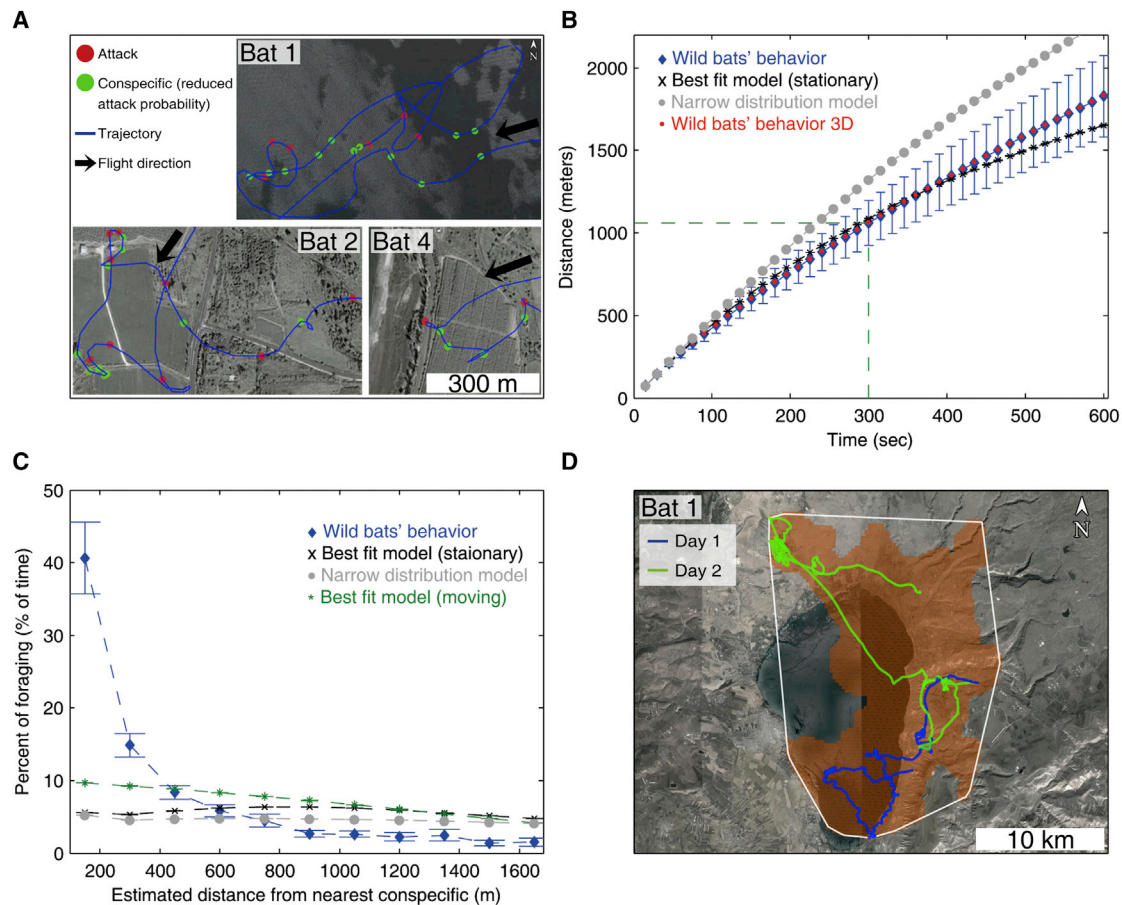


Figure 2. Bats Actively Aggregate in the Foraging Sites, Comparing the Observed Local Bat Density with Independent Bat Models

(A) Three examples of local foraging sites showing how bats interacted with conspecifics and often attacked prey briefly thereafter. This suggests that the interference observed near conspecifics was local and temporary and not a result of food depletion. Scale bar is the same for all three examples.

(B) The model's parameter (the width of the turning-angle distribution) was adjusted to best fit the bats' movement over time. Blue diamonds indicate absolute distance traveled over time by the real bats (2D beeline distance, mean + SE for all bats). Black X's indicate the distance over time in 2D for the best fitted model. Gray bullets indicate the narrow distribution model (strongly correlated movement model; [Supplemental Experimental Procedures](#)). Red dots show the movement of the real bats over time in 3D. The bats' movement was mostly in 2D, and thus, a 2D model (as we used) could capture the essence of the system. For all models, the mean + SE of 100 simulations are presented.

(C) The density predicted by several tested models (all of independent bats) is shown next to the real observed density (blue diamonds, mean + SE for all bats). The models include the best fitting model of a stationary conspecific (black line in B), the best fitting model of a moving conspecific (green stars), and a narrow distribution model (gray bullets). All models predicted a local bat density that is dramatically lower from the actual observations (blue). The stationary and moving conspecific simulations gave very similar results. For all models, the mean + SE of 100 simulations are presented.

(D) Foraging area of our bats. White line delineates the convex hull of the activity of 12 bats, while brown shaded areas show regions within the activity area that were searched by the bats. The searched area reached 75% of the entire area. Green and blue curves show the flight trajectory of the same bat over two consecutive nights, demonstrating how bats often did not search the same sites nightly and how they performed wide searching on each night.

estimations showed that bats flew within eavesdropping range at least 41% of the time (Table 1). Such group searching should be advantageous when prey is not uniformly distributed [6, 33]. This was most likely the case because during this season, bats mostly forage on *Camponotus* queen ants, which occur in patches [34]. We therefore suggest the existence of a social foraging trade-off: bats aggregate to improve foraging but when the local conspecific density becomes too high, they must allocate sensory resources to conspecifics at the expense of detecting prey (Figure 3A). This implies an intermediate local bat density, which enables efficient prey detection.

We already established above that high conspecific density can impair prey detection. The following results suggest that increasing the local conspecific density up to some degree will improve foraging. (1) Bats were more efficient near conspecifics (Figures S3A1 and S3A2). This does not contradict

the fact that when conspecifics were too close (<12 m), significantly fewer attacks were performed. (2) There was a (marginally) significant negative correlation between time spent within 12 m from conspecifics and the total number of attacks, suggesting that frequent flying in densities that were too high reduced the overall performance (Spearman correlation, $R = -0.61$, $p = 0.08$). Note that this is not the same as the reduced probability to attack near a conspecific, which we show above. (3) The most common distance bats traveled between two conspecific encounters was approximately 50 m (Figure S3B, blue line). This maximum in the distribution was unexpected if the bats were moving independently (Figure S3B, black line), suggesting that bats might have avoided densities that were too high.

To examine whether the two contradicting processes described above could theoretically generate a foraging

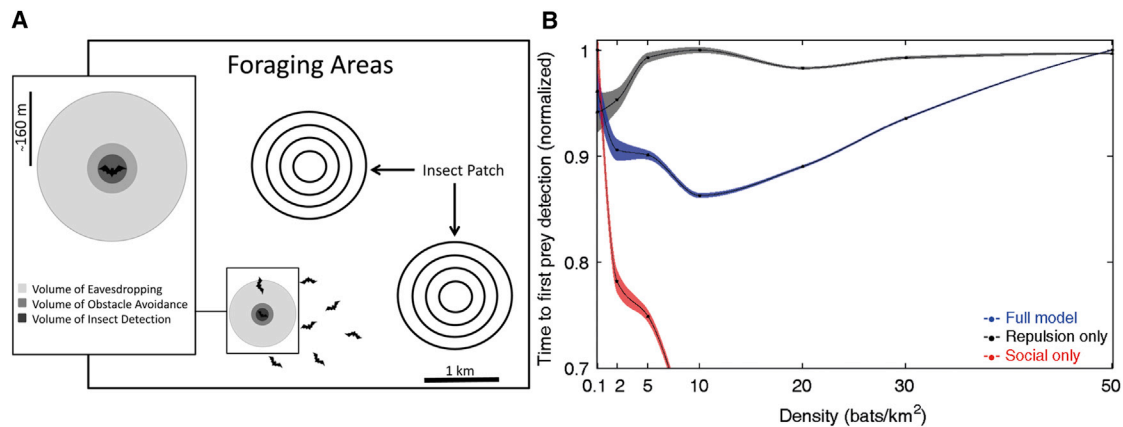


Figure 3. The Social Foraging Trade-off Model

(A) Schematic describing the model. Bats must scan the foraging areas in search of insect patches. Bats (not drawn to scale) search these areas, maintaining a distance that allows eavesdropping on conspecific foraging (less than 160 m), and thus, the group acts as an array of sensors. Bats can detect insects from up to 10 m, and they are repelled by other bats when coming as close as 20 m to each other. See top left sketch for the three volumes that play a role in the social foraging trade-off. We modeled spherical zones for simplicity, but in reality, zones are supposed to be cone shaped due to echolocation beams. We hypothesize that when conspecific density increases and bats enter each other's volume of avoidance too often, they will consider changing the foraging site.

(B) A simple model confirmed the feasibility of the social foraging trade-off. The blue line presents the foraging efficiency (normalized time to finding the first prey; see [Supplemental Experimental Procedures](#)) as a function of bat density for the full model, which includes both repulsion and eavesdropping. Shaded areas show the models' SE (over 100 simulations for each model). An optimum is achieved at an intermediate bat density. The black line shows the same but for the repulsion-only model, in which bats are not eavesdropping and thus not gaining from the group foraging. Here, foraging efficiency decreases with local bat density. The red line shows the attraction-only model, in which bats eavesdrop but are not repelled. This model drops quickly, exhibiting the advantage of social foraging in this system.

trade-off, we simulated the most naive model we could think of. The simulated bats searched for prey independently and were able to detect prey from 10 m. They were repelled by nearby conspecifics within 20 m (the sonar detection range of a conspecific; [Supplemental Experimental Procedures](#)). Notably, in this model, bats did not intentionally aggregate, but if by chance there was a conspecific within 160 m, they were attracted to it only in the case that it attacked prey. We simulated a wide range of global bat densities (10–5,000 bats per 100 km²), including the actual estimated global bat density. It is important to note that we did not tune any of the model parameters. The prey detection range and the conspecific attraction and repulsion ranges were all determined according to the physics of sound. The behavior was not weighted, i.e., bats were either repelled or attracted. We tested several models of nonuniform Gaussian prey distributions, whose centers were randomly positioned in the foraging area and whose widths were changed. Results proved that this very simple social strategy, which did not include any kind of collective movement [35, 36], already improved prey detection efficiency. Moreover, this model demonstrated how increasing the bats' local density should improve foraging efficiency, but only up to a certain point in which repulsion interactions become too frequent, impairing foraging efficiency (Figure 3B). The results of this oversimplified model should not be taken as an exact prediction for comparison with reality. It only aimed to show the feasibility of the social foraging trade-off. We expect that more complex models, which include attraction between moving bats [7], will further emphasize the existence of an intermediate efficient density.

An intermediate density, which is most efficient for foraging, might be relevant to other systems as well. For instance, in birds that search for seeds on the ground, the visual detection range of a seed is much shorter than that of seeing a pecking

conspecific. Birds can thus gain from searching together. The upper bound for the group density in this case, however, is probably not a sensory attention trade-off (as we suggest in bats) but the direct competition over food, which increases with density.

Finally, we never recorded any social calls outside the roost, though many were recorded inside it. Because echolocating bats constantly emit sound to perceive the environment, providing public information about their detection of prey [29, 37], social foraging in bats could have evolved with no need for costly social communication, which is often considered to be a bottleneck for the evolution of social foraging in other animals [10].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, three figures, one table, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.11.010>.

Author Contributions

N.C. created the research plan, gathered data, carried out data analysis, and wrote the manuscript. K.E.B. was responsible for the modeling. E.L., E.H., I.B., A.B., and E.A. gathered data. Y.Y. created the research plan, gathered data, and wrote the manuscript.

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