Insectivorous bats form mobile sensory networks to optimize prey localization: The case of the common noctule bat

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Animals that depend on ephemeral, patchily distributed prey often use public information to locate resource patches. The use of public information can lead to the aggregation of foragers at prey patches, a mechanism known as local enhancement. However, when ephemeral resources are distributed over large areas, foragers may also need to increase search efficiency, and thus apply social strategies when sampling the landscape. While sensory networks of visually oriented animals have already been confirmed, we lack an understanding of how acoustic eavesdropping adds to the formation of sensory networks. Here we radio-tracked a total of 81 aerial-hawking bats at very high spatio-temporal resolution during five sessions over 3 y, recording up to 19 individuals simultaneously. Analyses of interactive flight behavior provide conclusive evidence that bats form temporary mobile sensory networks by adjusting their movements to neighboring conspecifics while probing the airspace for prey. Complementary agent-based simulations confirmed that the observed movement patterns can lead to the formation of mobile sensory networks, and that bats located prey faster when networking than when relying only on local enhancement or searching solitarily. However, the benefit of networking diminished with decreasing group size. The combination of empirical analyses and simulations elucidates how animal groups use acoustic information to efficiently locate unpredictable and ephemeral food patches. Our results highlight that declining local populations of social foragers may thus suffer from Allee effects that increase the risk of collapses under global change scenarios, like insect decline and habitat degradation.

automated radio tracking | ephemerality | group foraging | simulation | sociality

Animals can use social information inadvertently provided by con- and heterospecifics to locate food resources (1). The use of social information, delivered via the location and performance of other foragers, becomes particularly beneficial when the occurrence of food varies unpredictably in space and time (2–5). The most prominent mechanism for social information transfer among foragers is termed "local enhancement" (6): foraging individuals spot and approach nearby feeding con- or heterospecifics, and consequently aggregate at food patches. However, local enhancement may be an insufficient mechanism for animals that must search for food across large areas, can detect feeding con- or heterospecifics only at relatively short distances, or feed on rapidly depleting or spatiotemporally ephemeral resources. For predatory fish, and recently also for vultures and insectivorous bats, it has been suggested that individuals can overcome the limitations of individual prey detection by forming foraging "arrays" or "chains" (7–10). We term these assemblages "mobile sensory networks," based on a similar term used in robotics and control systems (11), to emphasize the key elements of this social foraging mechanism.

In contrast to local enhancement, members of a mobile sensory network do not only use information from others that already found prey, but constantly exchange information while searching for food. Food-searching individuals move while actively sensing both their environment and the behavior of their neighbors, allowing each forager to gather sensory information across a much larger area than it alone could scan. Mobile sensory networks are more efficient in gathering information than groups of solitary foragers, but require frequent coordination of movements among individuals (Fig. 1). Cohesion of moving groups can be maintained by simple movement rules that lead to the alignment of neighboring individuals (12). Theoretical studies have explored the idea of mobile sensory networks maximizing the efficiency of foragers that depend on ephemeral and patchily distributed food resources (7, 9, 13, 14). Empirical studies suggest the existence of mobile sensory network formation in bats, yet this is based only on observations that foraging individuals were attracted to the broadcast of specific echolocation calls from successfully foraging conspecifics, so-called feeding buzzes (15),

Significance

For predators that depend on ephemeral prey patches, like aerial-hawking insectivores, searching for prey is akin to finding the proverbial needle in a haystack. Global change and resulting insect decline and habitat degradation make finding prey even more challenging. Simultaneous high-throughput radio-tracking of common noctule bats suggests that social strategies may be the key to mastering this challenge. When searching for insects, bats adjusted their movements to their neighbors consistent with the formation of mobile sensory networks. A simulation model confirmed that the observed behavior leads to increased search efficiency when prey is patchily distributed. However, the model also revealed that mobile sensory networks become unstable when the group becomes too small, indicating synergistic negative effects of local population declines.

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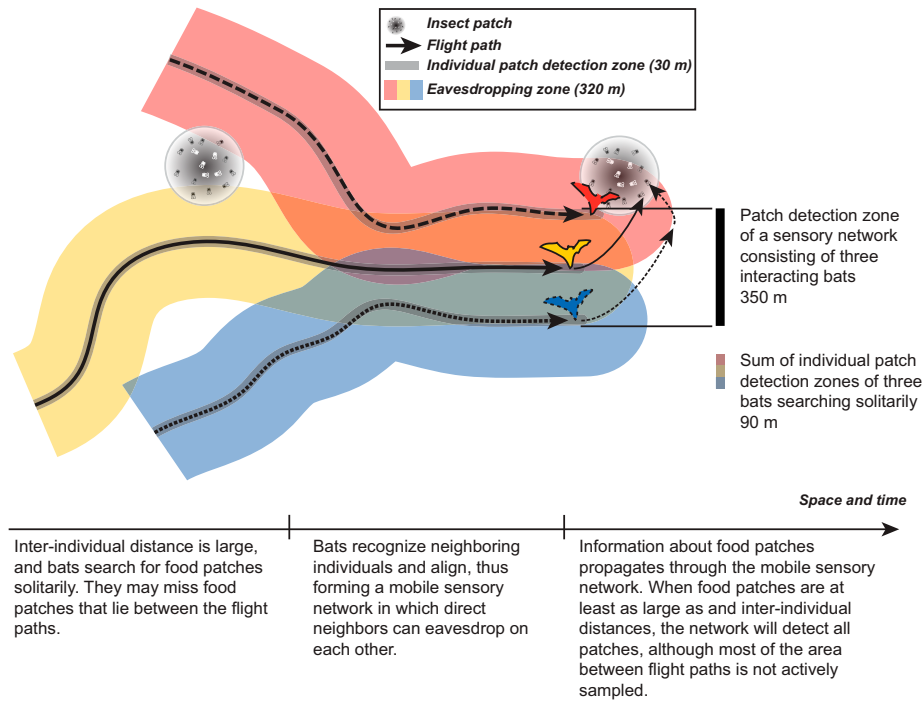
Fig. 1. Concept of a mobile sensory network, illustrated for insect-feeding bats. Three insectivorous bats align their flight paths (simplified as two-dimensional trajectories) while flying from left to right. Bats can detect insect patches using echolocation at distances of up to 15 m, but can eavesdrop on conspecifics as far away as 160 m. When a bat finds a food patch and starts hunting for single prey items (red bat), it uses specific hunting calls, so-called feeding buzzes (25), which alert its direct neighbor (yellow bat) to the patch location. The yellow bat would then abruptly change its flight direction to approach the patch, leading its other neighbor (blue bat) to reorient as well, and so on, until all bats in the network get close enough to the food patch to eavesdrop on the feeding buzzes of conspecifics that indicate active insect pursuit and therefore the presence of food. Thus, the information can slowly propagate across the network through changes in flight and echolocation behavior of chains of neighboring individuals. Searching for food in a network is most effective when interindividual distance and patch diameter match, and therefore, all food patches that lie in the flight direction of the network will be found, even though individual bats actively scan only a small portion of the total area. In this example, every additional bat may increase the zone scanned by the network by 160 m, while only actively sampling a zone of 30 m. Thus, a mobile sensory network consisting of only six bats may create a moving scanning zone of more than 1 km in width.

or by the fact that foraging individuals encountered conspecifics more often than expected (5, 8, 16). Indeed, feeding buzzes indicate that bats are actively attacking prey, and therefore convey information on prey availability that can induce local enhancement in food searching bats (17). Yet, these previous studies cannot explain the formation of mobile sensory networks as they missed the dynamic nature of the interactions of bats during food search. Direct evidence of interactive movement responses of free-ranging animals that lead to the formation of mobile sensory networks during prey search is still lacking. Observing the formation of mobile sensory networks in natural systems requires simultaneous monitoring of many individuals at high resolution, a feat that has been challenging to achieve in empirical studies thus far. Recent technological advances in tracking systems, which provide high-throughput data collection, now make it possible to shed light on the fine-scale patterns emerging from interactive movements in the wild (18).

Here, we used a fully automated radio tracking system based on trilateration (ATLAS) (19), to simultaneously record the movements of dozens of common noctule bats (*Nyctalus noctula*) at higher spatiotemporal resolutions than so far achieved for aerial insectivores. Aerial-hawking insectivorous bats are particularly suited for studying social aspects of foraging ecology since they face the dilemma of finding ephemeral patches of insects while being severely constrained in the distance at which they can detect prey. Distances at which echolocating bats may detect large insects or insect patches are usually below 10 to 15 m, due to the rapid attenuation of ultrasound

in air (20, 21). In contrast, the distance at which bats can eavesdrop on echolocating conspecifics is more than 10-fold larger, reaching up to 160 m under optimal conditions (22–24). This notable difference between prey detection distance and conspecific detection distance may promote the evolution of group-foraging strategies. For bats, group foraging via eavesdropping on the foraging calls of hunting conspecifics leading to local enhancement is indeed well documented (15, 17), but the formation of mobile sensory networks during prey search still lacks solid evidence from dynamic movement interactions of bats (5, 8). Assuming that aerial-insectivorous bats depending on ephemeral prey apply a mobile sensory network search strategy as proposed by Egert-Berg et al. (5) and Cvikel et al. (8), we hypothesize that food-searching common noctule bats adjust their movements to food-searching neighbors, and that such behavior will lead to the formation of mobile sensory networks that increase the efficiency of prey search. Specifically, we predict that bats align at the maximum eavesdropping distance of approximately 160 m by flying in parallel (Fig. 1), and that they decrease or increase distance to conspecifics when farther apart from or closer to conspecifics, respectively. We further present an agent-based simulation model and predict that modeled bats form chains of interconnected individuals. We also predict that, under realistic conditions of colony size and prey distribution, bats that apply a mobile sensory network search strategy will find food patches faster than bats searching for food solitarily.

Here, we combined empirical tracking data and simulations to explain the formation of mobile sensory networks in bats

hunting insects in open airspace and to investigate the benefits and constraints of mobile sensory networking. We recorded the movements of 81 common noctule bats during 359 foraging flights at 1/8 Hz resolution in five recording sessions (three spring sessions and two summer sessions over 3 consecutive years) (*SI Appendix*, Table S1). We defined flights as movements of a bat in a particular night, with data recordings for at least 15 min and no pauses longer than 5 min between datapoints (*SI Appendix, Data Filtering Protocol*). We analyzed the fine-scale movements of individuals in relation to tagged conspecifics and identified mechanisms by which they form and maintain mobile sensory networks. We subsequently built a theoretical model that was based on the empirically identified movement patterns to confirm the emergence of mobile sensory network in bats. Using the simulation, we predicted how benefits and stability of mobile sensory networks depend on group size and prey distribution.

Results

Flight Behavior Close to Conspecifics. In each of the five recording sessions, we simultaneously fitted between 14 and 19 bats with radio-transmitters and received movement data from 9 to 15 nights. We recorded up to 15 simultaneous flights per night (4 ± 3; median absolute deviation [MAD]), yet this number fluctuated due to varying bat activity, and decreased toward the end of the recording session, as animals left the tracking area or radio-transmitters ran out of battery (*SI Appendix*, Table S2). We estimate that ~160 common noctule bats inhabited the area [80 from the investigated colony that used a set of about 20 bat boxes located in a small forest (*SI Appendix*, Fig. S1), and another 80 from smaller colonies scattered in the tracking area]. We therefore designed our analysis to mitigate the effect of untracked bats on our models (see *Discussion* and *Methods and Materials* for details).

To study interactive movements, we only analyzed flights during which the focal bat flew closer than 240 m from other tagged conspecifics for at least 3 min of the entire flight (235 flights or 65% of recorded flights, stemming from 76 individuals: 13 males, 63 females, 94% of all tagged individuals) (*SI Appendix*, Table S1). The distance of 240 m is 1.5 times the maximum theoretical conspecific detection distance of 160 m for common noctule bats. This relatively short range is due to the fast dampening of ultrasounds (geometric and atmospheric attenuation), calculated for standard environmental conditions and assuming bat calls at a frequency of 20 kHz, a sound pressure of 120 dB at 1-m distance from the calling bat, and a hearing threshold of the listening bat of 0 dB (22–24, 26). During the analyzed flights, bats were near another tagged conspecific for 30 ± 22% (median ± MAD) of the entire flight, while individual continuous contacts had durations of 64 ± 72 s (median ± MAD).

To test whether bats reacted to conspecifics in terms of adjusting their distance, we applied an integrated step-selection analysis (iSSA) (27) with 10 random steps and logistic regression modeling to individual flights. The iSSA revealed that in 97 of the 235 analyzed flights (stemming from 54 different bats) tagged bats responded to other tagged conspecifics (iSSA estimates significant on an α-level of 0.1, relatively high significance threshold chosen to inform subsequent analysis on fine-scale reactions of potentially networking bats). Most flights with significant iSSA estimates could be grouped into two categories (Fig. 2, highlighted quadrants). First, in 53% of cases, bats flew toward conspecifics and decreased their directional
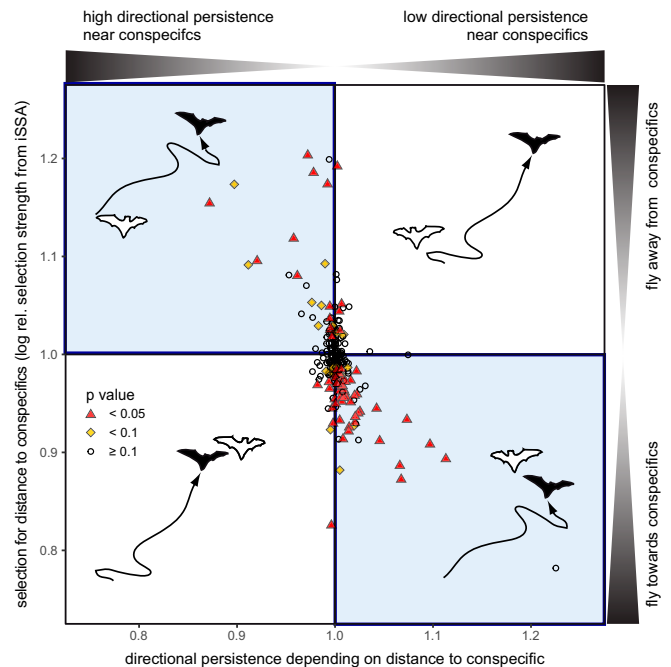
Fig. 2. Flight behavior of bats close to conspecifics. Relative selection strength of a focal bat (black bat) for distance to its nearest conspecific (white bat) and distance-dependent angle persistence of complete flights, as calculated from the iSSA. Deviation from random behavior concerning selection for the distance to conspecifics is indicated by symbol and color. During 53% of the flights yielding significant selection coefficients, bats flew closer to conspecifics than expected and decreased their directional persistence as they got closer (*Lower Right* quadrant). In an additional 23% of the flights yielding significant selection coefficients, bats flew away from conspecifics and decreased their directional persistence (*Upper Left* quadrant). For graphical reasons, coefficients for seven flights that fell outside the plotted range are not shown (four in *Upper Left* quadrant, two in *Upper Right* quadrant, one in *Lower Right* quadrant, six of them being significant on the 0.1 level).

persistence near them (Fig. 2, *Lower Right* quadrant), which indicates that bats aggregated for hunting (torturous movements during insect pursuit). Second, in 23% of cases, bats flew away from conspecifics but still remained within eavesdropping range, and directional persistence decreased with intraspecific distance (Fig. 2, *Upper Left* quadrant). Potential, nonexclusive reasons might be that bats kept a certain minimum distance to each other, either to avoid interference during hunting, or to space out while searching, as expected in a mobile sensory network.

Influence of Conspecifics on Fine-Scale Movements. Our iSSA model indicated that focal bats responded to tagged conspecifics in 41% of the analyzed flights. In these cases, bats spent 23 ± 17% (median ± MAD) of the time closer than 240 m from other tagged conspecifics. However, this analysis reveals general reactions toward conspecifics on the level of entire flights, whereas individual bats may still show contrasting behaviors throughout their flights. To identify conditions under which bats adjusted their flight trajectories to those of other tagged bats on finer temporal scale, we ran two linear mixed models for flights with a significant iSSA selection coefficient. For that, we only used locations during which focal bats were presumably searching for food (i.e., not actively hunting, high directional persistence, and comparably fast speeds of 5.6 ± 2.7 m/s [median ± MAD]), as classified by a two-state hidden Markov model. Following the previous results (Fig. 2) and knowledge of bat foraging patterns in landscapes with
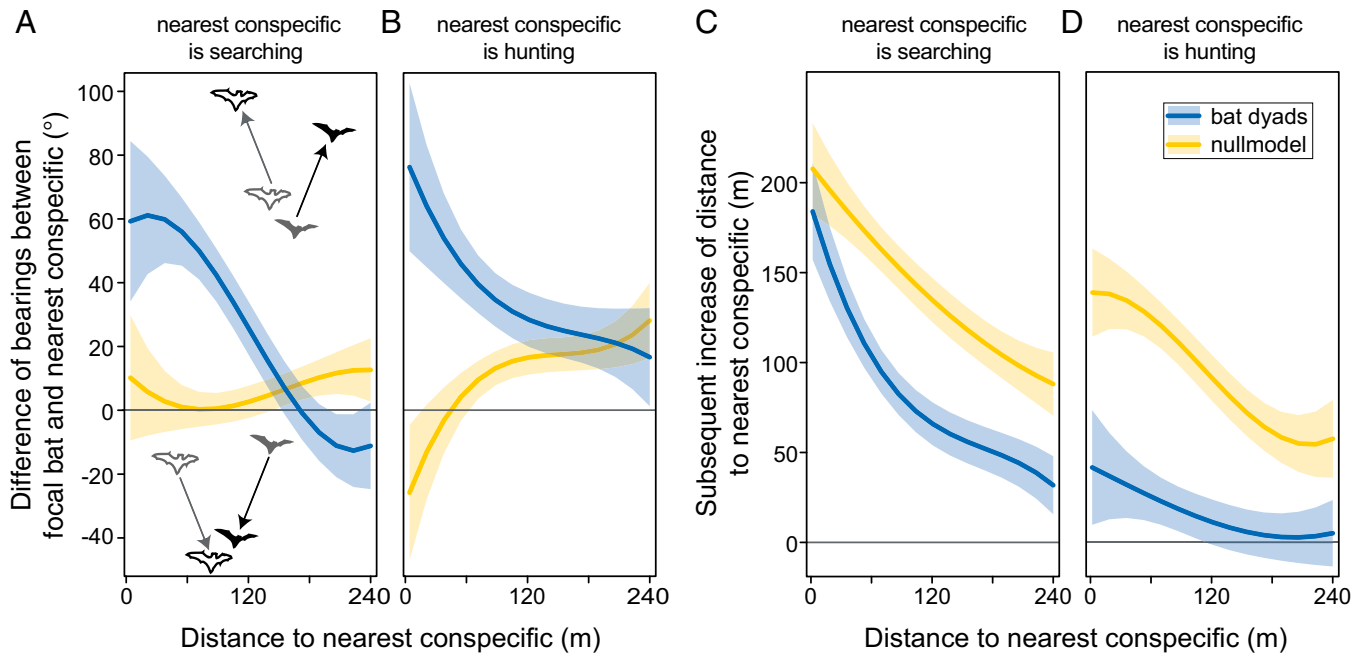
Fig. 3. Movement properties of interacting bats during search. Short-term response (32 s) of a focal bat searching for insects to its nearest (searching or hunting) tagged conspecific as a function of the initial interindividual distance. Blue lines depict the effect from the model on simultaneously flying bat dyads; yellow lines depict the effect of the null model based on pseudodyads where bats flew in the same area, but during different days. Bands represent the 95% confidence intervals. (A and B) Difference in bearings. Positive values indicate that bats moved in diverging directions, negative values indicate that bats moved in converging directions. (C and D) Change of interindividual distance.

patchy food distribution (16), we defined comparably straight and fast movements as food-searching behavior, and slow, tortuous movements (so-called area-restricted search) as hunting behavior. We compared the data from food-searching bat dyads to a null model using pseudodyads (28). Pseudodyads consisted of the respective focal bat and a tagged conspecific that used the same area but on a different day of the same experimental session. Our models for 96 flights stemming from 54 different focal bats revealed that bats adjusted their flight vectors, and their distance relative to conspecifics (Fig. 3), depending on the movement behavior of and the initial distance to the nearest conspecific (modeled as a third-order polynomial to allow for local maxima and leveling-off effects at large distances).

We observed that food-searching bats flew away from other searching conspecifics (diverging directions) when closer than about 150 m to each other, but tended to fly toward (converging directions) or align with conspecifics (no difference in bearing) at larger distances (Fig. 3A). When nearby conspecifics were hunting, focal bats also flew in diverging directions. However, there was no difference to the null model at interindividual distances larger than about 120 m (Fig. 3B). We also found that bats increased the distance to either searching or hunting conspecifics, but much less than expected from the null model (Fig. 3 C and D). These results further support the existence of mobile sensory networks, as searching bats tended to adjust flight direction according to their neighbors and to fly relatively close to each other (compared to pseudodyads).

As expected, focal bats increased distance to searching bats at small interindividual distances, and reduced their tendency to move away from conspecifics as interindividual distance increased (Fig. 3C). However, contrary to our expectations, a slight increase in distance to searching conspecifics remained even at comparably large interindividual distances, which were beyond the assumed eavesdropping range. A reason for this might be different flight speeds of bats. Nonetheless, at large interindividual distances, bat dyads stayed closer together than

assumed from independent movements in the null model. When conspecifics were hunting, bats exhibited only slight increases in interindividual distance and only for bats flying closer than 120 m from each other, while the null model predicted much stronger increases in distance across the entire range (Fig. 3D). We assume that bats investigated potential prey patches close to conspecifics, but maintained a minimum distance to avoid collision and sensory interference.

Overall, these results support expectations from mobile sensory networks, and suggest that simple movement metrics can be used to describe their formation and maintenance. Specifically, our data suggest that bats aligned their movements at distances of about 120 to 180 m while sampling the landscape for insects. The optimal distance to actively hunting bats was 120 m or more, probably to avoid collision and acoustic interference from other echolocating bats. The optimal distances during search and hunting, however, likely also depends on the investigated system, especially on its spatial resource distribution, the presence of competition or interference, and the sensory modalities of species involved in the mobile sensory network.

Simulation of Mobile Sensory Networks. We built an agent-based simulation model to evaluate whether the empirically demonstrated movement patterns (i.e., adjustment of flight direction to conspecifics) leads to the formation of mobile sensory networks (Fig. 4), and whether such movement behavior impacts individual foraging efficiency (Fig. 5). We simulated different scenarios (500 model runs each) with increasing numbers of bats (5, 10, 20, 40, 80, 160, whereas we deem 80 bats to be the most realistic scenario estimated from bat colony size), and increasing number of food patches (1, 2, 4, 8, 16, 32, 64, 128, 213, where the number of cells containing food was estimated from empirical data and kept constant at 213). From each model run, we randomly picked one bat and recorded its network size for all timesteps from the model run.
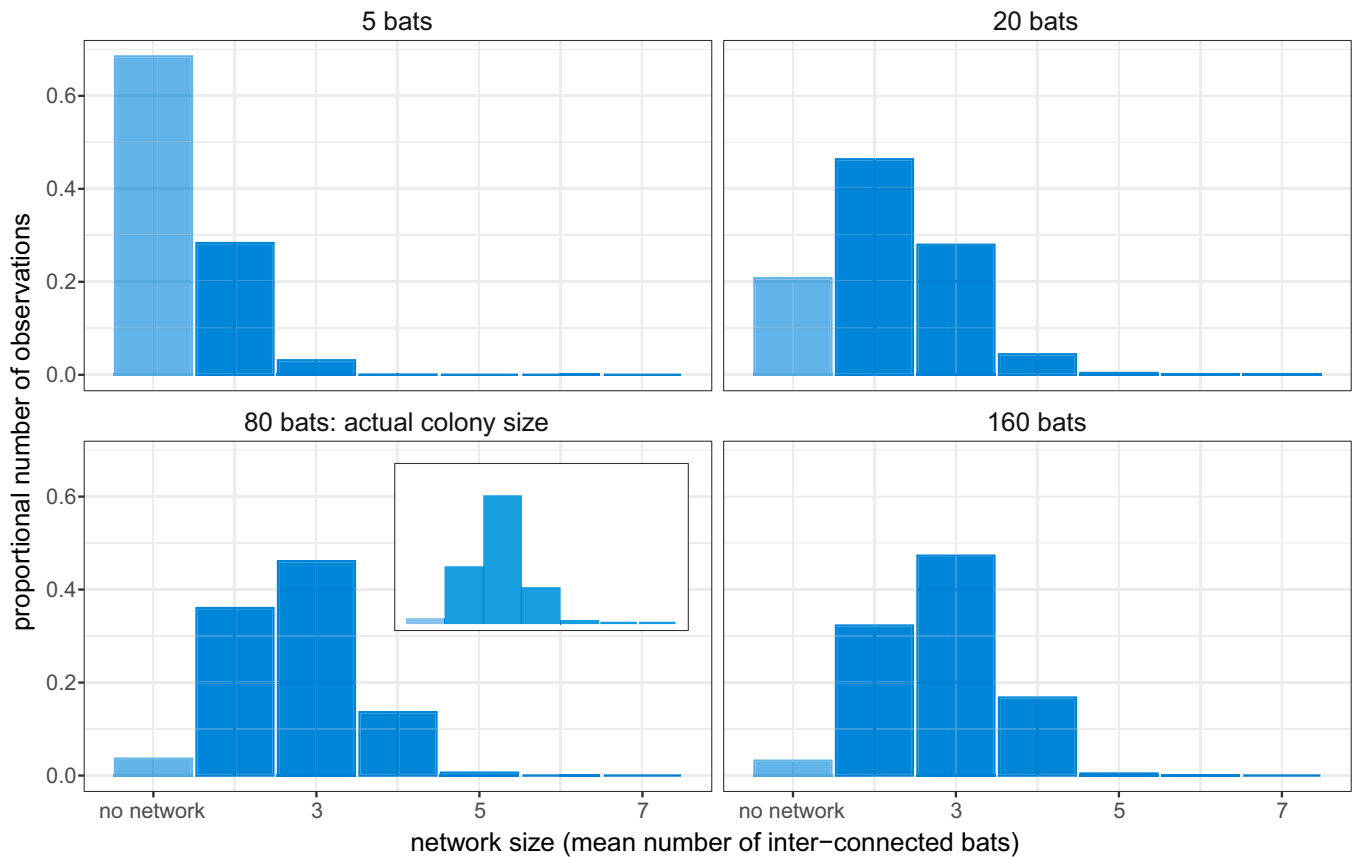
Fig. 4. Distributions of the mean network sizes, calculated for one randomly chosen focal bat per model run, shown for different numbers of modeled bats and aggregated over the nine different levels of resource distribution (between 1 and 213 patches). A number of three means, that the focal bat was connected with a conspecific that was itself connected with another conspecific (chain of three bats). The *Inset* in the *Lower Left* panel shows the network size distribution for a model scenario with four food patches and 80 bats. *Inset* is to scale with the large panels.

Network size was calculated as the number of interconnected bats (including the focal individual): that is, the number of bats linked in a chain of nearest neighbors. While bats only occasionally formed networks when few conspecifics were modeled, the number of networking bats as well as the mean network size increased with increasing number of conspecifics in the model (Fig. 4). For the most realistic scenario with 80 bats and 4 food patches, the mean (over 500 model runs) of the mean network sizes (of one focal bat per model run) was 2.9 ± 0.7 bats (mean $\pm$ SD), and the maximum network size was 7.4 ± 1.4 bats (mean $\pm$ SD). The largest number of interconnected bats was 11 in the realistic model scenario.

To quantify differences in foraging efficiency between bats using different foraging strategies we ran simulations with varying food distributions (number of food patches) and group sizes (number of simulated bats). We used a paired design to calculate the difference in time bats took to find unoccupied food cells in the exact same landscapes when interactions with conspecifics were enabled or disabled. Each of these paired runs was repeated 500 times per scenario. The investigated foraging strategies were: 1) solitary foraging (bats ignore conspecifics), 2) local enhancement (bats fly toward conspecifics that are hunting within a range of 240 m), 3) flight alignment (bats align with conspecifics that are searching for food but do not use local enhancement), and 4) mobile sensory networking (bats use both flight alignment and local enhancement).

The mean distance of a randomly chosen bat to its nearest neighbor decreased with increasing numbers of simulated bats, but the foraging strategy influenced the distance between bats irrespective of the modeled scenario. Specifically, the distance was largest when bats ignored conspecifics, decreased when local enhancement or flight alignment were enabled, and was lowest when empirical found movement interactions (i.e., mobile sensory networking) were enabled (*SI Appendix,* Fig. S2A). Under a realistic scenario with 4 food patches and 80 bats, neighboring bats were most often close to each other when mobile sensory networking was enabled (72% of the time within 240-m distance), and least often when bats were foraging solitarily (54% of the time within 240-m distance) (*SI Appendix,* Fig. S2B).

The simulations further revealed a benefit of mobile sensory networking under certain prey distributions and network configurations (Fig. 5). Bats were most efficient in finding food as a mobile sensory network when food was spatially aggregated (landscape with few patches), and hence difficult to find without prior information. This matches with suggestions from theoretical and empirical studies (2–5, 16). Under such scenarios, bats also profited from local enhancement only, and even more when they aligned their flights, probably because the latter leads to a more systematic search of the area. However, the simulations clearly show that mobile sensory networks (i.e., coordinated search plus local enhancement) increase hunting efficiency further than only local enhancement as previously known from studying eavesdropping behavior of bats (e.g., ref. 15). Under conditions typical for our study system (i.e., four food patches in an area of ~22 km² and 80 bats), networking bats located food within 9 ± 4 min (median $\pm$ MAD). This represented 60% of the time required by solitarily foraging bats, and 74% of the
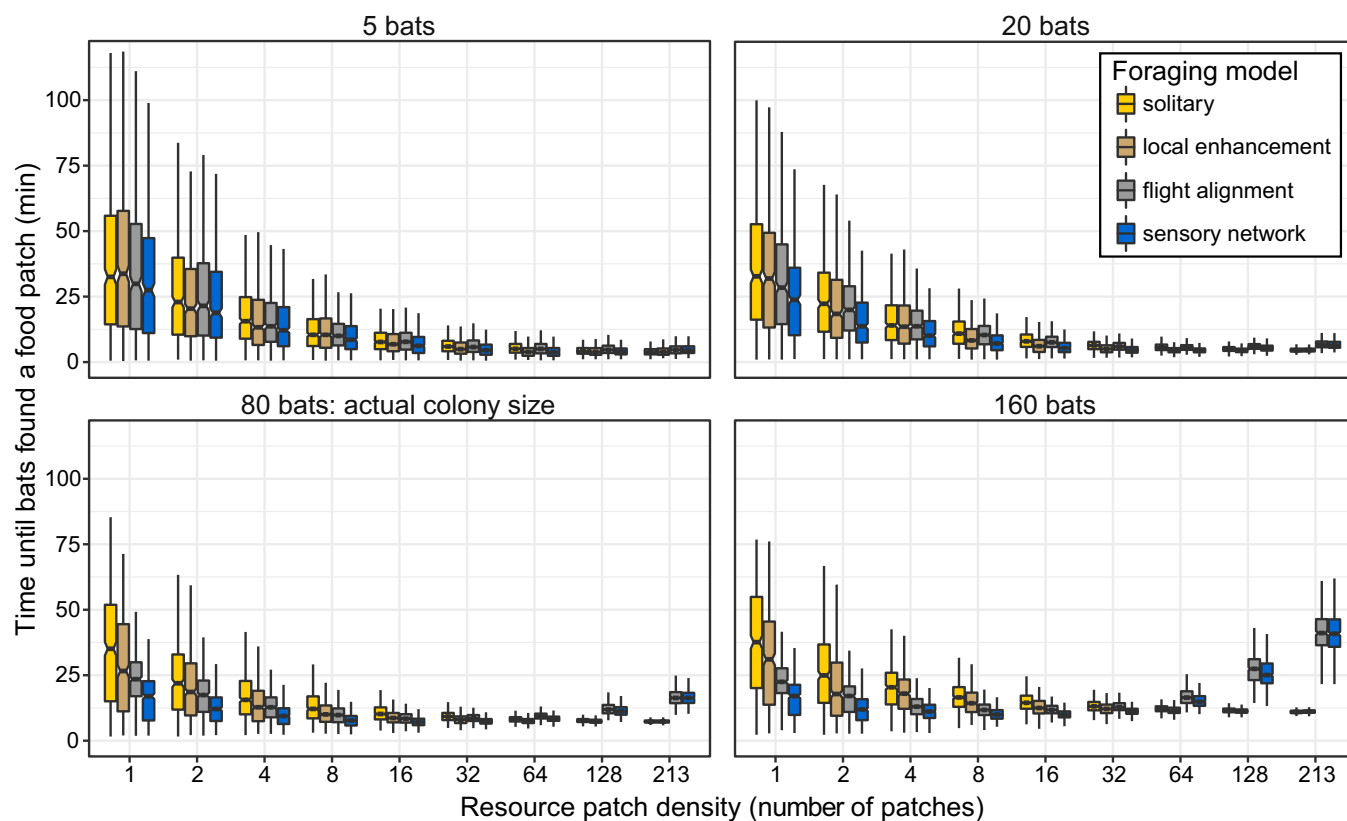
Fig. 5. Time until simulated bats found unoccupied food cells (median per model run), depending on whether bats used empirically derived movement strategies: that is, mobile sensory networking behavior, aligned their flights during prey search, used local enhancement or foraged solitarily. The modeled scenarios included different numbers of bats (whereas a number of 80 bats is the estimated colony size from the empirical study) and levels of spatial resource aggregation, as reflected by the number of food patches. The number of food cells in the model was fixed at 213 cells measuring 75 × 75 m, which represented the median area used for hunting per night by tracked bats in our study (based on kernel density estimates from localizations recorded during hunting). Tracked bats used ~5 ± 3 (mean ± SD) distinct patches for hunting per day, for which all scenarios showed an advantage of the mobile sensory network strategy over the other foraging strategies.

time required by bats either aligning during search or using local enhancement. However, foraging in a mobile sensory network became disadvantageous for large groups when food was homogenously distributed (many small patches), likely because bats aggregated at small food patches that did not contain enough food cells to support all bats in the network. The benefit of mobile sensory networking in aggregated landscapes grew with increasing number of bats, signifying that the advantages of social foraging can outweigh the disadvantages of intraspecific competition (Fig. 5). Moreover, this result indicates that there might be a critical minimum local population density of social foragers required to maintain foraging benefits when food is patchily distributed and ephemeral.

Discussion

High-resolution simultaneous tracking of common noctule bats revealed that nearby conspecifics coordinated their movements such that flight paths of neighboring individuals were separated but aligned (*SI Appendix*, Fig. S1), which is consistent with the formation of mobile sensory networks. Specifically, food-searching individuals aligned their movements at distances of about 120 to 180 m, matching an independent estimate of 160 m as maximum distance at which common noctule bats can eavesdrop on each other to detect searching or hunting activity through search calls or feeding buzzes. The alignment of individuals within eavesdropping distance during prey search supports the formation of mobile sensory networks. Searching for prey as part of a mobile sensory network can increase the

fitness of individual bats by improving the rate at which prey is found and captured, as well as the reliability of finding prey on a given day (29, 30).

Our simulation, developed using empirically identified movement behavior, showed that simple rules like distance-dependent attraction, alignment, and avoidance were sufficient to form and maintain mobile sensory networks (31) that outperformed solitary foragers when resources were patchily distributed. While there is extensive research on coordinated movements of flocking or schooling visual-oriented animals (32), our study is one of the few examples to evaluate the benefit of coordinated foraging behavior and investigate potential Allee effects (33, 34). Based on a realistic landscape scenario with about five different prey patches within a potential foraging area of ~36 km², groups of 40 or more bats outperformed smaller groups during prey search, indicating that the advantage of searching as a mobile sensory network outweighs competition effects. Our simulations also showed that foraging in a mobile sensory network is more efficient than relying on local enhancement to find food patches. This is due to the fact that while local enhancement allows animals to home in on nearby food that has already been located by conspecifics, flight alignment helps animals to indirectly widen their scanning area during food search, increasing their chance of encountering hunting conspecifics or finding prey that has not yet been located. Furthermore, the variation in time until food was found was shorter in sensory network scenarios than in corresponding solitary foraging scenarios, which signifies that individuals find food patches more consistently and reduce their

risk of starvation when participating in group foraging (35). On the other hand, these findings suggest that a minimum group size is required for successful foraging in mobile sensory networks. Allee effects may lead to collapses of groups when population and resource densities decrease (36).

We further observed that foraging in a mobile sensory network did not offer advantages over solitary foraging when resources were homogeneously distributed in many small patches. Indeed, mobile sensory networks might become disadvantageous at high bat densities under this scenario, likely due to competition arising from single patches being too small to support several members of the mobile sensory network. Since prey capture rate of bats is most likely limited by time to capture and handle prey (maximum of two insect catching attempts per second) when bats hunt for swarming insects, it is unlikely that bats compete for single prey items (37). However, the production of echolocation calls from several individuals can lead to sensory interference when bats are too close to each other, and bats may need to pay attention to conspecifics to avoid collisions when densities are high (38, 39). We therefore expect the existence of an optimal density of hunting bats. From the empirical data, we infer that bats kept a distance of at least 120 m to hunting conspecifics, which might set the limit for the spatial scale of sensory interference (8, 38, 40). Yet, the increase of distance to hunting conspecifics was comparably small, which suggests that bats aggregated at prey patches sufficiently large to support several individuals. In contrast, during search for prey, networking bats spaced out as far as eavesdropping range allowed, which optimizes search efficiency through maximizing the detection zone of the mobile sensory network.

As we tracked only a subset of all bats that were active in the study area, we were unable to observe interactions occurring with bats that were not tagged. We therefore designed our analysis to minimize sensitivity to untagged bats. To mitigate the unknown effect of untagged individuals in our empirical models, we weighed the observations at commonly used areas lower than observations at lesser used areas (*SI Appendix*, Fig. S1), since tracked bats in these areas were more likely to encounter untagged conspecifics. However, we expect that we would find even stronger intraspecific interactions if all bats in the area were tagged. Additionally, our movement data allow no direct inference on the searching or hunting behavior of the tagged bats, but only indirect inference via their movement behavior. However, tracking studies including acoustic records of insectivorous bats have shown that hunting behavior can be inferred from area-restricted movement behavior of species like the common noctule bat (i.e., bats hunting for ephemeral prey in open landscapes) (5, 16). Furthermore, observations were recorded as two-dimensional locations. Since neighboring bats can surely use different altitudes, distances between bats were likely underestimated. However, our assumption that bats which were close to each other in two-dimensional space generally used similar flight altitudes is supported by three-dimensional GPS data of simultaneously tracked bats from previous studies (16, 41). Indeed, our model results remained robust when simulating three-dimensional localizations (*SI Appendix*, Fig. S4).

In addition, we acknowledge that our study is based on a single species, and we do not expect that all insectivorous bat species form mobile sensory networks. As the results of our model scenarios indicate, mobile sensory networks are probably only beneficial when resources are aggregated in ephemeral and unpredictable patches (5). We believe that the common noctule bat investigated here serves as a model for several bat species that depend on ephemeral and unpredictable prey. We suppose that bat species that forage in unstructured habitat, like insectivorous bats hunting in the open airspace (e.g., many Molossids, Taphozous, Rhinopoma, and some Vespertilionidae with slender wings) or piscivorous bats that need to locate ephemeral fish swarms (5, 42, 43) may also form mobile sensory networks to optimize prey localization. The properties of the resulting mobile sensory networks (such as intraspecific distance and overall size of networks) will, however, depend on intraspecific communication distance, the size of the local population, and the size, yield, and density of resource patches. In contrast to species depending on ephemeral and unpredictable prey, we assume that bats which feed on predictably occurring resources (e.g., insects occurring in or close to vegetation or temporarily stable resources such as fruits or nectar) do not form mobile sensory networks.

Here we presented movement data of several simultaneously tracked insectivorous bats at high spatial and temporal resolution. While social hunting strategies have been described for many taxa that hunt for ephemeral and patchily distributed prey (2), this study provides strong evidence that some vertebrates may sample the landscape for food together by forming a mobile sensory network. We assume that individual bats deliberately aligned their flight paths with neighboring bats to indirectly increase their own detection range, and that this behavior led to the formation of a mobile sensory network that increases the fitness of the local population. Our simulation substantiated that the observed movement mechanisms can lead to the formation of mobile sensory networks, and identified under which circumstances networking is beneficial. Combining the analysis of fine-scale individual interactions based on high-throughput movement data with an agent-based theoretical model revealed that the formation of mobile sensory networks may influence individual fitness and enable species to efficiently exploit environments with varying resource distributions.

Methods and Materials

Study Area. The study took place in the Uckermark region (N 53.373945°, E 13.771231°), near the city of Prenzlau, northeastern Germany. The land is mainly used for agriculture (about 68% of land area), with wheat and corn being the main crops. Natural structures like forests or waterbodies are rare, making up about 5% and 6% of the landscape, respectively (44).

Bat Tracking. Over 3 consecutive years, we equipped a total of 81 (13 males and 68 females) common noctule bats (*N. noctula*) with radio transmitters to obtain their spatial positions during foraging flights. Experiments were conducted under the permits of the corresponding animal care and welfare committee (LAGV 2347-34-2017, 2347-23-19, 2347-6-2020) and the local conservation agency (LfU_N1-4743/128 + 7#56800/2018, LfU_N1-4743/130 + 1#19596/2019) and followed all national and institutional guidelines. Animals were tagged during five sessions: three sessions in spring (May 2018, May 2019, and May 2020), and two sessions in midsummer (August 2019 and July 2020). During each session, we tagged between 14 and 20 individual bats simultaneously (*SI Appendix*, Tables S1 and S2). All studied bats came from the same colony roosting in a set of about 20 artificial bat boxes within a small isolated forest patch. The colony consisted roughly of 80 bats distributed over a few of the available bat boxes (i.e., we tracked about 20% of the individuals in the colony in each session). However, it is likely that about the same number of conspecifics from other comparably small colonies were active in the same area. Models developed from the tracking data were therefore designed to be less sensitive to untagged bats (see below).

Bats were retrieved from a bat box during morning hours for tagging. We used surgical skin glue (Sauer Hautkleber, Manfred Sauer) to temporarily attach custom-made radio transmitters (type ATLAS, mass 0.9 to 1.35 g, which translates to 2.7 to 5.1%, median 4.4 ± 0.4% of individual bat body masses) (*SI Appendix*, Table S1) onto the dorsal fur of the bats. For each individual, the

tagging procedure took ~15 min, after which the bat was placed back into its roosting box. The radio transmitters had a ping rate of 0.125 Hz and a runtime of about 10 d. The automated radio telemetry system ATLAS was based on stationary radio antennas on 15-m poles that received the transmitter signals and synchronized computers to calculate the radio tags' positions using the time difference of signal arrival at the known antenna positions (so-called reverse GPS technology using trilateration; for more details on the ATLAS tracking system, see refs. 19 and 45). Based on prior knowledge of the bat colony's space use (16), we set up eight to nine antennas around the roosting forest and expected hunting grounds, resulting in a total trackable area of ~80 km², which bats left only occasionally.

Data Processing and Statistics.

Data filtering. Our system recorded ~3 million two-dimensional spatial positions of bats that had to be cleaned and filtered to obtain flight paths. During the cleaning procedure, we deleted spatial positions with low accuracy estimates. Additionally, we deleted localizations where bats were inactive in their roosts. We further deleted positions that suggested unlikely travel speeds between two positions, and then used a Kalman filter for data smoothing (details in *SI Appendix, Data Filtering Protocol*). To ensure that we only analyzed flights with foraging being the main motivation of animals, we only considered flights recorded during the first half of the night (i.e., we did not use occasionally recorded short drinking flights during the morning). Since we were interested in bat interactions, for subsequent analyses we used only flights during which at least two tagged bats were recorded closer than 240-m apart from each other for at least 3 min. Data filtering resulted in ~120,000 spatial positions in 186 flights from 66 individual bats for use in subsequent analyses. The threshold of 240-m distance from conspecifics was chosen as this is ~1.5 times the distance over which common noctule bats are able to hear echolocation calls of conspecifics under local ambient conditions, considering atmospheric and geometric attenuation (23, 24) and assuming a hearing threshold of 0 dB, a sound pressure level of 120 dB at 1-m distance (26), and a call frequency of 20 kHz, which is the typical frequency used by common noctule bats for insect search and orientation (46).

Movement classification. We classified bouts of area-restricted movements as foraging behavior following a two-step procedure. First, we built a two-state hidden Markov model [R package moveHMM (47)] with nearby conspecific presence (distance ≤ 240 m) as covariate. Whenever 75% of spatial positions within a 3-min sequence were classified with >80% likelihood as area-restricted movement (small step lengths and low concentration of turning angles) (*SI Appendix*, Fig. S3), this sequence qualified for the following step. Second, when the first criterion was met and the median first passage time of these localizations on a 200-m radius was larger than 200 s (i.e., clustered spatial positions), we classified these sequences as hunting behavior.

Selection for conspecific distance. To assess whether or not tagged bats were generally attracted to or repelled by tagged conspecifics, we used an iSSA (27) with 10 random steps per recorded step and the interaction between the dynamically calculated distance to conspecifics and the turning angle as an explanatory variable (48, 49). Significant deviation from indifferent behavior was estimate by a logistic regression model, with random or real step being the response, and the interaction between the dynamically calculated distance to conspecifics and the turning angle as explanatory variable (48, 49). The analysis was applied to entire flights of single bats during a given night.

Statistical models on flight behavior depending on conspecifics. For the insect search-flight sequences (i.e., no area-restricted movement behavior; see *Movement classification*, above) where we found coefficients from the iSSA to be significant on the 0.1 level, we performed two linear mixed models [R package lme4 (50)] to evaluate how bats changed their flight behavior (i.e., relative heading) and intraspecific distance in response to conspecifics that were within a maximum distance of 240 m. We chose the relatively moderate significance threshold of 0.1 since the iSSA was applied to entire flights and we did not want to be too restrictive for the subsequent fine-scale analysis.

For the first model, we used the difference of the flight vectors of the focal bat and its closest tagged conspecific on a 32-s interval as the response, and the interaction of prior distance between the two bats (modeled as third order polynomials) and the movement behavior of the conspecific (hunting or searching) as explanatory variables.

For the second model, we used the change of distance between the focal bat and its closest tagged conspecific within 32 s as response, and the interaction of prior distance between the two bats (modeled as third-order polynomials) and the movement behavior of the conspecific as explanatory variables.

We used individual bat identifiers nested within the recording session as random factors in both models. To account for potentially present untagged conspecifics and commonly known hunting grounds, which might have influenced movement decisions, we weighed model observations by the negative scaled density of hunting bats within a certain tracking session, calculated as kernel density estimates of the hunting points of all bats within one session (*SI Appendix*, Fig. S1). Thus, reactions of the focal bats near heavily frequented and thus potentially commonly used hunting spots were weighed less in the models, which should reduce the effects of untagged conspecifics and a priori knowledge of common hunting grounds in the models.

To account for the effect of flight behavior independent from conspecifics, we compared both models to null models. These null models were based on distance and relative bearings of pseudodyads of bats (28), where dyads were built using the actual modeled flights and the flight of another bat that came closest but was recorded during another day of the same recording session.

To account for potential errors due to inaccuracy of the distances between tagged bats stemming from unknown altitudes in our two-dimensional data, we reran the two models 1,000 times with randomly assigned altitudes sampled from GPS data collected in previous studies on *N. noctula* (16, 41) in the same study area. Estimates and goodness of fit between the used two-dimensional models and the three-dimensional models with randomly assigned altitudes differed only marginally (*SI Appendix*, Fig. S3). All analytic steps were performed with the software R v4.0.2 (51).

Agent-Based Model Description. As a test of the potential benefits of sensory network foraging in insectivorous bats on the group-level, we developed an agent-based theoretical model in Netlogo (v6.2.0) using interaction-based movements. The model was parameterized using the tracking data findings. We used the model to assess if and under which conditions sensory networking can lead to observed differences in foraging efficiency, measured as the amount of time it took bats to locate food in varying environments. In the following we present a summary description of the model. A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (52, 53) can be found in *SI Appendix, ODD Protocol for a Bat Sensory Network Model*.

We simulated a colony of bats foraging in a landscape containing food resources over a period of approximately several minutes to a few hours (depending on simulation specifications). The model landscape is based on a simplified version of the empirical study site and covers an area of 6 × 6 km. A total of 213 food cells of 75 × 75 m are randomly distributed in the landscape in aggregations consistent with the specified number of food cell aggregations, called patches. Each food cell represents the necessary amount of food for a single bat agent, and can only be occupied by a maximum of one bat. Bats are characterized by their movement behavior, interactions with other bats, and whether they have located a food cell. Mobile sensory networks emerge from interacting movements inspired by vector-based Boids movement dynamics (54), where bats keep track of their nearest neighbor (hereafter "conspecific") and determine their movement direction using three distance-dependent vectors: attraction (bats turn toward conspecifics), alignment (bats maintain distance from conspecifics), and avoidance (bats turn away from conspecifics). Additionally, a random walk vector is executed, which entirely drives the movement direction of bats that have no conspecific or of all bats when the null model is run. The direction and strength of each of the four vectors are taken together to determine the final heading of the bat in each time step. The time it takes individual bats to locate a food cell then emerges from the movement behavior of and interactions between bats and the landscape configuration.

The model proceeds in 8-s time steps (sampling interval of empirical data) and continues until all bats have located an unoccupied food cell. Bats begin the simulation at a central roost and then leave to sample the landscape for food. In each time step, bats that have not located food check for neighboring bats. They then calculate their step length (i.e., flying speed) using values from the tracking data for food-searching bats. All bats that have a conspecific determine their attraction, alignment, and avoidance vectors, then all bats calculate their random walk behavior. Bats determine their resulting direction using the vector

directions and strengths and move. When moving, bats sample the cells within 15 m to check for food. Once food has been located by a bat, it continues to fly in the food cell area until the simulation run is complete.

While model processes are highly general and could be applied to many systems, we parameterized and evaluated the model using pattern-oriented modeling (55) to ensure that simulated bat movement behavior and interactions reflected the movement patterns revealed in the empirical portion of the study. The movement vector strengths were calibrated using two patterns: 1) the relationship between initial distance and changes in distance between focal bats and their nearest conspecific (Fig. 3 *C* and *D*), and 2) the overall shape of the density curve fit to distance changes. After calibration, the model was evaluated against three independent movement patterns: 1) Euclidean distance between the bat starting point and its final point at a food cell (beeline), 2) beeline divided by the sum of Euclidean distances between each 8-s time step (straightness index), and 3) time difference between the bat leaving the roost and finding a food cell.

To examine whether empirically informed movement patterns resulted in the formation of mobile sensory networks, for one focal bat per model run we calculated the distance to its nearest neighbor and the number of directly and indirectly connected neighbors (network size). To assess whether movements consistent with mobile sensory networking resulted in detectable differences in the time it took bats to locate prey resources, we ran simulations using the parameterized and evaluated model. We simulated landscapes with differing numbers of bats (5, 10, 20, 40, 80, 160 bats) and spatial food aggregation levels (1, 2, 4, 8, 16, 32, 64, 128, 213 patches). For each combination of these conditions, the median time it took the bats of each model run to locate food was collected and outputs were compared based on four different foraging models: 1) solitary foraging (bats ignore conspecifics), 2) local enhancement (bats fly toward conspecifics that are hunting within a range of 240 m), 3) flight alignment (bats align with conspecifics that are searching for food but do not use local enhancement), and 4) mobile sensory networking (bats use both flight alignment and local enhancement). Pairs of runs were simulated where the exact same randomly generated landscape was run using the four different foraging models. Each of these paired runs was repeated 500 times per tested number of bats and spatial food aggregation level.

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